IUCN Publications new series N° 9

Tenth Technical Meeting / Dixième Réunion technique

LUCERNE (SWITZERLAND - SUISSE)
June / juin 1966

Proceedings and Papers / Procès-verbaux et rapports

Towards a new Relationship of Man and Nature in Temperate Lands

Vers un nouveau type de relations entre l'homme et la nature en région tempérée

PART III

Changes due to introduced species
Modifications dues à l'introduction d'espèces

Published with the assistance of UNESCO

International Union
for Conservation of Nature
and Natural Resources

Union Internationale
pour la Conservation de la Nature
et de ses Ressources

Morges, Switzerland 1967

The International Union for Conservation of Nature and Natural Resources (IUCN) was founded in 1948 and has its headquarters in Morges, Switzerland; it is an independent international body whose membership comprises states, irrespective of their political and social systems, government departments and private institutions as well as international organisations. It represents those who are concerned at man's modification of the natural environment through the rapidity of urban and industrial development and the excessive exploitation of the earth's natural resources, upon which rest the foundations of his survival. IUCN's main purpose is to promote or support action which will ensure the perpetuation of wild nature and natural resources on a world-wide basis, not only for their intrinsic cultural or scientific values but also for the long-term economic and social welfare of mankind.

This objective can be achieved through active conservation programmes for the wise use of natural resources in areas where the flora and fauna are of particular importance and where the landscape is especially beautiful or striking, or of historical, cultural or scientific significance. IUCN believes that its aims can be achieved most effectively by international effort in cooperation with other international agencies such as UNESCO and FAO.

The World Wildlife Fund (WWF) is an international charitable foundation for saving the world's wildlife and wild places. It was established in 1961 under Swiss law and shares joint headquarters with the International Union for Conservation of Nature and Natural Resources (IUCN). Its aim is to support the conservation of nature in all its forms (landscape, soil, water, flora and fauna) by raising funds and allocating them to projects, by publicity, and the education of the general public and young people in particular. For all these activities it takes scientific and technical advice from IUCN.

Although WWF may occasionally conduct its own field operations, it tries as much as possible to work through competent specialists or local organisations.

Among WWF projects financial support for IUCN and for the International Council for Bird Preservation (ICBP) have highest priority, in order to enable these bodies to build up the vital scientific and technical basis for world conservation and specific projects. Other projects cover a very wide range from education, ecological studies and surveys, to the establishment and management of areas as national parks and reserves and emergency programmes for the safeguarding of animal and plant species threatened with extinction.

WWF fund-raising and publicity activities are mainly carried out by National Appeals in a number of countries, and its international governing body is made up of prominent personalities in many fields.

Fondée en 1948, l'Union internationale pour la Conservation de la Nature et de ses Ressources (UICN), dont le siège est situé à Morges, Suisse, est une institution internationale indépendante. Elle est composée d'Etats membres, sans discrimination de systèmes politiques et sociaux, de services administratifs et techniques gouvernementaux, d'institutions privées ainsi que d'organisations internationales. Elle groupe tous ceux que préoccupe le bouleversement du milieu naturel par l'homme, conséquence de l'expansion urbaine et industrielle rapide et de l'exploitation excessive des ressources naturelles, qui sont les fondements de la survie même de l'homme. Le but principal de l'UICN est de promouvoir ou de soutenir toute action devant assurer, sur le plan mondial, la pérennité de la nature à l'état sauvage et des ressources naturelles renouvelables, non seulement pour leurs valeurs culturelles ou scientifiques intrinsèques mais aussi pour le bien-être économique et social qui en découle à long terme pour l'humanité.

Ce but peut être atteint grâce à des programmes de conservation visant à une utilisation rationnelle des ressources naturelles renouvelables, spécialement dans les régions où la flore et la faune revêtent un caractère d'un intérêt particulier, où le paysage est d'une beauté exceptionnelle ou saisissante ou représente une valeur soit historique, culturelle ou scientifique. L'UICN est convaincue que ses objectifs peuvent être atteints avec succès par un effort international déployé en coopération avec d'autres agences internationales comme l'UNESCO et la FAO.

Le Fonds mondial pour la Nature — WORLD WILDLIFE FUND (W. W. F.) — est une fondation de bienfaisance qui se consacre à la sauvegarde de la vie et des lieux sauvages dans le monde entier. Il fut créé en 1961 comme fondation de droit suisse et partage à Morges le même siège que l'UICN. Il a pour but de soutenir la conservation de la nature sous toutes ses formes (paysages, sol, eaux, flore et faune) ; ses moyens pour l'atteindre sont : les collectes de fonds et leur affectation à des projets, les campagnes publicitaires et l'éducation du grand public et de la jeunesse en particulier. Le W. W. F. bénéficie des conseils de l'UICN pour la réalisation des aspects techniques et scientifiques de ces activités.

Bien que le W. W. F. s'occupe parfois de la conduite de ses propres opérations sur le terrain, il essaie, dans la mesure du possible, d'en confier l'exécution à des spécialistes ou à des organisations locales compétentes.

Parmi les projets du W. W. F., l'appui financier des programmes de l'UICN et du CIPO (Conseil international pour la Préservation des Oiseaux) figure au tout premier rang des priorités, de manière à permettre à ces organismes d'établir la base scientifique et technique essentielle à la conservation à l'échelle mondiale et à l'élaboration de projets spécifiques. Les autres projets couvrent une gamme très étendue de sujets comme l'éducation, les études et enquêtes écologiques, la création et l'aménagement de parcs nationaux et de réserves, les programmes d'urgence destinés à sauver de l'extinction certaines espèces animales et végétales menacées.

Les collectes de fonds et les campagnes de propagande du W. W. F. sont organisées surtout par ses sociétés auxiliaires nationales qui existent déjà dans plusieurs pays. L'autorité supérieure du W. W. F. est le Conseil d'Administration international qui est composé de personnalités éminentes dans de nombreux domaines.

Towards a new Relationship
of Man and Nature in Temperate Lands

Vers un nouveau type de relations
entre l'homme et la nature en région tempérée

IUCN Publications new series N° 9

Tenth Technical Meeting
held at Lucerne, from 26 to 30 June 1966,
in conjunction with the Union's Ninth General Assembly

Dixième réunion technique
tenue à Lucerne du 26 au 30 juin 1966,
conjointement avec la Neuvième Assemblée Générale de l'Union

Proceedings and Papers / Procès-verbaux et rapports

Towards a new Relationship of Man and Nature in Temperate Lands

Vers un nouveau type de relations entre l'homme et la nature en région tempérée

PART III

Changes due to introduced species
Modifications dues à l'introduction d'espèces

Published with the assistance of UNESCO

International Union
for Conservation of Nature
and Natural Resources

Union Internationale
pour la Conservation de la Nature
et de ses Ressources

Morges, Switzerland 1967

CONTENTS

EDITORIAL NOTE

The 10th Technical Meeting of IUCN held at Lucerne, Switzerland, on 26, 27, 29 and 30 June 1966, during the course of IUCN's 9th General Assembly, was devoted to problems affecting the future relationship of man and nature in temperate regions and, therefore, generally in countries which tend to be rather heavily populated and industrialised.

The theme, and the subject-headings under which it was to be discussed, namely:

The ecological impact of recreation and tourism upon temperate environment,
Town and country planning problems,
Changes due to introduced species,

had been selected by the late Edward H. Graham, in his capacity as Chairman of IUCN's Commission on Ecology. They were designed both to be complementary to the theme of the 9th Technical Meeting, " the ecology of man in the tropical environment ", and as of particular interest in the setting of the 10th Meeting, the host country of Switzerland. It was believed that they were also of specially topical importance in many other countries of the world.

The Papers presented at the Meeting, together with comments on the discussions, are being published in three Volumes of IUCN's Technical Series, corresponding with the three main subject-headings of the programme. The present Volume, No. 9 in the Series, covers Part III " Changes due to introduced species ". This subject was dealt with in two sections, in which the ecological effects of introduced plant species and of introduced animal species, respectively, were reviewed and discussed. Professor J. D. Ovington of the Australian National University acted as Rapporteur for the first section and Professor G. A. Petrides of Michigan State University for the second, and IUCN is much indebted to them for so generously giving of their time for the preparation, conduct and review of the discussions. Grateful thanks are also due to the nine contributors to section 1 and eleven contributors to section 2, whose Papers together with a synopsis of some of the points made in the discussions, and with introductory and concluding comments by the Rapporteurs, comprise this Volume.

SECTION I

Ecological effects of introduced plant species

Effets écologiques de l'introduction d'espèces végétales

PREFACE

by

Professor J. D. OVINGTON

Department of Forestry, Australian National University, Canberra

Rapporteur général

Man has long been an active agent, either deliberately or accidently, in modifying the natural distribution of plants throughout the world, but his capacity for this has increased rapidly within the last century with the growth of modern technology and greater mobility. The successes of agriculture, forestry and landscape planning bear witness to the great benefits that can accrue from such activities, but sometimes plant introductions have had unfortunate consequences and control measures have been costly.

The primary purpose of the session on plant introductions was to examine some case histories in an attempt to clarify the scientific basis on which to forecast the consequences of specific plant introductions and to formulate the principles on which an IUCN policy can be based. That no unanimous agreement could be obtained is not surprising in view of the complexity of the subject. However, there was general agreement on the difficulty of obtaining legislation that could effectively regulate plant introductions, and on the need for better coordinated and more intensive research. Both depend upon the public being made aware of the problem and IUCN can play an effective educational role in this.

Most participants emphasised the strong resistance of closed natural ecosystems to invasion by alien plants and how this resistance diminished with increasing human intervention. As the general public and scientists make fuller use of nature reserves and national parks, the degree of environmental modification and hence the opportunity for aliens to become established will increase. IUCN with its special interest in these areas must foster research on this subject and part of this research effort could be a continuing study of the vegetation of oceanic islands which, because of their isolation, enable ecological investigations to be carried out under more controlled conditions. Undoubtedly as the world population multiplies the demands placed on natural and recreational areas will increase, and conservationists need to develop management systems which enable them to keep invading plant species at an acceptable level.

INTRODUCTION OF WILD-LAND PLANTS INTO THE UNITED STATES—METHODS, LEGAL CONTROLS, AND ECOLOGICAL IMPLICATIONS

by

JAMES P. BLAISDELL

Forest Service, U. S. Department of Agriculture
Washington D. C. 20250
U.S.A.

PREFACE

Plant introduction in its broadest sense is merely the movement of a plant from an area where it now occurs to another where it does not. It is primarily an extension of the ecological process migration to include the activity of man as an important factor in plant mobility. Unusual, beautiful, or useful species have been particularly sought out and carried from place to place, some to become established successfully under cultivation, some to escape and become a part of the native flora, and some to die because of their inability to withstand the new environment.

Ecesis, or establishment of an immigrant plant in a new location, involves three essential phases—germination, growth, and reproduction. It is, therefore, the decisive factor in plant introduction, for the process cannot be considered successfully completed until a plant becomes firmly established in its new environment and begins to reproduce itself. Establishment is especially difficult for species which must invade wild areas without the help of cultivation, irrigation, or protection.

The importance of plant introduction to the United States is readily apparent because most of our agricultural crops came from other parts of the world. Corn, potatoes, and tomatoes originated in the Andes of Bolivia and Peru; wheat, rye, and lentils in the Euphrates basin of the Near East; soybeans in China; rice in southeastern India; citrus fruits in Burma; peas in mid-Asia and Ethiopia; cherries, apples, and plums in the Caucasian Mountains of the Near East; oats in northern Europe. Likewise, many of our important forage plants and ornamentals are naturalized aliens. Legumes, including alfalfa, clover, vetch, sweet clover, lespedeza, trefoil, and kudzu, are particularly valuable for forage production and soil improvement. And such widely used forage grasses as smooth brome, timothy, crested wheatgrass, weeping lovegrass, Kentucky bluegrass, orchardgrass, and tall fescue were all introduced from other countries.

Throughout the ages, migration of plants has been restricted by such barriers as oceans, mountains, deserts, and distances. However, with the ever-increasing mobility of man, natural barriers have become less and less effective in confining vegetation to its native habitat. For this reason it seems timely to consider just how introductions occur, methods of controlling introductions and their effectiveness, and ecological implications. " Wild " species and " native " communities are of special interest and will receive primary consideration in this paper.

How Introductions Occur

Plant introduction as used herein refers to movement of plants or germ plasm from one area to another through the activities of man. It occurs in many ways, primarily through the transport of seeds. Although several classifications are possible, for the purpose of this discussion all introductions are placed either in the deliberate or in the accidental categories.

Deliberate

Plant introduction into what is now the continental United States began with the Indians, who were responsible for moving crops northward from Central and South America some 5,000 years ago. Colonists from Europe found North American Indians growing corn, beans, and squash at various places from the eastern seaboard to the Rocky Mountains. Columbus began the introduction of Old World crops in 1493 when he brought barley, wheat, sugarcane, and grapes on his second voyage. Many prominent citizens of colonial America participated actively in plant introductions from abroad, and John Chapman earned the name of " Johnny Appleseed " through his efforts to establish orchards by planting seeds as he walked through the wilderness. Seeds are, of course, the most convenient and widely used germ plasm for introduction, but buds, scions, and clonal material have also been utilized. Incidentally, seed of wild species is usually collected by hand and is less subject to contamination than seed of crop plants usually collected by machines.

Informal plant introduction actions, which started with Columbus, have continued to the present. Travellers abroad continue to be impressed by seemingly useful or ornamental plants and exert considerable effort to bring back and establish them at home. Greatly improved transportation facilities and increased numbers of travelers are providing more and more opportunities for movement of plants from one country to another. Likewise, increased knowledge of plant requirements and their culture is contributing to successful establishment.

A formalized program for plant introduction was started by the U. S. Department of Agriculture in 1898. At that time a Section of Seed and Plant Introduction was established and given the assignment of " bringing into the United States for experimental purposes any foreign seeds and plants which might give promise of increasing the value and variety of our agricultural resources. " In addition, the Section was assigned the task of distributing all seeds that it introduced. These usually went to the State Agricultural Experiment Stations or to reliable cooperators. At present, plant introduction investigations are administrated by the New Crops Research Branch of the Agricultural Research Service and headquartered at the Plant Industry Station in Beltsville, Maryland. As with the original plant introduction unit, it has two primary functions : introduction of new plant materials from all parts of the world, and preliminary testing for agricultural use. Providing plant materials of the United States for foreign research workers is also an important function of the Branch. Other agencies of the Department of Agriculture actively engaged in plant introduction are the Soil Conservation Service and the Forest Service.

Although much of the plant material introduced from foreign sources is obtained through correspondence, actual explorations are continually being conducted. These produce some of our most valuable introductions—the wild relatives of our cultivated crops—which may have genetic characters very useful to the breeder. After an introduced plant has been identified, inspected, and declared free from insects and diseases, it is ready for increase propagation and testing. This is usually accomplished at field locations scattered throughout the country where first indications of potential usefulness are obtained.

Such deliberate actions as these have been responsible for most of our successful introductions; for example, hard red winter wheat, which is grown annually on some 27 million acres; soybeans, which support a billion dollar industry; and among forage plants, crested wheatgrass, which is now the dominant species on millions of acres of western rangelands.

Accidental

Plants are accidentally introduced in a number of ways, particularly through seeds carried in clothing, vehicles, or personal effects of travelers; as impurities in crop seeds or other plant materials; in wool, hair, or fur of domestic animals or in materials used for their bedding; in ballast from ships; in a variety of materials used for packing; and in grain screenings. Since accidental introductions must also rely on accidental opportunities for their establishment, chances for the required combination of circumstances are extremely limited. Only the most adaptable and aggressive species are able to become established in the face of many unfavorable circumstances; consequently, a high proportion of successful accidental introductions are, and will continue to be, pestiferous weeds. It must be recognized, however, that with the ever-increasing amount of international travel and commerce, it is inevitable that accidental introductions will continue, probably at an accelerated rate.

Legal Controls and Effectiveness

Controls on introduction of exotic plants into the United States have been notably lacking. Rather, introductions have been encouraged, even during the colonial period when such government leaders as Benjamin Franklin and Thomas-Jefferson made special efforts during their travels to send home seeds and cuttings of promising plants for establishment in America. Such practices were officially recognized in 1827 during the administration of President John Quincy Adams as indicated in a circular from the Secretary of the Treasury to the U. S. Consuls, a portion of which follows :

> " The President is desirous of causing to be introduced into the United States all such seeds and plants from other countries not heretofore known in the United States, as may give promise, under proper cultivation, of flourishing and becoming useful. To this end I have his directions to address myself to you, invoking your aid to give effect to the plan that he has in view. Forest trees useful for timber; grain of any description; fruit trees; vegetables for the table; esculent roots; and, in short, plants of whatever nature whether useful as food for man or the domestic animals, or for purposes connected with manufactures or any of the useful arts, fall within the scope of the plan proposed. "

Entry of plants into the United States is now restricted to some extent by the Federal Seed Act of 1939, which is designed to control introduction of certain noxious weeds, and the Federal Pest Act of 1957, which has the objective of preventing entry of injurious foreign insect and disease pests not already widely established in this country. Also, introduction of a few narcotic plants is restricted by the Narcotic Drugs Import-Export Act of 1922.

The Pest Act imposes quarantine on certain plants being brought into the country, but it is used only for the purpose of preventing the entry of foreign plant pests. After plant materials have been inspected and have met quarantine requirements or treatment, they are released to the importer. The Seed Act does not allow importation of crop seeds containing more than 2 percent of the following noxious weeds: whitetop (*Lepidium draba*), Canada thistle (*Cirsium arvense*), dodder (*Cuscuta* spp.), quackgrass (*Agropyron repens*), Johnsongrass (*Sorghum halepense*), bindweed (*Convolvulus arvensis*), Russian knapweed (*Centaurea picris*), perennial sowthistle (*Sonchus arvensis*), and leafy spurge (*Euphorbia esula*). Consequently, enforcement of this law restricts entrance of these nine weed seeds in substantial quantities, but it does not prevent importation of smaller amounts of such noxious weeds or the introduction of other weed species in contaminated lots of crop seeds. Although the Seed Act does prohibit entry of screenings from many seeds, it does not apply to screenings from wheat, oats, rye, barley, corn, and many other crops provided they are declared for cleaning, processing, or manufacturing, and not for seeding purposes. Nor does it prohobit entry of such materials as hay, straw, bedding, and packing, which can harbor a wide variety of viable seeds.

For all practical purposes, then, there is really no legal control on introduction of most exotic plant materials. Likewise, there is no apparent attempt to control plant introduction through informational or educational activities. However, the inconvenience of quarantine or required fumigation procedures probably serves as a deterrent to some casual efforts at plant introduction.

Case Histories

In order to provide a satisfactory background for considering effects of plant introductions, it seems desirable to examine in some detail the case histories of several wild or semi-wild species. Some of these are clearly weeds for which control measures are being actively sought; others are desirable plants for livestock or wildlife, soil protection, recreation, or merely natural beauty; and still others have a combination of good and bad features, which defy attempts to so classify. The latter is well illustrated by an invader to Australia, a species of *Echium* known on farmlands as " Patterson's Curse " and on rangelands as " Salvation Jane ".

Crested Wheatgrass

Crested wheatgrass (*Agropyron desertorum* and *A. cristatum*) is a vigorous perennial bunchgrass. It is drought resistant, winter hardy, and a valuable forage plant because it is palatable, nutritious, and resistant to grazing.

This grass was deliberately introduced into the United States from Siberia in 1898, but it did not attract much attention until after 1915 when it was reintroduced and tested in the northern Great Plains. It has been used to seed millions of acres of deteriorated rangeland in the Western States. Although most stands have been established by removal of competing vegetation and by drilling, once established they persist indefinitely and can tolerate considerable abuse. For example, in southern Idaho it has been more resistant to fire and severe grazing than many of the native grasses. Its seeds are large and not particularly mobile; however, it has spread more from volunteer seedlings than some of the native grasses. Crested wheatgrass appears fully compatible with native vegetation of the zone to which it is climatically adapted and often grows in mixtures with such species as sagebrush (*Artemisia* spp.) and rabbitbrush (*Chrysothamnus* spp.). It must be considered a naturalized species and a permanent member of many semi-arid plant communities of Northwestern United States.

Kentucky Bluegrass

Kentucky bluegrass (*Poa pratensis*) is a long-lived, sod-forming perennial grass which reproduces by seed and spreads vegetatively by rhizomes. It is a highly palatable grass and withstands abuse from grazing and trampling, but it is not drought resistant.

This grass was brought to the United States by early colonists and is now widely distributed in all except the southern parts of the country. It has been extensively planted in pastures, waterways, golf courses, lawns, parks, and other recreational areas; and has become naturally established in many forest and range communities, particularly meadows. Bluegrass now occurs as one of the major species on more than 100 million acres in the United States and is considered the most important introduced grass in North America.

Cheatgrass

Cheatgrass (*Bromus tectorum*), also known as downy brome and Junegrass, is an aggressive winter annual which was first reported in Pennsylvania in the mid-1890's and has spread rapidly, particularly on areas disturbed by cultivation, fire, or severe grazing. It is now a major component of the vegetation on an estimated 50 million acres and is believed to be the dominant species on at least half of this area.

Cheatgrass is a Jeckyll-and-Hyde grass. It fills the void when perennial grasses are destroyed and provides soil protection and considerable livestock forage. On the other hand, its production fluctuates greatly, and it is not dependable for either soil protection or forage. Furthermore, its early drying habit and high inflammability creates a serious fire hazard which is costly and contributes to further deterioration of the vegetation.

Its seeds have sharp awns which allow them to readily penetrate and become lodged in fabrics, wool, fur, etc.; consequently, it can be a nuisance and source of discomfort to man and animals. This characteristic, of course, provides an effective means for transporting seeds from one area to another and was probably responsible for the original introduction of this plant.

Saltcedar

Saltcedar (*Tamarix pentandra*), also known as tamarisk, is a native of Europe and Asia and now occupies approximately a million acres in Southwestern United States. Although saltcedar may have been introduced through Mexico by Spanish explorers, its lack of abundance in that country does not support this assumption. Rather, the first introduction of this species into the United States appears to have been by nurserymen in the early 1800's, as a number of nurseries along the east coast listed tamarisk in their catalogues between 1823 and 1835. Following its distribution for ornamental plantings, saltcedar gradually began to escape from cultivation, and by the early 1900's had become naturalized in many parts of the country and was beginning to spread aggressively, particularly in the stream valleys of the Southwest.

Saltcedar is a phreatophyte, that is, it depends on ground water and is usually confined to areas where its roots can reach the water table. It is very tolerant to saline or alkali soil and water. It has a very high rate of water use—dense stands can annually consume more than 9 acre-feet per acre. Consequently, control measures are being sought to curb the growth and spread of saltcedar. At the same time, saltcedar is being lauded for its esthetic values and as an excellent habitat for such wildlife as rabbits, quail, deer, and doves. For example, observations by the Arizona Game and Fish Department have shown an average of 24 white-wing and 6 mourning dove nests per acre, and up to 84,000 birds per section of this land. Recreational values should certainly be considered in the management of areas now covered by this naturalized plant.

Scotch Broom

Scotch broom (*Cytisus scoparius*), a native of Europe, is reported to have been brought into the United States about 140 years ago by the Hudson's Bay Company. It is a legume and consequently has some value for improving soil fertility. It has beautiful yellow flowers in the spring and has enjoyed considerable popularity as an ornamental; however, it has been planted chiefly for the control of dunes and for the stabilization of highway cuts and fills.

From these plantings it has spread aggressively to thousands of acres of forest and rangelands, particularly on the coasts of Washington, Oregon, and California. It is poor livestock forage, but provides food and cover for several species of wildlife. It often grows in fairly dense stands and prevents establishment of tree seedlings and desirable forage plants. It is reported to create a high fire hazard, but this is open to question.

Scotch broom, then, is a naturalized species which is becoming an increasingly important component of the Pacific Coast vegetation. Although it has esthetic and erosion control values, in many situations it must be considered a weed. It can be killed with chemical sprays, but such control is often too expensive for extensive use. At the present time biological control with stem-boring insects is being investigated.

Japanese Honeysuckle

Honeysuckle (*Lonicera japonica*) has a pleasant odor, it provides a good cover for preventing soil erosion, it provides emergency winter grazing for cattle, and it is such a favorite food of deer that game managers are planting it. But it has caused considerable damage to timber producers of Southeastern United States by ruining pole-sized stands of pine, smothering the reproduction, and preventing seedling establishment.

Japanese honeysuckle is an ornamental that was introduced from Asia. It escaped cultivation and has spread throughout the forests from Connecticut to Florida. It reproduces vegetatively and from seed which is spread by both water and birds. It occurs in varying densities on several million acres, with the rankest growth on the best timber producing sites. Economical methods of controlling this plant are being sought.

Multiflora Rose

Rosa multiflora is an Asiatic plant that has long been used as an ornamental in the United States, and nurserymen often use it as a hardy rootstalk on which to produce other ornamental varieties. Living fences of multiflora rose have become an accepted addition to the farm landscape, particularly in the Central and Eastern States where it attains a height of 8 or 10 feet on the best soils. A multiflora rose fence is a thing of beauty. In the spring it has masses of white blossoms, and in the fall its red fruits add to the color of the fields. It furnishes welcome cover for songbirds, game birds, rabbits, and other wildlife. The fruits are eaten by many kinds of birds, and will meet the food requirements of pheasants during winter emergencies.

Multiflora rose has made itself too much at home and has become a weed in numerous situations. Although it does not spread from rootstalks, drooping stems often take root and grow. In addition, seeds are widely scattered by birds, and new plants continually spring up and thrive, particularly in areas where other vegetation does not fully occupy the site. Consequently, control by herbicides or other measures is sometimes necessary.

Sweetclover

Both white sweetclover (*Melilotus alba*) and yellow sweetclover (*M. officinalis*) are natives of Europe and Asia, now widely naturalized in the United States. They are robust, biennial legumes adapted to a wide variety of soil and climatic conditions. Sweetclover first appeared in Virginia about 1740, but it did not become very widespread until a century later following the acquisition of seed from Chile for farm planting to produce hay and pasture.

Sweetclover is an outstanding soil improver. It makes good growth in poor soils, and its extensive taproots penetrate the subsoil and facilitate aeration and drainage. It is an excellent plant for adding both nitrogen and humus to the soil. It escaped cultivation long ago and has become established abundantly on abandoned farms, eroded hillsides, and along roads where it inhabits the infertile cuts and fills. Beekeepers have long recognized its value as a source of nectar; in fact, its early distribution was largely for its use in bee pastures. It is not only a good forage plant for livestock but also provides good food and cover for numerous species of wildlife.

Crownvetch

Crownvetch (*Coronilla varia*) is a perennial legume which has become naturalized in parts of the Northeast and the Corn Belt. A native of Europe, it appeared in Pennsylvania some 50 years ago, perhaps in a shipment of imported alfalfa or possibly as a deliberate introduction for ornamental purposes. It reproduces by seed and spreads vegetatively by fleshy rhizomes. Its normally profuse flowers vary in color from pinkish-lavendar to white. It will grow in a variety of soils, including those low in nitrogen and humus. Consequently, crownvetch is a valuable plant for erosion control and natural beauty on highway embankments, dikes, streambanks, and strip-mine spoil banks.

Eucalypts

Trees of the Australian genus *Eucalyptus* have been widely planted in every continent of the world. During the latter part of the nineteenth century and the early part of the twentieth, numerous plantations of eucalypts were established in California, Arizona, New Mexico, and Florida. Most of these plantations were in California where some 50,000 acres were planted, mostly to the species *Eucalyptus globulus*; only a small portion of these plantations have survived to the present time.

It was originally hoped that eucalypts would be an important source of saw timber; however, they were, for the most part, inferior to native American species. Distillation of the leaves to obtain cineole and utilization of the wood for pulp have not been particularly successful. Portions of the original plantations still exist, and numerous eucalypt windbreaks have been established. These add interest and beauty to the landscape, but otherwise are of little importance. Scarcely any natural spread of this species has been observed.

Russian Olive

Russian olive (*Elaeagnus angustifolia*) is a small tree that has been widely planted from New England to California as an ornamental and for windbreaks. It is a native of Europe and Asia.

It spreads by seed and by underground rootstalks and has been reported to have escaped cultivation in many areas. For example, it has become a pasture weed in parts of Nebraska and is being controlled with herbicides. Nevertheless, it is a valuable ornamental, an effective component of windbreaks, a source of food for birds, and undoubtedly provides good habitat for many species of wildlife.

Noxious Weeds

Any discussion of wild or semi-wild plant introductions into the United States would not be complete without mention of the numerous noxious weeds that have successfully invaded vast areas of forest and rangelands. Halogeton (*Halogeton glomeratus*), a poisonous plant native to northwestern China and southwestern Siberia, is believed to have been accidentally introduced into the United States about 1930, and has since spread to thousands of acres of rangeland throughout the West. Medusahead (*Elymus caput-medusae*), an annual grass native to Portugal and Spain, appeared in the United States near the end of the nineteenth century and is now widely scattered throughout the Western States. Another wild-land weed, which is a serious pest in the West, is St. Johnswort (*Hypericum perforatum*). This native of Western Europe first appeared in California about 1900 and has since made extensive invasions into rangelands; however, considerable control has been achieved through introduction of the beetle, *Chrysolina gemellata.*

Other prominent introduced weeds of croplands, grasslands, and open forests are Russian knapweed (*Centaurea repens*), Canada thistle (*Cirsium arvense*), Russian thistle (*Salsola kali* var. *tenuifolia*), and leafy spurge (*Euphorbia esula*). All are troublesome weeds introduced from Eurasia, probably in contaminated lots of agricultural crop seeds. Russian thistle has the additional distinction of being the alternate host of the beet leafhopper, vector of curly top disease of sugar beets and other crops, as well as a useful plant for livestock forage and control of soil erosion.

Ecological Implications

It is apparent from the preceding discussion that native plant communities are continually being modified by introduction of exotic species. Some of these owe their successful establishment to disturbance of the original vegetation or modification of the site and consequently may hold a rather precarious position in the plant community. Others are apparently so well adapted to their new home that they can be considered permanent members of the natural or climax vegetation.

It seems necessary, therefore, that we maintain a flexible concept of what is " natural " to allow inclusion of late arrivals to particular plant communities. An interesting example is cheatgrass, an annual grass discussed in the previous section, now widely established on western rangelands. This species forms its heaviest stands in disturbed areas such as abandoned croplands or where the native vegetation has been largely destroyed by grazing or fire. Once established in such situations, it relinquishes its dominance very slowly, apparently due to its ability to compete with seedlings of perennial grasses and forbs. It has also been able to successfully invade virgin prairies, where it maintains a small, evenly distributed population, with a life form and periodicity almost identical to that of the indigenous annual grasses. Many other species such as crested wheatgrass, Kentucky bluegrass, tamarisk, and Japanese honeysuckle have apparently found extensive environments ideally suited to their requirements.

The annual grassland of California represents an important plant community composed almost entirely of exotic species. As a consequence of overgrazing by domestic livestock, it has almost completely replaced the original perennial bunchgrass vegetation which once occupied all of the Great Valley as well as the valleys and foothills of the Coast Range and the Sierra Nevada. Annual species of *Avena, Bromus, Hordeum,* and *Festuca,* all natives of Europe, have formed such dense stands that it is doubtful if perennial grasses could regain control, even if given protection from grazing. Furthermore, the present naturalized vegetation may be preferable from the standpoint of forage production and utilization.

In the absence of completely effective controls to plant introduction, it must be assumed that more and more species will gain entry to the United States. The significance of these introductions, however, will depend on the degree to which they are able to invade native communities, whether they are desirable or undesirable additions to the original vegetation, and how their presence affects utilization and management of the forest or range resources.

Effects of Disturbance

Once an exotic has arrived by deliberate or accidental means, rate and degree of invasion are determined by its aggressiveness, adaptability to the new environment, and the condition of the native plant community. The latter is especially important because numerous observations in the United States and abroad indicate that introduced species rarely invade undisturbed climax vegetation. Conversely, elimination of the disturbance factors often results in re-establishment of the climax.

Most disturbance to native vegetation can be attributed either directly or indirectly to activities of man. Grazing by his livestock has reduced or eliminated certain species and even entire communities. His efforts to eradicate or control certain species by fire, herbicides, mechanical, or biological means has resulted in modification of many native stands. Logging and strip-mining activities have, of course, caused destruction of native vegetation and extreme modifications of the site. Less prominent, though perhaps equally extreme, site alterations have been brought about by fertilization and water spreading practices, which have caused corresponding changes in vegetation. Natural environmental factors such as insects and disease, wildlife, fire, or drought may also have severe impacts on native plant communities, but even here man often exerts considerable influence through his efforts to control these factors.

The rapidly accelerating use of wild lands for recreation is perhaps worthy of special mention. Recreational activities are not only the source of considerable disturbance to native plant communities, but also can result in transportation of seed to remote areas which might not be visited for other purposes. A case in point is the introduction of weeds into wild lands through hay or straw used for mattresses, livestock feed, and other purposes.

Importance of Individual Characteristics

It is readily apparent, then, that disturbances to natural sites or native plant communities have created and are continuing to create satisfactory conditions for invasion of exotic species. Also of major importance are inherent characteristics of the newcomers. These introduced species are late arrivals to native communities that have already crowded out the least adapted species through a long period of development. Consequently, the potential invaders must be particularly aggressive and well adapted to the new environment if they are to become permanent residents.

Reproductive characteristics are of special importance. Abundant production of good quality seed certainly favors invasion, as do mechanisms that aid in transporting seed from one place to another or in getting it planted. Ability to reproduce by vegetative means such as rhizomes or stolons may also be a way of entering communities closed to establishment of seedlings. Adaptations for competing with other plants may be the key to successful invasion. For example, seedlings that grow rapidly have a real advantage in developing an extensive root system before soil moisture supplies are depleted and competition for it really sets in.

Tolerance to unfavorable environmental conditions and quick response to improved circumstances are also helpful. Drought and temperature extremes in some environments can create severe stresses which can quickly nullify establishment attempts. Likewise herbage removal by grazing animals, damage by rodents, infestations of insects or disease, and fire can prevent an otherwise effective invasion. It should also be recognized that the phenomenal success of some exotics can be attributed to their arrival in new environments unaccompanied by their specific insect pests and disease, whereas others fail to become established because appropriate symbiotic bacteria are left behind.

Although individual plants are usually rooted in a particular spot, the rate of invasion into new areas can be extremely rapid and can compare favorably with the spread of birds, which are apparently much more mobile. As already mentioned, the annual grass, *Bromus tectorum,* apparently moved across the United States and dominated millions of acres in the brief period of 40 or 50 years. Other plants have demonstrated similar mobility. Yet it took about 50 years for the starling to move from the east to the west coast of the United States, and a somewhat similar spread was made by the collared dove, which required about 50 years to move from the Balkans across Europe to England. These two examples have been characterized as " wildfire colonization " and " extraordinary spread ", respectively. Apparently these birds were aided by settlement and other activities of man just as the spread of many introduced plants is furthered by man's modification of native plant communities.

Native Communities Modified by Introductions

As already indicated, some native plant communities have been only slightly modified by invasion of foreign species, whereas others have been almost completely replaced. Consequently, these modified communities must be evaluated, goals must be established, and appropriate management practices must be developed. Some immigrants are desirable additions to the native community and management should attempt to preserve a mixed stand. In other cases it may be preferable to maintain a more or less pure stand of exotics, and in still others, the only reasonable course seems complete eradication or at least control of the invaders.

The introduced species and the modified communities must be studied to determine their values and ecological peculiarities. Some are good forage plants; others are particularly valuable for erosion control, as food and cover for wildlife, for improving outdoor recreation facilities, or for beautification of the landscape. And some, of course, are noxious weeds with little or no apparent value.

The annual grassland of California is a good forage producer, and its replacement by the original perennial vegetation would be extremely difficult and expensive; consequently, present research aims to determine best management for sustained high forage production of this community. On the other hand, research in cheatgrass communities is still weighing the relative merits of this species versus the original native vegetation and attempting to determine whether conversion is desirable, possible, or practicable. Tamarisk, a notorious waster of valuable water, is being studied to determine means of control; however, wildlife values must also be studied and evaluated before extensive control programs are activated. Such species as Kentucky bluegrass and crested wheatgrass are generally desirable additions to or replacements for native vegetation, and research is simply directed at management for maximum production. Such species as Japanese honeysuckle and Scotch broom are certainly valuable for soil stabilization and beautification of scars necessitated by construction, but information is needed on how to restrict them to the desired sites. Halogeton, medusahead, Russian knapweed, Canada thistle, and other noxious weeds should be studied to determine methods for their eradication or control.

CONCLUSIONS

Since present or anticipated legal controls will not effectively limit plant introductions into the United States, it seems axiomatic that more and more correspondence, commerce, and travel will introduce more and more exotic germ plasm at the same time that more and more disturbances to native plant communities are creating more and more opportunities for invasion. Many native communities, then, will undergo considerable modification as the late arrivals are able to enter the successional patterns and become permanent residents.

Research, of course, is the key to effective vegetation management. Of particular importance is knowledge of characteristics and requirements of possible introductions in order to anticipate how they might react with new plant communities and environments. A desirable plant in one situation may become a noxious weed with slight changes in site, climate, or associated flora and fauna; consequently, information on aggressive plants is particularly needed.

Likewise, attention should be given to searching out other species that may be introduced to supplement or replace native vegetation for special purposes. As an example, the United States Forest Service is particularly interested in obtaining shrubs that are high producers of quality browse for wildlife and livestock, suitable for landscaping and screening on outdoor recreational areas, of low inflammability for use on firebreaks, or effective for stabilizing soil and improving natural beauty of disturbed sites. Resistance to disease, insects, fire, drought, and animal use would, of course, be desirable. Consequently, plans are being developed for a laboratory to develop superior native shrubs through selection and breeding, introduce and evaluate foreign shrubs, develop information on site adaptability and methods of establishment, and determine methods for seed production and storage.

Definition of various geographical units in agroclimatological terms is needed as background for possible introductions, both deliberate and accidental. Although similarities or differences in climatic and other environmental factors do not insure or preclude successful introduction of particular species, such information can be a valuable adjunct to physiological and ecological knowledge of the plant itself.

Management of modified communities will be primarily concerned with regulating introduced species at an acceptable density. This can often be achieved by judicious utilization or protection of the native vegetation, but it may require direct and perhaps selective control of the invaders by fire, chemicals, biological, or mechanical measures. Successful management may also require site modification by such means as fertilization and irrigation or perhaps seeding of native or exotic species. Certainly, an expanded research effort will be necessary to provide effective management guides.

REFERENCES

ADAMS, K. S. (1958). *Pasture and range plants.* Phillips Petroleum Co., Bartlesville, Okla. 176 p.

ANDERSON, W. L., and EDMINSTER, F. C. (1960). *The multiflora rose for fences and wildlife.* U. S. Dept. Agr. Leafl. 374. 8 p.

COOK, C. W., and STODDART,, L. A. (1953). *The balogeton problem in Utah.* Utah Agr. Expt. Sta. Bul. 364. 44 p.

CRONQUIST, A. (1955). *Vascular plants of the Pacific Northwest.* Part 5 : *Compositae.* Univ. Wash. Press, Seattle. 343 p.

DAUBENMIRE, R. F. (1942). An ecological study of the vegetation of southeastern Washington and adjacent Idaho. *Ecol. Monogr.* 12 (1): 53-79.

DAYTON, W. A. et al. (1937). *Range plant handbook.* Forest Service, U. S. Dept. Agr. 515 p.

FISHER, J., and PETERSON, R. T. (1964). *The world of birds.* Doubleday, Garden City, N. Y. 288 p.

GILSTRAP, Marguerite. (1961). The greatest service to any country. *In* SEEDS, *The Yearbook of Agriculture:* 18-27. U. S. Dept. Agr.

HARTLEY, W. (1954). The agrostological index : a phytogeographical approach to problems of pasture introduction. *Australian J. Bot.* 2 (1): 1-21.

HODGE, W. H., and ERLANSON, C. O. (1956). Federal plant introduction—a review. *Econ. Bot.* 10 (4): 299-334.

HODGSON, J. M. (1963). *Canada thistle and its control.* U. S. Dept. Agr. Leafl. 523. 8 p.

HUFFAKER, C. B. (1957). Fundamentals of biological control of weeds. *Hilgardia* 27 (3): 101-157.

KLEMMEDSON, James O., and SMITH, Justin G. (1964). Cheatgrass (*Bromus tectorum* L.). *Bot. Rev.* 30 (2): 226-262.

METRO, Andre. (1955). *Eucalypts for planting.* FAO Forestry and Forest Products Studies No. 11. Food and Agr. Organ. of the United Nations.

MOORE, R. M. (1957). Some ecological aspects of the weeds problem in Australia. *Fourth Int. Congr. of Crop Protect. Proc.* 1 : 447-449.

MORRIS, M., and MEUCHEL, J. (1956). *The problem of St. Johnswort—a noxious plant in western Montana.* Mont. Forest Expt. Sta. Bul. 4. 8 p.

NELSON, Thomas C. (1953). *Honeysuckle is a serious problem.* Southeastern Forest Expt. Sta. Res. Note 41. 2 p.

PIEMEISEL, R. L. (1932). *Weedy abandoned lands and the weed hosts of the beet leafhopper.* U. S. Dept. Agr. Circ. 229. 24 p.

ROBINSON, T. W. (1965). *Introduction, spread, and areal extent of saltcedar* (*Tamarix*) *in the Western United States.* U. S. Dept. Interior, Geol. Surv. Prof. Pap. 491-A. 12 p.

SIZER, Bill. (1965). Gila River wildlife—habitat or epitaph? *Wildlife Views* 12 (2): 4-9. Ariz. Game and Fish Dept.

TURNER, R. B., POULTON, C. E., and GOULD, W. L. (1963). *Medusabead—a threat to Oregon rangeland.* Oreg. Agr. Expt. Sta. Spec. Rep. 149. 22 p.

WEINTRAUB, Frances C. (1953). *Grasses introduced into the United States.* U. S. Dept. Agr. Handb. 58. 79 p.

WHYTE, R. O. (1958). *Plant exploration, collection, and introduction.* Food and Agr. Organ. of the United Nations, Rome.

WILLIAMS, D. A. et al. (1964). *Grass in conservation in the United States.* Soil Conserv. Serv. TP-143, U. S. Dept. Agr 43 p.

COMMENTS

D. Hey (S. Africa) stressed that plants deliberately introduced by humans not only seriously affect the indigenous vegetation but are often very expensive to control and cited Hachea and jointed cactus as examples. He suggested legislation to prevent the introduction of alien plants must be reinforced with educational programmes to make the touring public aware of the possible danger involved. *Z. Futehally* (India) pointed out the difficulties of distinguishing between useful and useless species before they are introduced and the problems this raised in legislation. *V. Puscariu* (Rumania) gave further instances, e. g. *Nytnphaea lotus thermalis,* of plant species introduced outside their natural range with disastrous results. *H. Zwölfer* (Switzerland) suggested that one ecological reason for the success of introduced, noxious weeds, e.g. Euphorbia spp., and Hypericum in N. America, is the absence of the appropriate biological control agents and suggested weed control could be achieved best by introducing such agents. In reply, *Blaisdell* emphasised the need for more research not only in regions where plants are being introduced but also in their native regions, in order to assess the risks involved and to determine control measures. He pointed out the need to ensure the controlling organism does not itself become a pest when introduced. He also felt that, despite legislation and research, plant introductions will continue to occur increasingly particularly, since humans are becoming more mobile.

INTRODUCED AQUATIC, FRESH-WATER AND SALT MARSH PLANTS—CASE HISTORIES AND ECOLOGICAL EFFECTS

by

D. S. RANWELL

The Nature Conservancy, Furzebrook Research Station,
Wareham, Dorset,
United Kingdom

The massive expansions of aquatic plant populations that have occured with what Elton (1958) has described as explosive violence during the 19th and 20th centuries are clearly associated with factors dependent on the scale of expansion of human populations and civilisation. These factors include : increased travel facilitating inter-continental spread of plants; increased leisure permitting the cultivation of aquatics in gardens and aquaria; increasing control over native aquatic species to provide open or flowing water resources required by modern civilisation ; and finally, increased conversion of land surfaces to provide new water resources to meet growing demands.

Water for navigation, irrigation, power and recreation is now, or is fast becoming, a limiting resource in many parts of the United States as Timmons (1962) points out in a recent review of aquatic weed control problems. This seems to be generally true of most countries judging from the spate of reservoir-building characteristic of the first half of this century, and the more intensive use of existing water resources which is clearly going to characterise the second half.

The utilisation of water resources most frequently requires an open water surface and free flow. This is a difficult achievement by contrast with the utilisation of land surfaces which is usually in terms of the replacement of one type of cover by another. The problem is made more acute by the fact that the aquatic habitat presents optimum conditions for dispersal and plant growth. These conditions include a transporting growth medium with an open surface which provides protection from sudden temperature changes, unlimited water supply, and abundant carbon dioxide. Thus they are peculiarly well suited for the establishment and spread of any accidentally or deliberately introduced species.

An *introduced* species is defined as one known, or believed on available evidence, to have been brought to a country accidentally, or intentionally, by man. An alien species is an introduced species that has become more or less naturalised or firmly established in its new home. Neither of these vague terms has much merit other than that of convenience and the emphasis in this account lies on case histories and effects of large scale plant invasions in aquatic and marsh habitats, rather than on fine distinctions about precise dates and sources of the introductions themselves. These are given where known, but their reliability is inevitably open to question.

Aquatic and marsh plants include a relatively small group of species within the flora of the globe which is largely composed of terrestrial species. In the British Isles for example they form only about 10 per cent of the flora. Within the British flora some 600 - 700 species of aliens are recorded (Dandy, 1958), and these are mainly weeds of cultivation. Only about 37 species (less than 10 per cent of the British alien flora) of aquatic and marsh plants are known to have been introduced and have become naturalised in historic times. Much the same picture is found in other countries. About half the British alien wetland flora has come via trade routes from N. or S. America. The majority of aliens in N. America, Australia and New Zealand come from Europe, the major source of settlers, while the high proportion of South American aliens in South-east Asia is attributable to Jesuit settlers from South America and the West Indies (Ridley, 1930).

In spite of the enormous interchange of plant material from one part of the world to another which has occurred in recent years through accidental or deliberate introduction (e.g. nearly 200,000 named species and varieties of plants officially introduced to the United States (Elton 1958)), only a very small proportion of introduced plants actually establish. Of those that do establish an even smaller proportion do so on a large enough scale to cause significant ecological changes. In the British Isles for example, 2 out of 37 species, both of American origin or parentage, *Elodea canadensis* Michx. in inland waterways and *Spartina townsendii* (*sensu lato*) in salt marshes come into this category. Although few in numbers, these rapidly spreading alien aquatic and marsh plants and others like them elsewhere in the world, can produce profound changes in the habitat, often, but not always, detrimental to human interests.

Before considering detailed examples it is as well to put the problem of large scale alien invasion into perspective by pointing out that paleontological evidence and current experience indicate that sudden population expansion is as much likely to occur with long established or cosmopolitan species as it is with aliens. Good examples are provided by the native species *Typha capensis* Rohrb., vast populations of which have recently developed in the pseudo-delta of the River Senegal, West Africa, and *Myriophyllum spicatum* L. [1], more or less cosmopolitan in the north temperate zone, recently described (Smith 1963) as the most obnoxious submersed aquatic in fresh and brackish water in America. Widespread species of toxic algae whose sudden population expansions have killed thousand of cattle (e.g. *Microcystis)*, in the Vaal Dam, South Africa in 1943 (Jackson, 1964) or tens of thousands of fish (e.g. *Prymnesium)*, in Israel fish ponds in 1945, provide further examples (Jackson, 1964).

Successful aliens may have a temporary advantage over long established species in that controlling organisms may not immediately be available in sufficient quantities to limit their spread. They may also provide opportunities for hybridization and genetic recombination with allied native species and this is most freely expressed in open habitats, like water or sparsely colonised marshland substrates, where a high rate of progeny survival can obtain.

[1] *M. spicatum* L. is perhaps not a good example to chose in this connection. SPRINGER et al. (1961) suggest that it may be an introduced plant in the United States, but give no evidence to support this. They also point out that it was collected in the Chesapeake Bay region as early as 1902, but did not become a troublesome aquatic until 50 years later.

The case histories of examples chosen are considered first and the ecological effects, many of which are common to all, discussed together afterwards.

Eichornia crassipes (Mart.) Solms, native to tropical south America, stands out as the world's worst aquatic weed at the present time. It is kept in check by other water plants e.g. *Leersia hexandra* in its native home and is said not to be a problem there (Allsopp, 1961). It was deliberately introduced to the Old World as a cultivar because of its attractive flowers in 1829 (Ridley, 1930); to Egypt in 1880 (Simpson, 1965 in litt.); the U.S.A. in 1884 (Austin, 1963); South Africa c. 1900 (Wild, 1961) and Australia, c. 1906 (Anon, 1906). In spite of the fact that only one sex was originally introduced in the East Indies and Australia (Ridley, 1930) it spread extremely rapidly by vegetative growth. Fragment dispersal against river currents was facilitated by buoyant stem bladders and sail-like leaf blades (Simpson, 1932). Significantly it has wide ecological tolerance, occurring in both fresh-water and slightly brackish conditions and occupies suitable habitats in the central one third of the earth's latitudes. In spite of strong recommendations for control by the Government botanist at a time when the plant was sufficiently localised to be dealt with in the Nile delta (Simpson, 1932), some £ 500,000 per annum are being expended in controlling infestations of *Eichornia* which threaten to block the White Nile at present (Little, 1965). Lebrun (1959) reports that in spite of the expenditure of 50 million Belgian francs on control in the Congo in 1956-1957, 150 tons (152 kilo), per hour of *Eichornia* were still passing through Leopoldville on the Congo river in 1959.

Trapa natans L. an old world species of the warm, north temperate zone, introduced, again as a cultivar, to Australia, and in 1884 (Greely, 1965), to the United States, has presented a similar problem. It took 20 years and an expenditure of several hundred thousand dollars to rid the Potomac river of this species (Martin, 1953). *Trapa natans* L. is an annual species but its seeds, which sink rapidly, may lie dormant for at least 5 years (Greely, 1965). Constant vigilance is therefore needed to control new outbreaks such as that in Maryland in 1956. This species has diminished in Western Europe in recent times (Arber, 1920), but has clearly found optimum conditions in its New World habitats.

Salvinia auriculata Aubl., a tropical, free-floating fern, native to South America, where it is of little importance, was introduced on an exchange basis from Germany to the Botanical Gardens in Calcutta in 1933. In 1939 it was sent to Colombo University. By 1942 large quantities were naturalised in the neighbourhood of Colombo and floods in 1947 spread plants widely so that 22,000 acres (8,902 ha) of cultivatable land and at least 2,000 acres (810 ha) of waterways were infested. In Ceylon reproduction appears to be entirely vegetative (Williams 1956). *Salvinia* was known to be present on the Zambesi in S.W. Africa in the 1950's. In 1962, 400 sq. miles (103,600 ha) were estimated to be occupied by this plant on Lake Kariba and at present about half this amount (equivalent to 10 % of the lake surface), due to a natural decline, is found there. *Salvinia* has also been found recently on the Congo river (Little, 1965).

Two other fern species related to *Salvinia, Azollo filiculoides* Lam. and *A. caroliniana* Willd. are thought to have been introduced to European botanic gardens from their native home in the New World. They spread widely over central and southern Europe in the late 19th century (Ridley, 1930). *A. filiculoides* has become naturalised in Australia, where its growth hinders stock from drinking and is said to taint the water.

ROOTED AQUATICS

The rooted or floating aquatic *Rorippa nasturtium-aquaticum* (L.) Hayek was probably introduced from Europe to New Zealand for cultivation. Its growth seriously impeded drainage and navigation. Of particular interest was the fact that its growth in height and vigour was far greater in the new habitat than in Europe. The annual cost of keeping the Avon river open for navigation through Christchurch in the last century exceeded £ 300 (Hooker, 1864).

The submerged rooted aquatic species *Elodea canadensis* Michx., native to North America, appears to have been introduced accidentally with imported timber or horticultural aquatics on several occasions to the British Isles. It first appeared in Ireland in 1836, in England in 1842. Its subsequent spread, probably aided by birds, was extremely rapid and by the 1850's was blocking medium-sized rivers. About this time it crossed the channel and reached France and Belgium (1860), Holland (1861) and subsequently extended to Scandinavia and Russia. During this period of active spread only the female plant was found, and spread was apparently entirely vegetative (Ridley, 1930). Rapid spread in a new locality was followed in some 5 to 7 years by a gradual decline (Siddall, 1885). By the beginning of the present century *Elodea* was so diminished as to be no longer a problem in the British Isles (Walker, 1909).

ECOLOGICAL EFFECTS OF INTRODUCED AQUATICS

The general effects of these rapid and extensive growths of aquatic species on the habitat, are common to all. They reduce the flow of canals and streams, promote silting, and in low lying topography, promote flooding in neighbouring habitats. When present in quantity they can de-oxygenate the water to the extent that fish and other animals die. For example, Penfound & Earle (1948) found that oxygen tensions at 15 cm depth beneath dense to moderately dense infestations of *Eichornia* varied from 0.1 to 1.5 p.p.m., as compared with 4.0 p.p.m. at the same depth in open water. They point out that few fish can tolerate oxygen tensions as low as 1 p.p.m. Values of pH also decreased from 7.2 to 6.2 in water infested with *Eichornia,* Dense growths smother other vegetation. Species closely related to the invading species, and therefore most likely to be in closest competition with it, may be replaced by the invader. *Salvinia auriculata,* for example, is replacing native *Salvinia* sp. in Ceylon (Williams, 1956). In tropical regions dense growths may transpire considerable quantities of water. Penfound & Earle 1948 found that *Eichornia* could transpire an average of 3 times the amount of water lost from an equivalent area of open water. Greely (1965) points out that decaying plants of *Trapa natans* increase the organic content of bottom deposits producing unfavourable but complex effects.

Secondary effects of these aquatic growths are the changes in the fauna of the habitat which they promote. *Salvinia* for example, although not supplying such a good habitat as the native species *Pistia stratiotes* L., has already acted as host for the eggs of *Mansonia* mosquitoes, which are in turn vectors of filariasis (Williams, 1956).

Extensive growths of *Salvinia* from which large sections may be detached by wave action, form floating mats or " sudd " mobilised by wind and current. These form the basis for new plant communities. Boughey (1963) reports up to 40 species of plants growing on *Salvinia* mats.

Further changes in the habitat result from control measures. These include mechanical techniques of dredging and wholesale removal of plants used in the control of rooted aquatics like *Elodea,* underwater cutting of *Trapa,* and large scale spraying with herbicides, used to control *Eichornia, Salvinia* and other aquatics. The latter results in extensive pollution with toxic chemical residues, the effects of which are still largely unknown. For example frogs, tortoises and small water snakes are said to be particularly susceptible to spray mixtures of emulsible oil and pentachlorophenol used on *Salvinia* in Ceylon (Williams, 1956).

Wild (1961) notes that when *Eichornia* is brought under control it is often replaced by equally undesirable growths of *Alternathera philoxeroides* (Mart.) Griseb., which has spread from South America to Louisiana, and is said to have been introduced recently to India (Little, 1965).

Biological control measures which are being developed are likely to result in introductions of new fauna likely to be of use in controlling aquatic growths. The S. American water snail *Marisa cornuarietis* L., introduced to Puerto Rico in 1957, successfully controlled heavy growths of water lillies in ponds, and at the same time, destroyed a snail host of bilharzia (Anon, 1962 a). An extensive collection of aquatic plant herbivores has been made in South America recently (Anon, 1962 b) and among them, a flea beetle (*Agasicles connexd*) is being tested for the control of *Alternathera philoxeroides.* Many fish have been introduced to control rooted aquatics and algal growths, notably species of carp (e.g. *Cyprinis carpio* L. and *Carassius carassius* L.) in temperate waters, and *Tilapia* spp. (e.g. *T. melanopleura* Dum.) in tropical waters (Swingle 1957). Recent experiments with the aquatic mammals known as Manatees (*Trichecus* sp.) native of S. America, and equally at home in fresh or salt water, show that they can control varied aquatic growths in British Guiana, and show promise for the control of *Eichornia* (Allsopp, 1964).

FRESH WATER MARSH INTRODUCTIONS

Two thirds of the alien wetland flora of the British Isles consists of aquatic marginal, fresh water marsh or bog species. This is not surprising, because relatively few species have become adapted to the more uniform fully aquatic, or salt marsh habitats. Marginal aquatic habitats on various types of substrate, from coarse gravel through silt and clay to peat, on the other hand, provide a very wide range of conditions for growth, and consequently can carry a very much greater range of different species.

Though richest in numbers of introduced wetland species, many of the species concerned retain only a toe-hold (e.g. *Calla palustris* L. from Eurasia and

N. America), remain localised (e.g. *Sarracenia purpurea* L. from N. America), or are thinly scattered in other vegetation (e.g. *Senecio fluviatilis* (Eurasia)). None have spread on the scale of *Elodea.* There are two clear reasons for this. Fresh water marshes normally carry closed communities which do not have space for the wholesale invasion of introduced species. They occupy fertile, comparatively easily-drained ground, and have therefore been reclaimed extensively in many countries. This has resulted in fragmentation of the fresh water habitat. This acts as a barrier to the spread of introduced species. Spaces are not so easily created by burning in temperate fresh water marshes as in more inflammable drier communities. Where spaces do occur through exceptional flooding, burning, or over-grazing, one or other species of the rich indigenous flora is much more likely to be adapted to the rapid invasion of the space, than the few introduced species of limited population that may be present during the temporary opening of the marsh. In a word, fresh water marsh introductions meet what Elton (1958) has called " ecological resistance ", consequent on the maintenance of cover and variety.

Where there is extensive cultivation of fresh water marsh as in rice growing areas, species already widely dispersed such as *Phragmites* and *Typha* spp. are probably more troublesome than introduced species.

Cyperaceae form an important element of the fresh-water marsh flora. Remarkably few of these are listed as aliens. Ewart (1928) notes that only one alien sedge has crept in among 111 native species of Cyperaceae in Victoria State, Australia. All of the 76 species of *Carex* spp. in the British Isles are apparently native, and only 4 of them are listed as introduced species in other parts of the world (Clapham et al, 1962). The majority of *Carex* spp. are heavy-seeded, tussock plants, with slow rates of vegetative growth which may account for their limited success as aliens. One exception to the above, and significantly a rhizomatous species, *Cyperus papyrus* L., is a serious problem in arid countries. This species, like *Typha, Phragmites, Salix* and *Tamarix,* belongs to the important group of marsh or riverside plants known as " phreatophytes ". They transpire large quantities of water in arid regions where it is badly needed for irrigation. In its native home, *Cyperus* is estimated to be responsible for the loss of 50 per cent of the White Nile's water through evapo-transpiration. It also blocks irrigation systems, interferes with navigation and fishing and promotes " sudd " formation on the Niger Delta and Lake Kariba (Wild, 1961). It has been introduced to the United States and is reported to be spreading aggressively in Louisiana (Martin, 1953). *Lythrum salicaria* L., introduced from Europe to N. America, had become a common species on wetland areas of New York State by 1925 and is said to be still extending its range. Impoundments in the Montezuma refuge, managed on the draw down principle, are regularly drained for control of carp in summer and sown with waterfowl foods. The spread of *Lythrum* during the drained phase has prevented this. Control by flooding has proved impraticable as *Lythrum* tolerates 2 ft. (0.6 m) of flooding at least, so control by spraying has had to be resorted too (Smith, 1959).

The work of Bakker (1960 a & b) on the biology of fresh-water marsh plants that have invaded, or been introduced to, polder reclamation areas in the Netherlands is of outstanding importance to the whole subject of introduced species and their effects. This is mainly because of its emphasis on thorough understanding of species biology, and the insight that this gives into their most subtle reactions on the environment.

Equally it is of importance because it has demonstrated how a plant introduction on a massive scale can be utilised as a potent tool in the management of marshland for wildlife and human benefit.

Studies on the natural invasions of *Senecio congestus* (R.Br.) DC on a bare mud polder in East Flevoland showed that this plant, whose light seeds are carried long distances by wind, had ideal conditions for germination in 1957. Subsequently Bakker (1960 a) demonstrated that drying of the soil and losses of ammonium nitrogen, consequent on the growth of the first generation, reduced further establishment. *Senecio* was thus well adapted to the extreme primary stages of succession, but produces quite subtle changes in the environment in the course of 2 years (it is a biennial) growth, which are inimical to subsequent seedling establishment.

For the control of this, and other invading weed species in the latest S.E. Flevoland polder, Bakker (1960 b) initiated one of the most dramatic and successful biological control measures that have yet been devised. He recommended the introduction of *Phragmites*, sown by air in 1957, on to 35,000 hectares of newly exposed mud. Its successful growth suppressed agricultural weeds, transformed the ecology of a region (the effects of which are still being worked out), and was itself readily controlled by cultivation and drainage when the area, clean of weeds for its first agricultural crop, was ploughed in 1964.

Salt marsh

The three most powerful agencies for dispersal from one part of the world to another, the oceans, man, and birds, meet in the vicinity of salt marshes at almost every shipping port. Many salt marsh species consequently are already widely dispersed within the limits of their climatic tolerance. Significantly, the salt marsh flora contains several of the most cosmopolitan species in the world. Among them, *Eleocharis palustris* L. (Roem. & Schult.), *Ruppia maritima* L., *Scirpus maritimus* L., and *Zostera marina* L., all important wildfowl foods and of no interest to early settlers, testify to the importance of birds as agents of dispersal. In tropical areas, the distribution of mangrove species fits the natural pattern of oceanic circulation, and there is little evidence of distribution by human agency. Current reclamation projects in the tropics are likely to alter this pattern in the near future, and experiments in the use of mangroves for coastal reclamation on the coast of Taiwan are in progress at present (K. van der Meer, in litt. 1965).

The grass *Spartina tovmsendii* (*sensu lato*), is of outstanding interest as perhaps the most recent, best-documented, widely-introduced, marshland plant in the world. As the history of its introductions and ecological effects have been reviewed recently (Ranwell 1963 and in press), only a brief resume is given here. The American species *S. alterniflora* Lois, was first reported from Southampton Water, in the British Isles in 1829, where it is presumed to have been introduced accidentally by shipping. A native European species, *S. maritima* (Curt.) Fernald, grew in the neighbourhood, and available evidence (Marchant, 1963), suggests that first a sterile, and then a fertile, polyploid form (*Spartina townsendii* (s.l.)) was derived by hybridization between these two species some time during the middle, or latter half, of the 19th century. *S. townsendii* (s.l.) was highly fertile, and a vigorous grower on mudflats below the normal limit of saltmarsh, where hitherto only low growths of algae and *Zostera*, which formed no barrier to its spread, occurred. Its potentialities for stabilizing mud, coastal protection, and reclamation, were quickly realised and the grass was despatched to over 40 countries in at least 7 of which it has survived. It appeared on the French coast in 1906 and was deliberately introduced with success to many other parts of the British Isles; New Zealand (1913); Netherlands (1924); Germany (1927); Australia (1930); Denmark (1931); Tasmania (? 1947, probably earlier); North America (1960), and has been in greenhouse cultivation in Argentina and China since 1965.

Spartina townsendii (s.l.) has replaced most of the salt marsh plant and animal communities, from the upper *Zostera marina* levels, to the mid-*Puccinellia maritima* zone, on parts of the European coast. It has invaded the territory occupied by its parent species and in most cases replaced them. It has stabilised many square miles of formely shifting mudflat, and speeded up the accretion of coastal marshland, by slowing up the movements of siltladen tidal water. Its growth, considered undesirable on amenity grounds on parts of the coastline in the British Isles and in Germany, has led to chemical spraying for control. Elsewhere in the British Isles and other countries it has provided additional salting pasture, and in several countries, notably in the Netherlands, has lead to large scale reclamation.

Finally, the introduction of the salt tolerant shrub, *Tamarix gallica* L., from the Mediteranean region to North America in the early part of this century, remains to be considered.

This shrub spread very rapidly over thousands of acres of marshland, and especially alongside watercourses in the S.W. United States. Judging from its distribution on remote oceanic islands, its seeds, which are chiefly wind dispersed, but also dispersed by water, can spread over long distances. In the United States it forms dense thickets and readily seeds into new areas. Martin (1953) records that its most serious effects include : interference with drainage; promotion of flooding; damage to grazing interests and waterfowl habitat, and, most seriously, extensive losses of irrigation water through evapo-transpiration.

Tamarix presents a serious problem as a phreatophyte in two ways. Optimal growth occurs on soils where the water table lies 6 to 8 ft. (1.8 to 2.4 m) below the surface. It not only utilises water from a considerable depth required for irrigation, but in marginal, slightly brackish areas, by transpiring water, it effectively alters the quality of that remaining to a higher salt content, which may limit the growth of agricultural crops like rice (Israelson and Hansen, 1962).

Conclusion

Several points emerge from a study of alien aquatic and marsh plants and their effects which deserve final emphasis.

1. Botanists, horticulturalists and aquarists who often have special facilities for importing and exporting plants, have been largely responsible for introducing many of the species discussed from one continent to another. Large scale disturbances of the habitat, to meet expanding human population needs, have been responsible for the explosive spread of most of these species.

2. The ecological effects of large scale aquatic and marsh plant invasions are profound, complex, and still little understood. The picture is further complicated by the chains of reaction set up by *ad hoc* control measures.

3. The scale of expenditure and effort on control measures is not matched by that on species biology studies fundamental to their success.

4. Where really large scale invasions take place some evidence suggests that the plant may so change the environment, that in the time required for its effective control by artificial means, in the few cases where this has been achieved, the chances are that the plant itself would create a new environment unfavourable to its growth. Premature control measures may therefore, in some cases, actually retard the rate of natural population decline by recreating optimal growth conditions.

5. Research into biological cropping techniques, and physical techniques for insulating water surfaces to limit plant invasions, should be brought into scale with the continued search for safe and effective chemical control methods.

6. Historical studies of conditions that preceded large scale plant invasions are needed to help in the recognition of potentially troublesome introductions. Recognition of such species should be communicated (cf. Wild, 1961), to as wide a public as possible so that their help can be enlisted for preventative control measures at the earliest signs of trouble.

SUMMARY

Factors favouring the establishment and spread of alien aquatic and marsh plant species are considered in relation to the water resource needs of expanding human populations. Reasons for the special suitability of the aquatic habitat for plant growth and the rapid spread of aliens are given.

Cases-histories of well-documented examples of aquatic aliens (e.g. *Eichornia crassipes, Trapa natans, Salvinia auriculata* and *Elodea canadensis),* which have seriously modified the habitat are discussed. Reasons for the generally less serious effects of aliens in bog and fresh-water marsh habitats are considered. The significance of recent studies on marsh weeds in Dutch polders to studies on the establishment and spread of aliens is noted.

The advantages and disadvantages of *Spartina* introductions to different parts of the world are contrasted with the serious problems created by alien phreatophytes (e.g. *Tamarix gallica*) in saline marshland habitats.

Conclusions drawn from the examples given emphasize the need for detailed biological studies of alien aquatic and marsh plants and for critical examination of the reactions of these species on the environment in relation to control measures.

RÉSUMÉ

Les facteurs favorisant l'établissement et la propagation d'espèces végétales aquatiques et marécageuses introduites sont examinés par rapport aux besoins en ressources aquatiques des populations humaines en expansion. Les raisons pour lesquelles l'habitat aquatique convient particulièrement bien à la croissance des plantes et celles pour lesquelles les espèces introduites se propagent avec rapidité sont exposées.

L'historique d'exemples bien documentés de plantes aquatiques introduites (comme *Eichornia crassipes, Trapa natans, Salvinia auriculata, Elodea canadensis)* ayant sérieusement modifié l'habitat est présenté. Les raisons pour lesquelles les effets d'espèces introduites dans les habitats de tourbières et de marais d'eau douce sont généralement moins graves sont examinées. Mention est faite de l'importance que revêtent les études effectuées récemment sur les mauvaises herbes de marais dans les polders hollandais pour les études sur l'établissement et la propagation d'espèces introduites.

Les avantages et désavantages pour différentes régions du monde découlant d'introductions de *Spartina* sont comparés avec les graves problèmes créés pas des phréatophytes introduits (comme *Tamarix gallica*) dans des habitats de marais salants.

Les conclusions dégagées des exemples donnés soulignent la nécessité de procéder à des études biologiques détaillées des plantes aquatiques et marécageuses et à un examen critique des réactions de ces espèces sur le milieu par rapport aux mesures de contrôle.

REFERENCES

ALLSOPP, W. H. L. (1961). Putting manatees to work. *New Scient,* 12 : 548-549.

ANON (1906). *Water hyacinth in New South Wales.* Agric Gaz. N. S. W.

ANON (1962 a). Snails weed waterways. *Agric. Res., Wash.* 11 : 8-9.

ANON (1962 b) Alligator weed... controlled by insects? *Agric. Res., Wash.* 10: 8-9.

ARBER, A. (1920). *Water plants.* Cambridge.

AUSTIN, W. G. L. (1963). Control of aquatic weeds. *Outl. Agric.* 4: 35-43.

BARKER, D. (1960 a). *Senecio congestus* (R. Br.) D. C. in the Lake Yssel polders. *Acta. hot. neerl.* 9: 235-259.

BAKKER, D. (1960 b). A comparative life-history study of *Cirsium arvense* (L.) Scop, and *Tussilago farfara* L., the most troublesome weeds in the newly reclaimed polders of the former Zuiderzee. *Biology of Weeds,* Oxford, 205-222.

BOUGHEY, A. S. (1963). The explosive development of a floating weed vegetation on Lake Kariba. *Addisonia* 3 : 49-61.

CLAPHAM, A. R., TUTIN, T. G. and WARBURG, E. F. (1962). *Flora of the British Isles,* 2nd edn. Cambridge.

DANDY, J. E. (1958). *List of British vascular plants.* London.

ELTON, C. S. (1958). *The ecology of invasions by animals and plants.* London.

EWART, A. J. (1928). Alien flora of Victoria. *Proc. R. Soc. Vict.* (N. S.) 41 : 59-62.

GREELY, J. R. (1960). Eurasian watermilfoil: a new threat to our waterways. *N. T. St. Conserv.* 14: 10-11.

HOOKER, J. (1864) Note on the replacement of species in the colonies and elsewhere. *Nat. Hist. Review,* 4 : 123-127.

ISEAELSON, O. W. and HANSEN, V. E. (1962). *Irrigation principles and practices.* 3rd ed. New York.

JACKSON, D. F. (ed) (1964). *Algae and man.* New York.

LEBRUN, J. (1959). La lutte contre le développement de *l'Eicbornia crassipes. Bull. agric. Congo beige* 50: 251-252.

LITTLE, E. C. S. (1966). *The invasion of Man-made Lakes by plants.* London.

MARTIN, A. C. (1953). Improving duck marshes by weed control. *Fish and Wildl. Circ.* 19: 1-49.

PENFOUND, W. T. and EARLE, T. T. (1948). The biology of the water hyacinth. *Ecol. Monogr.* 18: 447-472.

RANWELL, D. S. (1962). Conservation and management of estuarine marsh in relation to *Spartina* marsh in the British Isles. *Int. Un. Consv. Nat. publn.* 3 : 281-287.

RANWELL, D. S. (in press). World resources of *Spartina townsendii* (*sensu lato*) and economic use of Spartina marshland. *J. App. Ecol.*

RIDLEY, H. N. (1930). *The dispersal of plants throughout the world.* London.

SIDDALL, J. D. (1885). The American water weed *Anacbaris* (*Elodea*) *alsinatrum* Bab: its structure and habit. *Proc. Soc. Nat. Sci.* 3 : 125-134.

SIMPSON, N. D. (1932). *A report on the weed flora of the irrigation channels in Egypt.* Cairo.

SMITH, L. S. (1959). Some experiences with control of Purple Loosestrife at the Montezuma Wildlife Refuge. *Proc. 13th north east Weed Control Conf.,* 333-336.

SMITH, G. E. (1962). Eurasian watermilfoil (*Myriophyllum spicatum*) in the Tennesee Valley *Proc. 15th south Weed Control Conf.* 258-264.

SPRINGER, P. F., BEAVEN, G. F. and STOTTS, V. D. (1961). Eurasian watermilfoil — a rapidly spreading pest plant in eastern waters. *Proc. north east Wildl. Conf.,* 1-6.

SWINGLE, H. S. (1957). Control of pond weeds by the use of herbivorous fishes. *Proc. 10th south Weed Control Conf.,* 11-17.

TIMMONS, F. L. (1962). Status and prospects in aquatic weed control. *Proc. 18th west Weed Control Conf.,* 59-64.

WALKER, A. 0. (1912). The distribution of *Elodea canadensis* Michaux in the British Isles in 1909. *Proc. Linn. Soc. Land., 71-77.*

WILD, H. (1961). Harmful aquatic plants in Africa and Madagascar. *Publs. Cons. scient. Afr. S. Sahara* No. 73, 1-67.

WILLIAMS, R. H. (1956). *Sahinia auriculata* Aubl: the chemical eradication of a serious aquatic weed in Ceylon. *Trop. Agric, Trin.* 33 : 145-157.

COMMENTS

R. M. Moore (Australia) agreed on the dangers of applying control measures without understanding the ecology of the community in which the undesirable species has become established. In Australia the control of the introduced *Lantana lamera* led to an increase in another and perhaps more undesirable exotic species *Eupatorium adenophorum.* Similarly, the local control of *Hypericum perforatutn* in Victoria by *Chryosmelia gemellata* was followed by increases in bracken fern and blackberry.

THE STATUS OF INTRODUCED PLANTS IN THE NATURAL VEGETATION OF POLAND

by

JAN KORNAS and A. MEDWECKA-KORNAS

Institute of Botany, Jagellonian University,

and

Nature Conservation Research Centre,
Polish Academy of Sciences,
Kraków, Poland

INTRODUCTION

The aim of the present paper is to report the occurrence of foreign plant species, introduced by man, in different types of plant communities in Poland, and to discuss the bearing of these facts upon the conservation of natural vegetation. It is a matter of high importance for a conservationist to know whether and under what circumstances introduced plants are able to displace the native flora, and what are the best means to avoid this danger. In Poland the impact of man upon vegetation and the spread of foreign plant species have been extensively studied, especially in the last 15 years. Therefore it is already possible to give an adequate answer to both of these questions.

Various terms are used to classify introduced flora, but many of them are ambiguous. Therefore it seems reasonable to give here some terminological explanations. All the plant species " accompanying man ", especially those occuring in the artificial habitats of ruderal places and cultivated fields, will be referred to as synanthropic species (Kornas 1966: 119). Synanthropic species of alien origin will be called anthropophytes (= introduced or adventive species), and will be divided into (1) older immigrants, which arrived in prehistoric or early historic times, up to the end of the xvth century (archeophytes - Rikli 1903 : 74), and (2) newcomers, which were introduced in more recent times but are already well established in the country (neophytes *sensu* Meusel 1943 : 94, a.o.). The newcomers occur either (a) exclusively in ruderal places and/or in cultivated fields (epoecophytes - Thellung 1915), or they have already settled in more natural plant communities (agriophytes - Kamyshev 1959: 1614 = neophytes *sensu* Rikli 1903: 74, Thellung 1915, Kornas 1966: 121, a.o.). The data on the origin and history of archeophytes in Poland—as in all other countries—are rather incomplete and not very reliable. Therefore the only group of introduced plants to be discussed here are the newcomers. To permit more exact analysis of their occurrence, a further subdivision of agriophytes, the group of recent immigrants established in other than cultivated and ruderal sites, is proposed by the present authors : viz. into (b_1) newcomers established only in semi-natural secondary vegetation of meadows, pastures, disturbed riversides, forest clearings and forest edges, etc. (hemiagriophytes), and (b_2) newcomers which have become integral members of completely natural vegetation in waters, swamps, bogs, dunes, rocks, forests, etc. (holoagriophytes).

OCCURRENCE OF INTRODUCED SPECIES IN DIFFERENT TYPES OF PLANT COMMUNITIES

The Polish flora contains nearly 2,300 species of vascular plants, more than 2,000 species being native and about 250-300 species introduced by man and already well established in the country. Several hundred of temporarily introduced species have been also observed, but—as they are not able to maintain themselves permanently—they cannot be regarded as true members of the Polish flora.

More than 100 introduced species are believed to be new immigrants, arrived since the beginning of the XVIth century; the remaining are either archeophytes or foreign species of unknown history. The occurrence of 100 newcomers in plant communities of Poland have been carefully analyzed. 57 species proved to grow only in ruderal places and/or in cultivated fields (epoecophytes); 34 species are found usually in semi-natural vegetation (hemiagriophytes), while only 9 species are reported to grow permanently in undisturbed natural vegetation (holoagriophytes). Of the latter group only 2 species are really widely distributed throughout the country: *Elodea canadensis* Rich. in water plant communities (Potamogetonetalia) and *Acorus calamus* L. in reed-swamps (Phragmitetalia). Another newcomer, *Impatiens parviflora* D.C., quite recently became fully established in moist deciduous forests (Fagetalia, especially Alno-Padion) in several parts of Poland; the same is reported of *Impatiens Roylei* Walp. (= *I. glandulifera* Royle) in the willow-poplar riverside forest (Salici-Populetum) of the Szczecin region (Jasnowski 1961). Two foreign species occur along rivulets: *Mimulus guttatus* D.C. in different parts of the country, and *Lysimachia punctata* L. in southern Poland. Very locally established newcomers are : *Lactuca tatarica* (L.) C.A. Mey. on maritime sandy beaches in the Island of Wolin, *Sedum album* on limestone rocks in Silesia, and *Tunica Saxifraga* on gravel beds along the river Poprad in the Carpathian Mts. Only a very few other doubtful or extremely rare examples could be added to this list.

The distribution of 34 species established in semi-natural vegetation (hemiagriophytes) may be summarized as follows:

on disturbed edges of riverside forests and in secondary osier thickets .	12 spp.
on edges of other forest types, in hedges etc.	4 spp.
in dry secondary grasslands on sunny slopes	4 spp.
on disturbed, periodically inundated riverbanks	3 spp.
on sandy, dry riverbanks	3 spp.
in felled forest areas	3 spp.
in heaths and clearings in conifer forests	2 spp.
in meadows	1 sp.
in pastures	1 sp.
on grassy foot-paths	1 sp.

The above data clearly show, that in Poland, as in other Central European countries (Sukopp 1962), introduced plant species most often occupy only artificial habitats and very seldom succeed in establishing themselves as true members of the natural vegetation. The primitive plant communities seem to be highly resistant against invasions of adventives. This is especially evident in communities with a closed plant cover (forests, grasslands, bogs, etc.), but even some initial plant communities with much open spaces, e.g. on sand dunes, rocks, etc., offer only little opportunity for the newcomers to become established. The semi-natural types of closed vegetation (e.g. meadows and pastures) are similar in this respect. On the contrary, the open synanthropic vegetation of cultivated fields and ruderal places is a very favourable environment for the invaders; to a lesser extent this is also true of semi-natural secondary communities with much bare ground, disturbed by human agencies or even by natural factors, especially in river valleys, where more than 2/3 of all naturalized species of newcomers have been found. Open waters seem to be more accessible for adventives than the land. In the mountains there are far fewer introduced plants than in the lowlands, their number decreasing very rapidly with increasing altitude (Kornas 1955 : 174). Only one recently introduced newcomer is much more common in the lower montane zone than outside of the mountains (*Veronica filiformis* Sm.).

PENETRATION OF FOREIGN PLANTS INTO THE NATIONAL PARKS AND NATURE RESERVES

The spread of introduced plants into territories with natural vegetation may be especially well illustrated by data from some protected areas in Poland, recently studied in this respect. Only three national parks will be discussed here as examples; in two of them, the Bialowieza N.P. and the Tatra N.P., the first stages of transformation of the natural vegetation by man still predominate; in the Ojcôw N.P. this process is already much more advanced.

The Bialowieza N.P. consists of 4,716 ha of strict reserve in the central part of an extensive forest complex (about 125,000 ha), called the Bialowieza Forest (Puszcza Bialowieska) and situated at the frontier of Poland and the USSR. This flat lowland area of Pleistocene sands and loams is covered with beautifully preserved deciduous forests (*Tilio-Carpinetum, Circaeo-Alnetum, Carici elongatae-Alnetum,* etc.), mixed deciduous and conifer forests (*Pino-Quercetum*), as well as conifer forests (*Vaccinio myrtilli—Pinetum* s.l.); some bogs, swamps and open waters are also present (Matuszkiewicz & Matuszkiewicz 1954, Falinski & Matuszkiewicz 1963).

The historical changes of vegetation in the Bialowieza Forest have recently been summarized by Falinski (1966)[1]. Till the middle of the XVIth century the area was visited only by hunters and its vegetation remained nearly intact. In the XVIth century the first villages arose at the edge of the Forest; in the XVIIth century the establishment of permanent settlements began in more than 20 successively cleared glades inside of the wood. Roads were built and timber cut; the first ruderal places in the villages and cultivated fields around them appeared, with their specific synanthropic vegetation. In deforested river valleys reed-swamps developed, in which *Acorus calamus* L. soon became naturalized. From 1888 to 1914 the Bialowieza Forest was managed as a hunting ground of the tsars. Excessive increase of game population seriously damaged the woods;

[1] The authors are greatly obliged to Dr. J. B. Falinski (Bialowieza) for these unpublished data.

several foreign species were introduced with forage (*Bromus erectus* Huds., *Euphorbia virgata* W.K., *Galium cruciata* (L.) Scop., etc.) and two of them (*Sarothamnus scoparius* (L.) Wimm., *Lupinus polyphyllus* Ldl.) became established on forest edges. On foot-paths *Juncus macer* Gray appeared, and in waters *Elodea canadensis* Rich. The construction of two railroad lines into the Forest (1894, 1902) contributed very much to transference of new ruderal plants and field weeds. During World War I, the hunting park was done away with and the game shot down. Great quantities of timber were logged and in the felled forest areas the North American adventive *Epilobium adenocaulon* Hausskn. became naturalized. After the war a nature reserve in the nearly intact central part of the forest was set aside, and in 1932 it became a National Park. On felled areas outside of it *Sambucus racemosa* L., a garden escape, settled; some most recent ruderal newcomers appeared in the villages (*Galinsoga quadriradiata* Ruiz et Pav., *Lepidium densiflorum* Schrad., etc).

The vascular flora of the Bialowieza Forest contains some 970 species; the percent rate of introduced species is here much lower than in the whole flora of Poland, and the share of new immigrants in plant communities very insignificant. Only two newcomers established themselves in wholly natural environments (*Acorus calamus* L., *Elodea canadensis* Rich.), and only a very few of them grow in semi-natural vegetation. Many species which are naturalized on semi-natural habitats in other parts of Poland did not reach such places in the Bialowieza Forest, e.g. *Impatiens parviflora* D.C., North American species of *Solidago, Aster, Rudbekia,* etc., though some of them already occur in the villages of this region. From all these facts it must be concluded that in the Bialowieza Forest the introduced plant species do not compete directly with the native flora, as far as undisturbed habitats are concerned. However, the growing traffic in the National Park (at present some 60,000 visitors yearly) more and more seriously contributes toward the ruderalization of the environment, especially along the roads and trails, and thus opens the gates for future invasions of anthropophytes,

The Tatra N.P., established in 1954, covers 21,546 ha - nearly the whole area of the Polish part of this highest range in the Carpathians [1]. The Tatra massif is composed chiefly of granite and limestone, and clad up to about 1550 m a.s.l. with heavy montane forests (*Fagetum carpaticutn, Piceetum tatricum*); higher up there is a subalpine elfinwood zone of *Pinus mughus* Scop. (up to 1800 m), an alpine zone (up to 2300 m) and a subniveal zone (up to 2499 m on the Polish side and 2663 m on the Czechoslovak side of the range). The whole Tatra territory remained always beyond the limits of human settlement; nevertheless man's impact on the vegetation is very well marked here. Initially, this was due especially to the seasonal grazing (since the XIVth century) rather than to the lumbering, and for more than 100 years to the rapidly growing flow of tourists and mountain climbers. At present there are 2,350 ha of strict reserves in the Polish Tatra N.P., and the remaining territory is under partial protection, permitting moderate grazing and tourism. In summer, chalets on about 24 alps are occupied by herdsmen with sheep and cows; more than 10 mountain hotels are open all the year round, and the number of visitors to the National Park is about 1,000,000 people (!) yearly.

[1] In the Czechoslovak Tatra a National Park of 50,000 ha was established in 1948.

Some 1,300 species of vascular plants have been found in the Tatra Mts. As in the Bialowieza Forest, the percentage of introduced species is rather low, and their local distribution is strictly, limited to places where the natural plant cover has been previously destroyed : roadsides, trails, waste places near buildings, dung heaps by the chalets, etc., and to a lesser extent to some most heavily grazed alps and forest glades (Radwanska-Paryska 1963). Not one newcomer has succeeded in being established in the natural plant communities of forests, scrubs, alpine grasslands, rocks, etc. A few of them appear temporarily on gravel banks along the torrents. One introduced species became established on wind-throw and felled forest areas (*Digitalis purpurea* L.), another on grassy slopes by highways (*Lupinus polyphyllus* Ldl.), and a third one on foot-paths (*Juncus macer* Gray). Four newcomers were found in ruderal places near hotels and chalets (*Veronica persica* Poir., *Matricaria discoidea* D.C., *Galinsoga parviflora* Cav., *G. quadriradiata* Ruiz et Pav.). In secondary hay meadows of the forest zone only 14 rather rare species appear (= 8 % of the whole meadow flora), which are believed to be not indigenous in the Tatra Mts. (Pawlowska 1965 : 52). Only one meadow species, found exclusively at the foot of the Tatra (*Bunias orientalis* L.), is a recent newcomer (arrived about 1930). This must be especially emphasized, because at the end of the XIXth century experiments were started to acclimatize foreign meadow plants in the Tatra; of about 10 species imported from the Alps only one still persists near the former culture plots (*Sanguisorba dodecandra* L.), and another one was able to spread somewhat into the nearby meadows (*Crepis aurea* (L.) Cass.).

The local distribution of the newcomers in the Tatra Mts. shows very clearly that they are penetrating from the villages at the foot of the range up and into its centre. The same has been observed in other parts of the Polish Carpathian Mts. (Kornas 1955 : 175, 1966 : 135). It is only man, who—by destroying the natural plant cover and creating ruderal habitats—permits the adventive plants to invade the mountains. However, this process becomes more and more intensive in the Tatra Mts. because of the enormous influx of visitors.

The Ojców N.P. near Cracow was established in 1956 to protect a small complex of natural and semi-natural vegetation (1570 ha), surrounded by vast agricultural land. The river Pradnik cut here a deep and picturesque rocky valley through a limestone plateau covered with loess. The altitudes reach 300-470 m a.s.l.; the slopes are covered with neutrophilous deciduous forests (*Tilio-Carpinetum, Fagetum carpaticum*), on the plateau acidophilous conifer-deciduous forests (*Pino-Quercetum*) dominate, while on rocks there occur epilithic grassland (*Festucetum pallentis*) and xerothermic brushwood (*Corylo-Peucedanetum cervariae*) (Medwecka-Kornas & Kornas 1963). A relatively extensive area in the Park is occupied by secondary meadows and pastures, and there are even some cultivated fields within its limits. On the valley bottom a small village is situated. The human influence upon the vegetation of this region dates from prehistoric times: the area has been populated since the stone age and already in the Neolithic wheat was cultivated on the loess soils of the plateau.

The flora of the Ojcôw N.P. is composed of some 900 species of vascular plants (Michalik mscr.) [1]; the percentage of anthropophytes is approximately as

[1] The authors are greatly obliged to Mr. S. Michalik, M. S. (Krakow) for these unpublished data.

high as in the whole flora of Poland. Only one newcomer is already well established in natural forest vegetation on moist habitats (*Impatiens parviflora* D.C.); on the edges of riverside willow thickets the North American species of *Rudbekia* and *Aster* occur; on grassy paths another American plant, *Juncus macer* Gray is quite abundant. In secondary grassland on sunny slopes *Onobrychis viciaefolia* Scop. and *Medicago sativa* L. are rarely found. All other recently introduced species grow only on fields and around the buildings (*Veronica persica* Poir., *Oxalis stricta* L., *Galinsoga parviflora* Cav., *G. quadriradiata* Ruiz et Pav., etc.); near half-abandoned gardens some ornamental plants escaped from cultivation (*Parthenocissus quinquefolia* (L.) Planch., *Deutzia scabra* Thunb.). Thus, in the Ojcôw N.P., in spite of its vegetation being much more influenced by man than in the Bialowieza N.P. and the Tatra N.P., the same course of penetration of introduced plant species is clearly visible; at first the destruction of the natural plant cover and then the establishment of the newcomers.

Many similar data from other national parks and nature reserves in different parts of Poland have been collected. An especially interesting example in this respect is the steppe reserve Skorocice near Busko, district Kielce, studied by Medwecka-Kornas (1959), where a very small, isolated piece of xerothermic grassland (7,7 ha) effectively resists invasion by foreign plant species from the surrounding fields and ruderal places.

CONCLUSIONS

The natural plant communities in Poland have proved to be highly resistant to invasions of foreign plant species. The open habitats in the river valleys seem to be so far an exception, as they are apparently more accessible for adventives (especially of North American origin); but these valleys constitute the type of environment which has been most altered by man's activities. Generally speaking, the danger of penetration by newcomers into any area in Poland is rather low as long as the primitive plant cover remains undisturbed. There are many good reasons (the possible invasions of pests and parasites, introgressive hybridization with native species, and so on) to protect the national parks and nature reserves by legal regulations against the introduction of any foreign plant species. But the best way to prevent the newcomers from becoming established is to protect the natural plant cover against any damage (caused e.g. by trampling, grazing, manuring, littering, burning, etc.). This becomes especially important at present because of the constantly growing influx of visitors.

The result of our investigations agrees very well with the general opinion that intact native vegetation is able to withstand successfully the invasions of introduced species (see e.g. Ridley 1930: 658, Meusel 1943 : 94, Wulf 1943 : 111, Szafer 1949: 127, Dansereau 1959: 268, Kornas 1966: 129, and many others). However, this conclusion apparently cannot be generalized for all territories because the open plant communities of arid climates, as well as the vegetation of biologically isolated regions (e.g. islands), seems to be less resistant to foreign invaders.

SUMMARY

1. The distribution of 100 plant species, recently introduced to Poland, has been analyzed. 58 of them proved to occur only in artificial habitats of ruderal places and cultivated fields, 34 established themselves in semi-natural secondary vegetation, but only 9 became true members of natural plant communities.

2. Introduced plant species are generally able to penetrate only into places in nature reserves where the native vegetation has been previously destroyed. Therefore the best way to prevent the newcomers from becoming established is to protect the natural plant cover against any damage caused by man.

RÉSUMÉ

1. La répartition de 100 espèces de plantes, récemment introduites en Pologne, a été analysée. Cette étude montre que 57 d'entre elles ne se rencontrent que dans les habitats artificiels d'endroits rudéraux (dépôts d'immondices, fosses à ordures, décombres) et de champs cultivés, que 37 se sont établies dans la végétation secondaire semi-naturelle mais que 9 seulement d'entre elles sont devenues des membres véritables d'associations végétales naturelles.

2. Dans les réserves naturelles, les espèces végétales introduites ne sont généralement capables de pénétrer que dans les endroits où la végétation indigène a été détruite auparavant. Par conséquent, le meilleur moyen d'empêcher les nouvelles venues de s'établir est de protéger la couverture végétale naturelle contre tout dégât causé par l'homme.

REFERENCES

DANSEREAU P. (1957). *Biogeograpby—an ecological perspective.* 394 p. New York, The Ronald Press Co.

FALINSKI J. B. (1966). *La végétation anthropogène de la Grande Forêt de Bialowieza.* Publ. de l'Univ. de Varsovie (sous presse).

FALINSKI J. B., MATUSZKIEWICZ W. (1963). La Grande Forêt de Bialowieza. *Materialy Zakl. Fitosocjol. Stosow. Uniw. Warsz.* 2: 31-54.

JASNOWSKI M. (1961). *Impatiens Roylei* Walpers — eine neue Auenwaldpflanze in Polen. *Fragm. Flor. et Geobot.* 7 (1) : 77-80.

KAMYSHEV N. S. (1959). K klassifikatsii antropokhorov. *Bot. Zhurn.* 14 (11): 1613-1616.

KORNAS J. (1955). Caractéristique géobotanique des Gorces (Karpathes Occidentales Polonaises). *Monogr. Bot.* 3: 1-216.

KORNAS J. (1966). Influence of man and his economic activities on the vegetation of Poland —the synanthropic flora. In: *The Vegetation of Poland,* ed. by W. Szafer, p. 97-137. Oxford etc. Warszawa, Pergamon Press, PWN.

MATUSZKIEWICZ A., MATUSZKIEWICZ W. (1954). Die Verbreitung der Waldassoziationen des Nationalparks von Bialowieza. *Ekol. Polska* 2 (1) : 36-60, Vegetationskarte 1 :25.00c

MEUSEL H. (1943). *Vergleichende Arealkunde.* I. 466 p. Berlin-Zehlendorf, Verl. Gebr. Borntraeger.

MEDWECKA-KORNAS A. (1959). La végétation de la réserve steppique « Skorocice » (District Kielce, Pologne méridionale). *Ochrana Przyrody* 26 : 172-260, carte de végétation 1:170c

MEDWECKA-KORNAS A., KORNAS J. (1963). Vegetation map of the Ojców National Park. *Ocbrona Przyrody* 29: 17-87, vegetation map 1 :10.000.

MICHALIK S. Mscr. *Vascular flora of the Ojców National Park.*

PAWIOWSKA S. (1965). La provenance de la flore des prairies fauchables de la partie septentrionale des Tatras et de la Région Subtatrique. *Fragm. Flor. et Geobot.* 11 (1) : 33-52.

RADWANSKA-PARYSKA Z. (1963). La végétation synanthrope de la flore des Tatras. L'influence des bovins, des ovins et de l'homme sur la végétation. In : *Pasterstwo Tatr Polskicb i Podhala,* red. W. Antoniewicz, 5 : 233-281. Wroclaw etc., Zakl. im. Ossolinskich.

RIDLEY H. N. (1930). *The dispersal of plants throughout the world.* 744 p. Ashford, L. Reeve & Co.

RIKLI M. (1903). Die Anthropochoren und der Formenkreis des *Nasturtium palustre* D. C. *Ber. Schweiz. Bot. Ges.* 13, Anhang.

SUKOPP H. (1962). Neophyten in natürlichen Pflanzengesellschaften Mitteleuropas. *Ber. Deutsch. Bot. Ges.* 75 (6): 193-205.

SZAFER W. (1949). *Zarys ogolnej geografii roslin.* (An outline of general plant geography). 409 p. Warszawa, Czytelnik (in Polish).

THELLUNG A. (1915). *Pflanzenwanderungen unter dem Einfluss des Menscben.* Beibl. z. Englers Bot. Jahrb. 53 (3/5) Nr. 116.

COMMENTS

J. D. Ovington (Australia) discussed the implications of the author's conclusion that degree of closure of natural plant communities indicates ability to resist invasion by introduced species, and considered the concept in relation to the management of open communities in national parks and nature reserves. *R. M. Moore* (Australia) agreed that climax communities undisturbed by man are not invaded other than perhaps temporarily by exotic species, but suggested invasion of unstable communities by exotics is more lasting where disturbance is continuous. Since disturbance by man is often continuous, human interference becomes a prime factor in the naturalization of plants.

ALIEN PLANTS IN THE TRISTAN DA CUNHA ISLANDS

by

N. M. WACE

Department of Geography, University of Adelaide,
Adelaide, South Australia

The breakdown by man of the biotic realms established during the Tertiary Era has been one of the most striking biogeographic phenomena of the last millenium. The effects of the human introduction of alien species into their native ecosystems, and the attendant ecological explosions (Elton, 1958) and disruptions of the native biota, seem to have been most pronounced in the long-isolated lands (mostly of the Southern Hemisphere) which man with an agricultural and commercial economy reached in post-Colombian times. This process of the invasion and spread of alien plants has in general only been studied at a comparatively late stage, when the alien species concerned had attracted attention by their spectacular increases in numbers, or become a nuisance to man as weeds of cultivated land or pastures grazed by alien stock. The spread of the cardoon on the South American pampas, of the prickly pear in Southern Queensland, and of gorse and a host of other alien plants in New Zealand are well known examples which escaped early study.

In no case has it been possible to study the spread of alien plants in the absence of any man-induced disturbance of the pre-existing ecosystems. Because of the all-pervading effects of modern man (and especially his early importation of alien animals), it has thus been difficult for workers in New Zealand to decide whether the spectacular successes of alien plants there are due to some general competitive superiority of the aliens over the native species, or whether the aliens are simply better at exploiting the disturbed situations created by man and his imported animals (Allan, 1936). But the ecological performance of alien species in *undisturbed* native communities is a matter of considerable theoretical interest for students of plant dispersal and the past movements of vegetation and floras. However, there are now few habitable areas of the earth's surface where the native biota has not been to some extent disturbed by the direct or indirect effects of man, and in which the critical early stages of these alien invasions of unaltered ecosystems can be investigated. Yet some of the most interesting questions concerning alien invasions, and especially the correctness of such ideas as the " pre-adaptation " and " superior competitive ability " often attributed to alien species, can only be evaluated by study of these early stages of invasion of undisturbed environments.

Some of the most catastrophic effects of man upon native biota have taken place in oceanic islands, which appear to be particularly vulnerable to the invasion and sudden spread of alien plants and animals when their isolation is broken down by man (Fosberg, 1963 ; Wace, 1965). Few such islands enjoying climates mesic enough to enable them to support any considerable native biota, now exist in an undisturbed condition. Hawaii, Juan Fernandez, the Mascarenes and St. Helena all present well known examples of destruction of native biota and invasion by aliens since their settlement by Europeans (Wace, 1966). The four islands of the Tristan da Cunha group in mid-South Atlantic (37°-40° S.), however, still provide a valuable series of sites invaded by aliens: ranging from radical alteration of habitats and considerable alien invasion on one island, to almost complete lack of any habitat alteration and few aliens on others. For this reason, I intend to use the history and performance of alien plants in the Tristan da Cunha islands to illustrate the following points:

a) The human history of the islands, in relation to the likely methods of arrival of the aliens;

b) The geographic areas of the world to which the alien species were originally native, and the areas from which the aliens have been recruited;

c) The performance of the alien species under differing degrees of habitat disturbance ;

d) The biological characteristics of some of the more aggressive alien species.

General geographic descriptions of the islands are found in Holdgate (1958) and Dickson (1965). Full accounts of present knowledge concerning the native and alien vegetation and flora (Wace & Dickson, 1965) and fauna (Holdgate, 1965) have recently appeared. Alien flowering plants only are considered, although it is possible that some cryptogams owe their presence in the islands to man.

HISTORY OF THE ISLANDS AND THE ARRIVAL OF ALIEN PLANTS

The Tristan islands were uninhabited by man when discovered in 1506, and there is no evidence of any aboriginal inhabitants, or of any visits by primitive man. The first recorded landing took place (on the main island) in 1643. Sealing gangs are known to have lived ashore intermittently (and cultivated potatoes, and probably other plants) from about 1790 (Brander, 1940). Settlement of Tristan by a self-supporting human population has been continuous since 1815, except for the temporary evacuation of 1961-63 following the volcanic eruption of October 1961. None of the other three islands has yet been settled by a permanent human population, although there has been a manned weather station on Gough Island since 1955. The various phases of human contact with all the islands are summarised in Table I.

On the evidence of pollens from Tristan bogs, Hafsten (1960 a, b) has suggested that *Rumex acetosella* and *Holcus lanatus* (which are important dominants in the present upland vegetation—see below) may have invaded Tristan at about the same time as its discovery, and some three centuries before settlement.

Plantago lanceolata pollen, thought to be a reliable indicator of cultivation, (Godwin, 1956), occurs in peat a metre below the present surface of a lowland mire on Tristan, and Hafsten tentatively suggested a much earlier phase of human contact to account for it. This seems very unlikely on historical grounds (Uhden, 1939), and no pollens of undoubted aliens have been found in peat deposits on Nightingale or Gough Island (Hafsten, 1951, 1960 a, b). *Holcus lanatus* and *Plantago lanceolata* were not recorded from Tristan until 1908 (Phillips, 1913), but a specimen of *Rumex acetosella* in the Kew herbarium is noted as having been collected on Tristan in 1832.

The first botanical collections on the islands were made in 1793, before permanent settlement (Dupetit Thouars, 1811), when lettuces and radishes were recorded as persisting from previous cultivations on Tristan. Botanical collecting following the settlement of the main island in 1815 was sporadic: only four collections were made on Tristan, and only one on Inaccessible and Nightingale before 1900, and the first collections from Gough Island were not made until 1904. The build-up in numbers of alien species was probably continuous during the nineteenth century (Table II), but is obviously not fully recorded in the few accounts of botanists' visits. An examination of unpublished collections in herbaria could add considerably to knowledge of the rate of alien increase. By the time of the first scientific investigations by shore-based Expeditions which made some attempt at complete collecting, there were about 40 alien flowering plants established in the three northern islands (1937: see Dyer 1939, Hafsten 1951, Wace & Holdgate 1958), and 12 on Gough Island (1955: see Wace 1961). Today about 83 species of aliens are known from all the islands (about twice the number of indigenous flowering plants), but more are undoubtedly established which have not yet been collected.

By far the greatest number of aliens is found on Tristan, which has suffered the most disturbance to its native ecosystems. Of the 83 aliens at present recorded from all the islands, only one (*Brassica rapa*, on Inaccessible, which is obviously an escape from cultivation there) is not recorded from Tristan itself. The settled island has obviously acted as a pool from which aliens are distributed to the others.

The first aliens to be recorded from the several islands are of considerable interest, despite the fact that the records are obviously incomplete. The early escape of cultigens on Tristan and Inaccessible, largely preceeding the influx of alien weeds, seems to have a parallel on Masatierra in the Juan Fernandez group, where radishes and turnips escaped from cultivation covered considerable areas of ground in 1740 (Skottsberg 1953). The early arrivals of aliens on Tristan are very similar to those recorded on the Chatham Islands (43° S, 177° W) within about 30 years of their settlement by Europeans (Madden & Healy 1959). In spite of their wide longitudinal separation, the aliens which early colonized these two island groups are remarkably similar, and the aliens show little influence of the indigenous floras of their nearest continental lands (see below). Ridley (1930) believed that the first insular aliens to appear in " cold climates " were *Poa annua, Poa pratensis, Plantago major, Stellaria media* and *Sonchus oleraceus.* To this list might perhaps be added *Anagallis arvensis, Bromus catharticus/unioloides, Cerastium* spp., *Hypochoeris* spp., *Rumex acetosella* and *R. obtusifolius* (Table II).

Almost all the aliens recorded from the islands have light, scabrid or adhesive diaspores, and it is notable that at least the early arrivals are quoted by Ridley

(1930) as being dispersed in a variety of ways, but especially in mud on shoes etc., and in association with various domestic animals. The few aliens with bulky or heavy diaspores (*Ulex europaeus, Physalis peruviana, Romulea bulbocodiutri*) have probably been introduced intentionally. It seems likely that most of the aliens have been introduced accidentally with stock or their fodder, in packing materials, or with seeds etc. of domesticated plants.

PROVENANCE OF ALIENS IN THE ISLANDS

The alien flora in the islands is predominantly northern hemisphere in origin. The majority of species, including almost all the earlier arrivals (and all the most aggressive aliens - see Table III) are natives of Europe and the Mediterranean region. An attempt is made below to analyse the areas of origin of the aliens, by adding the points allotted to each species according to the probable extent of their native ranges over the biogeographic realms. Many of the aliens now have such a wide range, that it is difficult to define their pre-human areas of occurrence, but relative sizes of the totals give some idea of the areas from which the alien flora was ultimately derived :

Palearctic realm	58
Nearctic realm	12
Ethiopian realm (including the Cape)	14
Oriental realm	3
Neotropical realm	8
Australian realm	7

Although the alien flora seems to have been derived originally from the northern hemisphere, it may have been recruited from areas closer at hand, especially the Cape region. Only fifteen of the aliens in the islands are not recorded as present in the Cape peninsular in Adamson & Salter's (1950) flora:

Ranunculus acris
Rorippa spp.
Ulex europaeus
Bellis perennis
Crepis spp.
Veronica agrestis
V. serpyllifolia
Prunella vulgaris
Agrostis tenuis
A. stolonifera
Festuca rubra
Poa trivialis
Cerastium caespitosum
Chrysanthemum leucanthemum

It is likely that some of these are in fact now established in the Cape region, but the rich *native* flora of that area seems to have contributed little to the alien flora in the islands, despite the fact that most of the human traffic with Tristan since the decline of sailing ships in the latter half of the last century, has been by way of the Cape. The following natives of the Cape region are now established as aliens in the islands:

Oxalis purpurea	Leonitis leonurus
Crassula pellucida	Romulea bulbocodium
Centella asiatica	Sporobolus capensis
Lobelia erinus	Cyperus congestus, C. tenellus

These, and other species possibly native to the Cape region, were comparative latecomers to Tristan (or were not collected there until the 1930's). It is probable that this influx of Cape species reflects the greater traffic with South Africa in later years. During the time of the explorers and the sealers, and especially before the cutting of the Suez Canal in 1869, most of the sailing ships calling at Tristan would have come more-or-less direct from Europe and North America.

In 1937 efforts were made to establish a number of species of African fodder grasses on the island, and some prospective timber trees originally from warm temperate zones (*Cupressus macrocarpa,* 4 species of eucalypts, 4 species of pine and *Phytolacca dioica*), together with three Australian hedge plants (*Hakea saligna, Leptosperum laevigatum* and *Myoporum insulare*) (Dyer, 1939). Most of these died, and none is reproducing spontaneously now. The contribution of the southern cold temperate and circum-Antarctic floras to the aliens in Tristan has been negligible, but it is likely that these are the regions of moist, cool isothermal climates from which useful woody plants for introduction might be procured in future.

THE PERFORMANCE OF THE ALIEN SPECIES

In the islands, as elsewhere, alien species tend to grow in areas which have suffered some disturbance to their native plant communities. The majority of the island aliens are confined to the radically altered communities which are subjected to continual disturbance by cultivation or grazing, and which are themselves dominated by aliens. Most of these non-aggressive aliens seem to be confined to Tristan on the lowland plains, which are heavily grazed by cattle, or where potatoes or other vegetables are grown (Table III).

A second group of about 14 species of aliens also grow in communities which are dominated by native species, but which have suffered some disturbances (usually from grazing animals). These somewhat aggressive aliens mostly grow on some of the smaller islands, as well as Tristan itself.

A third small group of about 12 highly aggressive alien species appear to be capable of penetrating native vegetation on the smaller islands which have not suffered any human disturbance, nor been subjected to the grazing of imported animals. It is important to note, however, that even these most aggressive aliens all appear to exploit habitats which have been disturbed through non-human causes. Thus, many of them are predominantly coastal species, growing in open communities above the beaches; others are associated with the trampled and disturbed vegetation around penguin and albatross nesting sites; while some exploit the bared hillsides which have been swept by landslides and rock falls. On Gough Island, these aggressive aliens can be ecologically segregated (although there is some overlap between coastal and penguin rookery species):

coastal sites	*nesting sites*	*landslides* etc.
Stellaria media	Stellaria media	Agrostis stolonifera
Sonchus oleraceus	Poa annua	Holcus lanatus
Plantago major	Rumex obtusifolius	Sonchus oleraceus
Rumex obtusifolius		

There is no evidence to show that even these aggressive aliens are invading native vegetation which has never been subjected to grazing or other disturbance, and study of all the smaller islands strongly suggests that some disturbance to the native ecosystems is a necessary condition for the successful invasion of the aliens.

These observations thus support the view of Allan (1936) in New Zealand and Egler (1942) in Hawaii that the alien species there owe their success to the disturbances made by man, and especially by the alien herbivores that he imports. They refute the view of Hooker (1853) that the alien species from northern lands are inherently superior to the native species in the absence of any habitat disturbance.

Alien species can enter the native vegetation, as on Gough Island, even in the absence of human disturbance because of the effects of natural erosion and native avifauna. But even under conditions of severe and continued disturbance by man, some native species seem able to survive in competition with the aliens. Thus, on the grasslands of the Tristan coastal plains, *Blechnum penna-marina* and *Hydrocotyle capitata* are frequent amongst the aliens despite very heavy grazing. But few of the native species in the islands appear to be capable of exploiting continuously disturbed sites, and the great vulnerability of the insular vegetation to alien invasions may be largely due to just this lack of competitors for the aggressive aliens. It is notable, however, that the most successful flowering plant colonist ot the new volcanic material on Tristan in 1966 was the native *Scirpus thonansianus* (J. M. Dickson, *in litt.*).

The biological spectra (Raunkiaer, 1934, 1947) of the alien and native species differ considerably from one another. The greatest change is in the much higher proportion of therophytes in the alien flora, than amongst the natives; and the lower proportion of chamaephytes (and woody plants generally) :

Percentage proportion of life forms	*Number of species*	*Phanaerophytes*	*Chamaephytes*	*Hetni-cryptophytes*	*Geophytes*	*Therophytes*
Tristan-Gough native species	38	5	27	63	0	5
Tristan-Gough alien species	83	1	3	52	1	43

Some of the species here regarded as therophytes, however, may overwinter successfully in the mild and equable oceanic climate of the islands, but the proportional representation of life forms within the different groups of aliens, arranged according to the disturbance of the habitats they occupy, varies considerably. Whereas the most labile habitats (Groups A and B, Table III) are invaded by about equal numbers of therophyte and hemicryptophyte species, the less labile areas (Group C) support mostly hemicryptophytes. The latter may correspond to Ehrendorfer's (1965) perennial polyploid colonizers.

It is notable that the alien flora contains few woody species. *Ulex europaeus,* the only phanerophyte listed in Table III, has shown no signs of the aggression that it manifests in New Zealand and elsewhere, although it has been present on Tristan for at least 30 years. None of the woody species which has been planted from time to time, such as the fig, apples, various willows, eucalypts and pines (see above) regenerates freely. This is in marked contrast to some other oceanic islands, where aggressive shrubs have invaded the native vegetation and even altered the whole character of the landscape. *Aristotelia maqui* and *Rubus* sp. in Juan Fernandez (Skottsberg 1953); *Lantana camara* in the Hawaiian group, and many other parts of the tropics and subtropics (Fosberg 1954); and *Rubus* spp. in the moister parts of Ascension Island (Duffey 1964), and on St. Helena (Wallace 1895) are all outstanding examples of highly aggressive woody aliens in islands. If the native vegetation in the Tristan islands is to be preserved, special care should be taken to exclude these aliens from them—particularly the brambles — and also the cool temperate representatives of such southern continental genera as *Leptospermum, Metrosideros, Tepualia* and *Fuchsia.*

BIOLOGY OF SOME AGGRESSIVE ALIENS

Certain alien species in the islands are of particular interest, due to their history and ecological performance there, and will be discussed below.

Rumex acetosella was probably an early arrival in the islands (see above). Together with *Holcus lanatus* it now dominates an entire altitudinal belt of vegetation on the main island, around the bottom of the Peak between altitudes of about 900 to 1200 m. above sea level. The early accounts of Dupetit Thouars (1811) and Carmichael (1819), suggest that tussock-forming grasses (probably *Deschampsia sp.* and *Spartina arundinacea,* and possibly also *Poa flabellata*) inhabited this region. The spread of *Rumex acetosella* seems to have coincided with the increase in numbers of sheep on the Peak, and possibly with that of goats and rabbits also (both the latter not now present in the islands - see Table I). Moore (1954) pointed out that the *Rumex acetosella* communities on Tristan seem very similar to those in parts of New Zealand, South Island. In both cases the *Rumex* forms patchy communities on stony soils in wet regions beneath the snow line, and has replaced tussock grass communities which developed in the absence of grazing animals. " In each case, *R. acetosella* seems to fill a niche that is prepared by the animals, and in which no indigenous species is sufficiently aggressive and resistant to attain immediate dominance. " On the smaller islands of the group, which have been less disturbed by grazing animals, *Rumex acetosella* is far less important. On Gough Island in 1955-56 (up to which time there had been no grazing animals ashore) it was absent from the upland regions, although some of these regions present conditions very similar to those in which it is so successful on Tristan. The only plant of that species recorded on Gough until then had been imported with some vegetables, and was destroyed, although it has probably re-established itself on the island since then. It will be interesting to see whether it eventually spreads into the upland regions in the continued absence of sheep and other introduced herbivores. No chromosome counts have yet been carried out on the Tristan plants, but from existing herbarium collections it seems that only the diploid form (*R. angiocarpus* Murb.) is present on Tristan.

Rumex obtusifolius has already been noted as one of the earliest arrivals in the islands, which now grows throughout the group. Like *Sonchus oleraceus* and *Poa annua* it seems to owe its initial success largely to its preference for sites rich in soil nitrogen. These early colonists become easily established on beach detritus and on dunged ground in seal wallows and breeding grounds and in penguin rookeries. All these species, and also *Stellaria media* and *Chenopodium album,* which often inhabit rather similar situations, grow to a greater size than is common (at least in Britain) where they are presumed native.

Oxalis purpurea on Tristan is the only alien species which has a clear morphologically marked outbreeding system: like most species of *Oxalis* (but not *O. corniculata,* which is also established on Tristan), it has trimorphic flowers. Although common around the Tristan settlement in October 1955, it was found that all the plants there were long styled. It is probable that the importation of single diaspores (in both the alien and the native flora) may force vegetative or subsexual reproduction on plants which are obligatory outbreeders in their native range. This hypothesis would be worth testing on the alien hemicryptophytes in the islands. The adoption of vigorous vegetative reproduction by sterile pentaploids of *Oxalis pes-caprae* in South Australia (Symon, 1961) where it is also established as an alien from South Africa, may provide a parallel case to that of *O. purpurea* on Tristan. But the specialisation to vigorous outbreeding in *Oxalis purpurea* is probably exceptional in the alien flora as a whole. It seems that almost all the alien species display what Baker (1965) has called « general purpose genotypes », and show at least some of the characteristics of this « ideal weed ».

There is no doubt that more alien plants will establish themselves in the Tristan islands in future, and more are certainly present now than are recorded in these lists (Table III). But quite apart from the value of the islands for a study of their native biota (Wace, 1965, 1966), they will be increasingly useful for investigations into the whole ecological and evolutionary process of alien invasions. Some control of human activities (especially on the smaller islands), linked to continuing research on the flora, is therefore needed in future.

Table I. SOME CHARACTERISTICS OF THE ISLANDS, WITH A SYNOPSIS OF THE MAIN EVENTS LEADING TO THE DISTURBANCE OF NATIVE VEGETATION

Dates in parentheses indicate that the animals concerned are not now present on the islands in question. Taken from Holdgate & Wace (1961), and Wace & Dickson (1965).

	Tristan	*Inaccessible*	*Nightingale*	*Gough*
Physical Characteristics and Native Biota :				
Area (sq. km.)	86	12	4	57
Max. altitude (m.)	2060	c. 700	c. 300	910
Native Land Flora (*species*)				
Angiosperms	32	26	17	31
Gymnosperms	0	0	0	0
Pteridophytes	29	27	14	26
Bryophytes	230	110	42	146
Native Fauna (*species*)				
Freshwater fish	0	0	0	0
Amphibia	0	0	0	0
Reptiles	0	0	0	0
Breeding land birds	2	4	3	2
Breeding seabirds	13	17	14	20
Land mammals	0	0	0	0
Arrival of Man (*dates AD*)				
Discovery	1506	1506	1506	1505?
First known landings	1643	1656	1656?	1810?
Parties living ashore (ie. sealers, weather stn., scientists & c.)	1790-1815	1871-73 1936	visited annually by islanders from Tristan	1810-11 1888-92 1955-
Settlement (ie. breeding and self-supporting population)	1815-1961 1963-	none	none	none
Introduction of Alien Vertebrates				
Cattle	pre-1817	(1937)	—	—
Donkeys	pre-1867	—	—	—
Goats	(pre-1790 - 1870)	(c. 1820-33)	—	(1958)
Poultry	1811	—	—	1956
Rabbits	(?pre-1829-c. 1873)	—	—	—
Sheep	pre-1817	(?-1938-?)	—	1956
Pigs	(pre-1810 -?)	(1873-1938?)	—	—
Mice	? 1810	—	—	pre-1887
Rats	1882	—	—	—
Cats	c. 1810	—	—	—
Dogs	pre-1824	(occasional)	—	1959 (not breeding)

Table II. THE NUMBERS OF ALIEN SPECIES KNOWN TO BE ESTABLISHED IN THE TRISTAN ISLANDS AT VARIOUS TIMES, TOGETHER WITH THE EARLIEST ARRIVALS COMPARED TO THOSE RECORDED FROM THE CHATHAM ISLANDS WITHIN THIRTY YEARS OF EUROPEAN SETTLEMENT. (CHATHAM ISLANDS DATA FROM MADDEN & HEALY, 1959).

		Tristan	*Inaccessible*	*Nightingale*	*Gough*
1793	Dupetit Thouars, 1811	3	—	—	—
1816	Carmichael, 1819	3	—	—	—
1873	Hemsley, 1885	c. 10	c. 5	0	—
1904	Rudmose Brown, 1905	—	—	—	5
1909	Phillips, 1913	c. 26	—	—	—
1933	Christophersen, 1934	—	—	—	5
1934	Christophersen, 1937	c. 34	—	—	—
1937	Dyer, 1939	38	—	—	—
1955	Wace, 1961	—	—	—	12
1962	Wace & Dickson, 1965	82	14	4	12

Chatham Islands (until 1873)	*Tristan* (until 1900)	*Inaccessible* (until 1900)	*Gough* (until 1905)
Anagallis arvensis	Anagallis arvensis	Rumex acetosella	Plantago major
Bellis perennis	Bromus unioloides	Sonchus oleraceus	Poa annua
Brassica nigra	Cerastium triviale		Rumex obtusifolius
Bromus catharticus	Chenopodium album		Sonchus oleraceus
Capsella bursa-pastoris	Gnaphalium luteo-album		
Cerastium glomeratum	Hypochoeris glabra		
Chenopodium sp.	Lactuca sativa		
Dactylis glomerata	Malva sylvestris		
Fumaria officianis	Oxalis corniculata		
Geranium molle	Poa annua		
Holcus lanatus	P. pratensis		
Hypochoeris radicata	Raphanus sativus		
Leycesteria perenne	Rumex acetosella		
Phalaris canariensis	Senecio vulgaris		
Plantago lanceolata	Sonchus oleraceus		
P. major	Vulpia myuros		
Poa annua			
P. pratensis			
Polygonum aviculare			
Prunella vulgaris			
Ranunculus repens			
Rumex acetosella			
R. obtusifolius			
Setaria viridis			
Silene anglica			
Solanum nigrum			
Sonchus oleraceus			
Stellaria media			
Trifolium dubium			
T. repens			

Table III. THE PERFORMANCE OF THE ALIEN FLOWERING PLANTS

This division of the alien flora according to the ecological behaviour of the species in the islands is largely subjective (specially as between groups B and C), but the groups A-B-C represent a series of which the species are increasingly aggressive in invading the native vegetation. A few aliens have been omitted because of uncertainty of status, or taxonomic confusion. From Wace & Dickson 1965.

Life Forms are indicated as follows :

P : Phanaerophyte
Ch : Chamaephyte
H : Hemicryptophyte
Ge: Geophyte
Th: Therophyte

Distribution of each species within the islands is indicated by the following abbreviations:

T : Tristan (main island)
I : Inaccessible
N : Nightingale
G : Gough Island

A. *Species which are more or less confined to communities dominated by introduced plants* (i.e. alien species in alien communities):

H	T	Ranunculus acris
Th	I	Brassica rapa
Th	T	Coronopus didymus
?H	T	Rorippa nasturtium-aquaticum
Th	T	Polycarpon tetraphyllum
?Th	T	Scleranthus sp.
Th	T	Malva parviflora
H	T	M. sylvestris
H	T	Oxalis purpurea
H	T	Trifolium repens
?Th	T	Trifolium cf. micranthum
Th	T	T. dubium
P	T	Ulex europaeus
?Th	T	Crassula pellucida
Th	T	Anthemis cotula
H	T	Bellis perennis
H	T	Cotula anthemoides
?Th	T	Crepis sp.
Th-H	T	C. capillaris
Th	T	Conyza bonariensis
?Th	T	Gnaphalium purpureum
Th	T	Senecio vulgaris
Th	T	Sonchus asper
Th	T	Lobelia erinus
Th	T	Anagallis arvensis
?	T	Lithospermum sp.
Th	T	Myosotis discolor
H	T	Convolvulus sp.
Ch	TI	Physalis peruviana
H	T	Verbascum virgatum
Th	T	Veronica agrestis
H	T	Verbena officinalis
H	T	Leonitis leonurus
H	T	Prunella vulgaris
H	T	Polygonum aviculare
H	T	Rumex crispus
Th	T	Euphorbia peplus
Ge	T	Romulea bulbocodium
Th	T	Juncus bufonis
H	T	J. effusus
H	T	J. macer
H	T	Cyperus tenellus
H	T	Scirpus cernuus
H	T	Agrostis tenuis
Th	T	Bromus unioloides
H	T G	Dactylis glomerata
Th	T	Digitaria sanguinalis
?Th	T	Eleusine indica
H	T	Festuca rubra
H	T	Lolium perenne
H	T	Paspalum dilatatum
H	T	Poa trivialis
Th	T	Polypogon monspeilensis
H	T	Sporobolus capensis
Th	T	Vulpia myuros

B. *Species growing in alien communities, but also extending into native vegetation which has been affected by man or his animals* (i.e. alien species in both alien and semi-native communities).

Th	TI		Oxalis corniculata	H	T		Plantago lanceolata
H	TI		Centella asiatica	Th	T		Chenopodium album
Th	TI		Gnaphalium luteo-album	?H	TI		Mariscus congestus
Th	T	G	Hypochoeris glabra	Th	TI		Aira caryophyllea
H	TI		Calystegia sepium	H	T		Cynodon dactylon
Th	TI		Solanum nigrum	H	T	G	Poa pratensis
H	TI		Veronica serpyllifolia	Th	T		Vulpia bromoides

C. *Species growing in alien and semi-native communities, but which are also successful invaders of native vegetation which has not been affected by man or his animals* (i.e. alien species in alien, semi-native and fully native communities).

Ch	TI		Cerastium holosteoides	H	TI	G	Rumex acetosella
Th	T	G	Stellaria media	H	TIN	G	R. obtusifolius
H	T		Chrysanthemum leucanthemum	H	TI	G	Agrostis stolonifera
H	TIN	G	Sonchus oleraceus	H	T		Anthoxanthum odoratum
H	TI		Calystegia soldanella	H	TIN	G	Holcus lanatus
H	TI	G	Plantago major	Th	TIN	G	Poa annua

SUMMARY

The four islands of the Tristan group were uninhabited when discovered in 1506, and only one island has been settled by man. They present a series of sites with differing degrees of habitat disturbance and invasion by aliens. Pollen finds suggest that invasion of Tristan main island by a few alien flowering plants may have preceeded settlement, but numbers of alien species increased greatly with the introduction of sheep, goats and cattle there. *Holcus lanatus* and *Rumex acetosella* came to dominate a zone from 900 to 1200 m above sea-level, and the coastal strips are now largely covered by alien grasses. The number of alien flowering plant species on the main island (82) now greatly exceeds the number of native species (c. 32). The three smaller and unsettled islands have fewer aliens, and these only seem to invade disturbed sites (whether the disturbance is man made or natural in origin). The earliest recorded aliens seem in general to be the most aggressive species, now invading native vegetation on several of the islands (notably *Sonchus oleraceus, Plantago major, Rumex acetosella, R. obtusifolius, Agrostis stolonifera, Holcus lanatus* and *Poa annua*). The majority of alien species are natives of the Palearctic Region, although most may have come to the islands from the Cape Region where they are also adventive.

RÉSUMÉ

Les quatre îles du groupe de Tristan étaient inhabitées lorsqu'elles furent découvertes en 1506, et une seule d'entre elles a été colonisée. Elles offrent une variété de sites présentant des degrés divers de perturbation de l'habitat et

d'invasion par des éléments exotiques. Des analyses de pollen tendraient à faire supposer que l'invasion de l'île principale de Tristan par quelques plantes exotiques à fleurs pourrait être antérieure à sa colonisation, mais le nombre d'espèces allochtones augmenta considérablement avec l'introduction de moutons, de chèvres et autre bétail domestique. *Holcus lanatus* et *Rumex acetosella* en sont arrivées à dominer une zone située entre 900 et 1200 m au-dessus du niveau de la mer, et le littoral est maintenant couvert dans une large proportion de graminées exotiques. Le nombre de plantes exotiques à fleurs dans l'île principale (82) dépasse maintenant de loin celui des espèces indigènes (c. 32). Il y a moins d'espèces exotiques dans les trois autres îles, plus petites et non colonisées, et celles-ci ne semblent avoir envahi que des sites perturbés (que les perturbations soient anthropiques ou d'origine naturelle). Les tout premiers exotiques enregistrés semblent appartenir en général aux espèces les plus agressives et ont maintenant envahi la végétation sur plusieurs des îles (notamment *Sonchus oleraceus, Plantago major, Rumex acetosella, R. obtusifolius, Agrostis stolonifera, Holcus lanatus* et *Poa annua*). La majorité des espèces exotiques des îles sont originaires de la région paléarctique, quoique la plupart d'entre elles puissent provenir de la région du Cap, où elles sont aussi adventices.

REFERENCES

ADAMSON, R. S. and SALTER, A. B. (1950). *Flora of the Cape Peninsular.*

ALLAN, H. H. (1936). Indigene versus alien in the New Zealand plant world. *Ecology,* 17: 187-193.

ALLAN, H. H. (1937). The origin and distribution of the naturalized plants of New Zealand. *Proc. Linn. Soc. London,* 150: 25.

BAKER, H. G. & STEBBINS, G. L. (1965). *The genetics of colonizing species.* Proc. 1st Int. Symp. Biol. Sciences.

BRANDER, J. (1940). *Tristan da Cunba,* 1506-1902. London, Allen and Unwin.

CARMICHAEL, D. (1819). Some account of the island of Tristan da Cunha and its natural productions. *Trans. Linn. Soc. London,* 12: 483.

CHRISTOPHERSEN, E. (1934). Plants of Gough Island (Diego Alvarez). *Set. Results Norwegian Antarctic Exp.* 1927-28: 13.

CHRISTOPHERSEN, E. (1937). Plants of Tristan da Cunha. *Sci. Results Norwegian Antarctic Exp.* 1927-28 : 16.

DICKSON, J. H. (1965). General introduction to the Biological Report of the Royal Society Expedition to Tristan da Cunha, 1962. *Phil. Trans. Roy. Soc. London,* B 249.

DUFFEY, E. (1964). The terrestrial ecology of Ascension Island. *J. appl. Ecol., 1,* 219-251.

DUPETIT THOUARS, A. (1811). *Melanges de Botaniques et des Voyages:* 5. *Description de l'île de Tristan d'Acugna et esquisse de sa Flore.* Paris, Arthus Bertrand.

DYER, R. A. (1939). The flora of Tristan da Cunha : HMS Carlisle Expedition, 1937. *Bothalia,* 3 : 589-607.

EGLER, F. E. (1942). Indigene versus alien in the development of arid Hawaiian vegetation. *Ecology,* 23 : 14-23.

EHRENDORFER, F. (1965) in Baker H. G. & Stebbins, G. L. (q. v.).

ELTON, C. S. (1958). *The ecology of invasions by animals and plants.* London, Methuen.

FOSBERG, F. R. (1954). *Protection of Nature in the islands of the Pacific,* 8th Int. Congr. Botany 104-152.

FOSBERG, F. R. (1963). Man's place in the island ecosystem. *Proc. 10th. Pacific Sci, Congress* (1961).

GODWIN, H. (1956). *The history of the British flora.* Cambridge University Press.

HAFSTEN, U. (1951). A pollen analytic investigation of two peat deposits from Tristan da Cunha. *Results Norwegian Scientific Exped, to Tristan da Cunha,* 22.

HAFSTEN, U. (1960 a). *Pleistocene development of vegetation and climate in Tristan da Cunha and Gough Isld.* Arbok for Universitetet Bergen Mat-Naturv. serie 20.

HAFSTEN, U. (1960 b). Quaternary history of vegetation in the South Atlantic islands. *Proc. Roy. Soc. London,* B, 152: 516-29.

HEMSLEV, W. B. (1885). Report on the botany of the Bermudas, and various other islands in the Atlantic and Southern Oceans. *Challenger Reps. Botany* (1) 3.

HOLDGATE, M. W. (1958). *Mountains in the sea.* London, Macmillan.

HOLDGATE, M. W. (1965). The fauna of the Tristan da Cunha Islands. *Phil. Trans. Roy. Soc. London,* B 249 : 403.

HOLDGATE, M. W. and WACE, N. M. (1961). The influence of man on the floras and faunas of Southern Islands. *Polar Record,* 10: 475-493.

HOOKER, J. D. (1853). *The botany of the Antarctic voyage of HM Discovery ships Erebus and Terror in the years 1839-1843,* Part 2, *Flora Novae Zelandiae.*

MADDEN, E. A. and HEALY, A. J. (1959). The adventive flora of the Chatham Islands. *Trans. Roy. Soc. NZ,* 87: 221-228.

MOORE, L. B. (1954). Some *Rumex acetosella* communities in New Zealand. *Vegetatio,* 5-6: 268-278.

PHILLIPS, E. P. (1913). A list of phanerogams and ferns collected by Mr. P. C. Keytel on the islands of Tristan da Cunha, 1908-09. *Ann. S. African Museum,* 9: 53-103.

RAUNKIAER, C. (1934). *The life forms of plants and statistical plant geography.* Oxford, Clarendon Press.

RAUNKIAER, C. (1937). The life form spectrum of some Atlantic islands. *Bot. Stud.* 4.

RIDLEY, H. N. (1930). *The dispersal of plants throughout the world.* Ashford, Kent, Reeve.

RUDMOSE BROWN, R. N. (1905). The botany of Gough Island, I: phanerogams and ferns. *Jour. Linn. Soc. Bot.,* 37: 238-250.

SKOTTSBERG, C. (1953). *The vegetation of the Juan Fernandez Islands.* Nat. Hist. Juan Fernandez and Easter Is. Vol. 2, 793.

SYMON, D. E. (1961). The species of *Oxalis* established in South Australia. *Trans. Roy. Soc. S. Australia,* 84: 71-77.

UHDEN, R. (1939). The oldest Portugese original chart of the Indian Ocean, AD 1509. *Imago Mundi* 3 : 7-11.

WACE, N. M. (1961). The vegetation of Gough Island. *Ecol. Monogr.,* 31 : 337-367.

WACE, N. M. (1965). Future of the Tristan da Cunha Islands. *Nature,* London, 207 (5003), 1232-34.

WACE, N. M. (1966). The Last of the Virgin Islands. *Discovery,* 27 (2).

WACE, N. M. and DICKSON, J. H. (1965). The terrestrial botany of the Tristan da Cunha Islands. *Phil. Trans. Roy. Soc. London,* B 249: 273-361.

WACE, N. M. and HOLDGATE, M. W. (1958). The vegetation of Tristan da Cunha. *Jour. Ecol.* 46 : 593-620.

WALLACE, A. R. (1895). *Island life* (2nd ed.) London, Macmillan.

COMMENTS

D. Hey (S. Africa) said that in the Cape Province of South Africa the spread of alien plants is promoted by disturbance of the natural vegetation and, once established, the aliens continue to invade even undisturbed veld. One factor encouraging the spread of invasions is fire which is not caused entirely by human agencies since it can result from lightning and rolling boulders. Introduced plants such as Hochea and the Australian Acacias reseed the burnt areas. *R. A. Falla* (New Zealand) asked what evidence there is that burning is a regular form of disturbance. He pointed out the long lasting effects of burning of vegetation on oceanic islands in the cool temperate climatic zone, where conflagration may occur rapidly over short periods and cause an impermeable crust on burnt peat. *M. Holdgate* (U. K.) confirmed that burning had occurred locally on Tristan da Cunha and said he had seen evidence of burning even in remote Southern Chile, which has a very wet climate. *L. W. McCaskill* (New Zealand) supported Wace in his plea to protect the three smaller islands from alien introductions and human interference and suggested a continuing research programme is necessary to complement that on Galapagos. Such islands suitably protected are living museums for the study of insular evolution and I.U.C.N. should take positive action to protect them.

CONSÉQUENCES ÉCOLOGIQUES DE LA MONOCULTURE DES CONIFÈRES DANS LA ZONE DES FEUILLUS DE L'EUROPE TEMPÉRÉE [1]

par

A. NOIRFALISE

Faculté des Sciences agronomiques de l'Etat
Gembloux, Belgique

La monoculture intensive des conifères a débuté il y a près d'un siècle et continue à s'étendre dans la zone des plaines et basses montagnes de l'Europe tempérée, appartenant à la ceinture naturelle des forêts de feuillus. Ces boisements ont permis de valoriser, avec grand succès, les parcours pastoraux, les landes et les terres marginales libérées par la reconversion agricole du 20[e] siècle. Leur rentabilité pousse aujourd'hui les propriétaires publics et privés à convertir également en plantations de conifères les forêts de feuillus, dont la production n'est plus adaptée aux besoins actuels des pays.

Cette nouvelle politique modifie considérablement les écosystèmes naturels de la forêt de feuillus et les conditions de vie des organismes qui leur sont inféodés. Ses conséquences écologiques méritent donc d'être confrontées, d'une part avec les impératifs économiques, d'autre part avec ceux de la conservation de la nature et de ses ressources.

Le présent article concerne principalement les monocultures artificielles de conifères d'origine européenne ou américaine, notamment l'épicea, le pin sylvestre et les sapins (*Abies*, *Tsuga* et *Pseudotsuga*). On examinera leurs effets sur le sol, les eaux et la vie sauvage.

I. Influence des conifères sur le sol

La substitution des forêts denses de conifères aux forêts naturelles de feuillus entraîne des modifications qui affectent la biologie du sol, son système d'humidification, son bilan minéral et sa pédogenèse. Ces effets sont, en général, plus marqués pour les conifères sclérophylles, à feuilles dures, tels que l'épicéa ou le pin, que pour les conifères à feuilles tendres, tels que les sapins.

1. *Modifications biologiques*

a) Des recherches effectuées en Allemagne, Autriche, Belgique et Danemark ont montré que la substitution des conifères aux feuillus provoque une forte

[1] Etude effectuée sous l'égide du Comité des Experts pour la Sauvegarde de la nature et du paysage. Conseil de l'Europe, Strasbourg (France).

diminution sinon la complète disparition des *lombricides.* Sous les conifères sclérophylles, leur biomasse est 100 fois plus faible que sous hêtraie et 300 à 800 fois plus faible que sous la chênaie mélangée à charme et tilleul. L'influence dépressive des conifères à feuillus tendres (sapins, mélèze) est moins prononcée (Franz, 1950; Wittich, 1953; Ronde, 1954, 1957; Bornebusch, 1953; Galoux, 1953).

La régression porte davantage sur les lombrics consommateurs de feuilles, qui sont également ceux qui affouillent le sol en profondeur, que sur les lombrics consommateurs d'humus (Bornebusch, 1953). La cause principale réside dans les propriétés organoleptiques des feuilles de conifères, mais il faut y ajouter les températures plus basses du sol sous conifères que sous feuillus.

b) La biomasse de la *microfaune* des litières et du sol diminue également sous les conifères. Certains groupes sont plus affectés que d'autres, notamment les Diplopodes, Gastéropodes, Myriapodes, Tardigrades, Rotifères et Nématodes. Parmi ces groupes, il en existe plusieurs qui interviennent activement dans l'attaque mécanique des litières. Le maintien ou l'introduction d'îlots feuillus conserve ou reconstitue à bref délai la microfaune endogée des forêts de feuillus (Galoux, 1953 ; Pschorn - Walker, 1953 ; Rabeler, 1964).

c) La *flore bactérienne* subit aussi une véritable inhibition, aussi bien dans l'humus que dans le sol minéral, où elle ne se maintient qu'au contact des racines (rhizosphère) (Rudnov et Zolannikova, 1960). Ainsi, dans les horizons minéraux du sol, Sonn (1960) évalue la régression à 99 %.

Celle-ci porte, en particulier, sur les fixateurs d'azote libre (Azotobacter) et sur les bactéries de la nitrification (Brouwers, 1947; Simonart et Huyghe, 1953 ; Ambroz, 1954; Warteresiewicz, 1954; Krasiljnikov et al. 1955; Veregina, 1958). La minéralisation de l'humus d'épicéa est, de ce fait, 3 à 6 fois plus lente que celle de l'humus de hêtre (Meyer, 1960).

L'inhibition bactérienne trouve ses causes dans l'acidification de l'humus et du sol, dans l'antagonisme exercé par les colonies mycéliennes et dans les propriétés antibiotiques des dérivés terpéniques libérés par les litières et les humus de conifères, dont Moreau (1959) et Bublitz (1959) ont établi expérimentalement la nocivité.

d) En revanche, la flore *mycélienne* est notablement favorisée dans l'humus des conifères, spécialement les basidiomycètes qui décomposent la lignine et les hémicelluloses (Feher, 1933; Hartmann, 1952; Ambroz, 1954; Barnat, 1954; Meyer, 1960; Rudnov et Zolannikova, 1960; Sizova et Suprun, 1962). Toutefois, dans le sol minéral lui-même, où l'humus incorporé est moins abondant sous les conifères, les colonies mycéliennes sont plus pauvres que sous la hêtraie, en particulier les consommateurs d'hydrates de carbone, tels que les ascomycètes (Mikola, 1954; Warteresiewicz, 1954). Le développement d'un tapis de mousse, fréquent sous les conifères, appauvrit davantage encore l'image fongique du sol minéral (Barnat, 1954).

2. *Transformation du type d'humus*

a) La régression de la biocénose du sol a pour conséquence un ralentissement de la division mécanique et de la décomposition des litières forestières qui, sous les conifères, s'accumulent en une couche épaisse, représentant les chutes foliaires de plusieurs années. Pareil phénomène est exceptionnel sous feuillus, même dans les sols réputés les plus pauvres. L'accumulation d'aiguilles ne résulte pas de retombées foliaires plus abondantes sous conifères que sous feuillus, mais de leur résistance spécifique à l'attaque biologique (Ovington, 1954; Handley, 1954; Gennsler, 1959; Manil et al., 1963).

Les pesées de litières, effectuées par Ovington (1954) montrent que le phénomène d'accumulation et de retard à la décomposition est le plus notable sous épicéa, mélèze et pin noir, moindre sous pin sylvestre et surtout sous le sapin géant et le sapin de Douglas, dont les retombées foliaires ne sont cependant pas négligeables. La dureté relative des feuilles semble donc bien jouer un rôle déterminant.

b) L'humidification des litières de conifères et spécialement des conifères à feuilles dures produit un *humus brut*, holorganique, noir et souvent poussiéreux, appelé « mor » et parfois « tourbe sèche » (Hartmann, 1952). Cet humus provient d'une activité largement prépondérante des champignons par rapport à la microfaune et aux bactéries (humus mycogène). Sa décomposition libère des acides fulviques et humoligniques dont les propriétés sont réputées podsolisantes (Hartmann, 1952; Ambroz, 1955). Cette déviation du type d'humidification est spécialement marquée sous l'épicéa et le pin sylvestre.

c) L'incorporation de l'humus au sol est fortement réduite sous les conifères et généralement limitée aux 2 - 3 premiers cm. L'épaisseur totale du sol influencé par l'humus (*solum* biodynamique) passe de 50 cm sous hêtraie à 20 - 25 cm sous pessière (Manil et al. 1963). Ce fait explique la pauvreté du sol minéral en microorganismes et en azote mobilisable.

d) Le changement du type d'humus se traduit par une acidification des horizons humifères et de l'horizon minéral supérieur, qui peut atteindre 0,5 à 1 unité de pH (Maran, 1959 ; Hartmann, 1960 ; Meyer, 1960 ; Gennsler, 1961 ; Duchaufour et Bonneau, 1961 ; Neuhausl, 1963; Manil et al. 1963). L'effet sur l'acidité d'échange paraît moins constant.

L'acidification n'a sans doute, pour les conifères eux-mêmes, qu'une importance physiologique mineure et peut même leur être favorable sur certains sols. Mais dans le cas des substrats pauvres, elle peut engendrer des effets secondaires en stimulant la podsolisation et la destruction des argiles, la mise en solution d'ions toxiques (aluminium, manganèse) et la rétrogradation des phosphates, qui peuvent se combiner avec le fer libre, quand le pH descend au voisinage de 4 (Laatsch, 1952).

3. *Modifications du bilan minéral*

a) L'accumulation de la litière et de l'humus brut immobilise un stock important de matières minérales, qui se trouve temporairement soustrait à la circulation dans l'écosystème forestier. Ce fait concerne en premier lieu l'*azote* qui se trouve immobilisé, sous les conifères, dans une proportion deux ou trois fois plus élevée que sous les feuillus, dans le cas de l'épicéa, du pin noir et du mélèze (Pohiton, 1958; Ovington, 1954). L'immobilisation est moins importante pour le pin sylvestre et les sapins (Ovington, 1954). Il faut ajouter que les feuilles de conifères ont souvent une teneur en azote plus basse que celle des feuillus, de sorte que leur décomposition n'en réincorpore que de faibles quantités dans le cycle annuel de cet élément (Wittich, 1954).

L'appauvrissement ou l'élimination de la végétation herbacée sous les conifères ou leur remplacement par des mousses et des éricacées diminue encore les restitutions annuelles d'azote (Sonn, 1960; Ovington, 1954). De même, l'abaissement du taux d'humus incorporé dans le sol minéral se solde par une carence relative d'azote accessible aux racines et aux mycorhizes ; Gennsler (1959) évalue ce déficit à 25 - 30 % par rapport aux sols homologues sous hêtraie.

Il résulte de ces faits que les monocultures de conifères souffrent fréquemment d'une « faim d'azote » (Duchaufour, 1953), spécialement dans les premières années de leur développement. Les replantations, après la coupe à blanc des peuplements, exigent au préalable une activation de la décomposition des litières par voie naturelle — œuvre du temps — ou par voie artificielle (chaulage, engrais), afin de remettre en circulation l'azote qui s'y trouve bloqué. C'est une des raisons pour lesquelles la seconde génération de conifères est parfois difficile à réussir sur certains sols.

b) L'immobilisation dans les litières et dans le peuplement lui-même concerne aussi le *calcium*, le *magnésium*, le *phosphore* et la *potasse* ; si les conifères prélèvent ces éléments dans le sol en quantités moindres que les feuillus (Wittich, 1954), le taux d'immobilisation est tel que le sol lui-même apparaît appauvri. Pour le calcium, cet appauvrissement est de l'ordre de 25 à 30 % (Gennsler, 1959; Sonn, 1960; Duchaufour et Bonneau, 1961), parfois plus élevé, par exemple sous le pin (70 % selon Sonn, 1960, par rapport au hêtre). Les résultats sont moins probants pour les autres éléments que le calcium et sont infirmés par certaines mesures. Les recherches d'Ovington (1954) confirment que les déficits minéraux du sol sous les conifères ne résultent pas d'une perte par lessivage mais d'un déplacement dans l'écosystème par immobilisation dans les litières, l'humus et le peuplement.

c) Les données sont rares et d'interprétation délicate en ce qui concerne les *oligoéléments.* Sonn (1960) signale une augmentation de l'alumine libre, qu'il attribue à la plus grande teneur des aiguilles en cet élément plutôt qu'à l'acidification du milieu. Le manganèse donnerait lieu à des observations similaires. Simonart et Huygh (1953) ont trouvé moins de cuivre dans le sol sous les pinèdes que sous les feuillus, mais la différence tient peut-être à une podsolisation antérieure sous la lande qui a servi d'assiette aux reboisements de pins.

4. *Altérations pédogénétiques*

a) L'acidification du sol, la formation d'humus brut, l'accumulation des litières et les régressions biocénotiques du sol constituent-elles des phénomènes réversibles ou consacrent-elles une dégradation authentique du sol? Sur cette question, les avis sont partagés.

Pour certains, ces processus traduisent un nouvel équilibre comparable à celui qui prévaut dans les forêts naturelles de conifères, défavorable aux feuillus mais nullement aux conifères eux-mêmes. Il semble bien que ce point de vue soit défendable pour les sols bruns montagnards des massifs hercyniens très pluvieux de l'Europe occidentale, comme ceux de l'Ardenne, du Massif schisteux rhénan ou du Harz. Gennsler(19S9) n'a pas observé, sur les sols bruns acides de ces contrées, des signes patents de podsolisation, ni une aggravation de l'état des humus, ni une chute de productivité de l'épicéa, même après un ou deux siècles de culture intensive.

b) Les conclusions ne sont pas aussi optimistes dans les cas des sols sablonneux, spécialement en Europe centrale, où l'on attribue à la monoculture de l'épicéa une podsolisation du sol, considérée comme préjudiciable au rendement soutenu des conifères (Hartmann, 1952 ; Smirnova et Gromajeva, 1955 ; Skrynnokova, 1958; Verigina, 1958; Vascis, 1958; Maran, 1959; Neuhausl, 1963). Pour la Tchécoslovaquie, par exemple, Maran (1959) et Maran et Lhota (1954) attribuent à la monoculture des conifères la dégradation qui frappe de vastes étendues de sols, dont certaines paraissent difficilement restaurables par des mesures sylvicoles simples, telles que le mélange de feuillus aux conifères.

c) On a également souligné le danger des monocultures de conifères sur les sols lessivés à pseudogley, très fréquents dans la zone des feuillus de l'Europe. Dans ces sols, l'épicéa ou le sapin de Douglas forment un enracinement tabulaire et n'exploitent plus l'horizon B. Le sol se podsolise peu à peu en surface, tandis que l'horizon B s'altère par tassement, marmorisation et imperméabilisation. Ce processus peut conduire, dans les cas extrêmes, à un relèvement des nappes suspendues, à l'envahissement du sol par la molinie et même parfois par les sphaignes.

d) Les sols de la forêt de feuillus offrent donc des résistances variables à la monoculture des conifères ; il convient de tenir compte de ces propriétés dans les projets d'enrésinement et dans le choix des conifères eux-mêmes, les espèces à feuilles tendres apparaissant à priori moins nocives que les espèces à feuilles scléreuses. L'éventuelle dégradation du sol dans les régions ou dans les sites inappropriés n'est d'ailleurs pas la seule menace à laquelle sont exposées les monocultures intensives de conifères. Il convient aussi de tenir compte du danger de l'extension des pourridiés radiculaires dans les terrains secs et du danger de chablis dans les terrains compacts ou hydromorphes, deux circonstances qui peuvent, à la longue, déprécier notablement des peuplements très prometteurs dans le jeune âge.

II. Influence des conifères sur la qualité et le bilan des eaux

1. *Altérations de la qualité biologique des eaux*

a) Les boisements de conifères, dans les vallées, le long des ruisseaux et des rivières ont des effets sur la capacité biogénique des eaux courantes. Huet (1951, 1952) en décrit comme suit les conséquences. On assiste à une régression sinon à l'élimination complète, sous l'effet de l'ombrage, du phytoplancton, des plantes aquatiques et des formations herbeuses ripicoles, servant d'aliment ou d'habitat au plancton animal et à de nombreux insectes, qui constituent la nourriture des poissons d'eau douce. En outre, l'élimination des plantes ripicoles herbacées ou ligneuses favorise l'éboulement des berges et supprime les refuges naturels des salmonidés. Enfin, l'enrésinement des prés et des vallons supprime les lieux propices aux frayères ou à l'alevinage artificiel.

b) Certaines recherches (Ebeling, 1930 ; Huet, 1951) ont aussi montré que l'humus d'épicéa libère des substances toxiques qui, entraînées par ruissellement vers les sources et les ruisseaux, ont une action toxique sur certains poissons, comme la truite, le vairon ou le chabot, cet effet pouvant se manifester à partir des zones fortement enrésinées, sur plusieurs kilomètres en aval.

c) Le boisement en conifères des tourbes acides à sphaignes exige, au départ, un drainage intensif et régulièrement entretenu. Selon des observations faites en Belgique, les eaux courantes peuvent se charger de matières humiques en suspension, qui retardent la décantation des argiles et peuvent complexer les oxydes de fer et de manganèse, ainsi que le plomb ou le cuivre, dans les conduites d'alimentation (Van Beneden, 1958, 1961, 1963). Il est d'ailleurs reconnu que les sols tourbeux sont inaptes à la culture des conifères quand l'épaisseur de tourbe dépasse un certain seuil, variable selon la perméabilité du sous-sol, et que les peuplements souffrent fréquemment, dans ces sites, d'importantes pertes par chablis (Pahaut, 1961). Le boisement des sols tourbeux doit donc être réalisé avec circonspection aussi bien dans le but de sauvegarder la qualité des eaux que sur le plan même de la rentabilité économique.

2. *Modifications du bilan hydrologique*

a) L'interception de la pluie par les forêts denses de conifères dépasse notablement celle des forêts à feuilles caduques. Des valeurs assez concordantes ont été établies ; généralement exprimées en pour-cents des précipitations, elles varient évidemment avec leur régime et leur intensité. Dans les régions à climat pluvieux (plus de 1000 mm par an), on a établi pour les monocultures d'épicéa des taux d'interception dépassant ceux de la hêtraie de 15 à 20 % (Eidmann, 1959, 1962; Engler, 1919; Noirfalise, 1963), et pour des régions à pluviosité plus faible, des surplus de 30 % (Valek, 1959). L'interception des peuplements d'épicéa se situe, selon les climats, entre 28 et 50 % des précipitations, celle du pin entre 25 et 30 %, soit notablement plus, dans le cas de l'épicéa, que les forêts naturelles de feuillus que ces peuplements ont remplacées.

b) On attribue aussi aux épicéas et aux sapins une transpiration totale plus élevée que celle des feuillus, sur la foi des mesures transpiratoires comparatives (Polster, 1950 ; Huber, 1953), des mesures d'assèchement du sol (Utenkova, 1962) ou des observations lysimétriques (Wind, 1958). Toutefois, ces présomptions n'échappent pas à la critique et les chiffres qui les étayent sont encore discutables et trop peu nombreux.

c) Dans les pentes boisées de conifères, le ruissellement est deux ou trois fois plus intense que sous feuillus, comme l'ont montré notamment des expériences de pluie artificielle (Valek, 1959). Cet effet est surtout sensible après une période de dessèchement des litières (Mesmer et Feldmann, 1953). Ces circonstances, ajoutées à la forte interception des monocultures de conifères, expliqueraient le tarissement de certaines sources dans les versants (Hempel, 1956) et la conclusion générale émise par plusieurs auteurs (Eidmann, 1962 ; Valek, 1959) que l'épicéa, en particulier, déprime significativement la balance hydrologique des territoires où il remplace les feuillus sur de grandes étendues.

d) Il est admis que les tourbières bombées jouent un rôle important comme régulateurs de l'écoulement dans le système hydrographique (Bouillenne, 1934; Van Beneden, 1963). Les plantations de conifères dans ces milieux impliquent un drainage intensif et un assèchement des masses de tourbe, qui ont une répercussion défavorable sur leur rôle régulateur. En outre, les zones tourbeuses agissent probablement comme des pièges à rosées et brouillards, ce qui compense l'intense transpiration dont elles sont le siège. Néanmoins, les avis demeurent très partagés sur le point de savoir si le boisement en conifères se solde effectivement par une balance hydrologique moins favorable que celle des tourbières hautes intactes (Nys, 1957; Nathlich, 1955; Eggelsmann, 1950).

III. Influence des conifères sur la vie sauvage

a) Le boisement des landes, des pelouses naturelles, des tourbières basses et des tourbières hautes par des conifères peut entraîner l'extinction locale d'espèces rares qui avaient trouvé refuge dans ces milieux; des disparitions sont citées en Belgique qui résultent incontestablement de l'enrésinement. Mais pour ce qui concerne la flore typiquement forestière, si les remaniements en sont profonds et l'appauvrissement notable sous les plantations de conifères, (Ovington, 1954; Kornen, 1952; Gennsler, 1959; Becher, 1963; Lohmeyer, 1965; Thill, 1965), sa reconstitution spontanée paraît possible si l'on revient à la culture des feuillus.

La faune entomologique est également modifiée dans la mesure où sont affectés les biotopes ou les espèces auxquels elle est inféodée. On signalera en particulier la multiplication dans les forêts artificielles de conifères de certains phytophages et lignicoles immigrés, qui sont à l'origine de dégâts parfois spectaculaires.

b) En ce qui concerne la faune aviaire, la culture des conifères dans la zone des feuillus explique peut-être certaines immigrations récentes signalées dans l'ouest de l'Europe, par exemple celle du casse-noix de Sibérie (*Nucifraga caryocatactes*) qui est indigène dans l'étage des conifères de l'Europe centrale, du pic noir naturalisé depuis quelques décennies en Belgique et aux Pays-Bas, du bec-croisé dont on a relevé plusieurs vagues d'immigration en Europe occidentale. De même, diverses espèces de la faune aviaire des feuillus et notamment les mésanges, certaines grives, le tarin et les roitelets fréquentent volontiers les peuplements artificiels de conifères où ils trouvent de la nourriture et des abris propices pour nicher (Rabeler, 1965; Fitter, 1960; Muyldermans, 1965).

c) Si les boisements de conifères créent des refuges hivernaux favorables au gibier, ils diminuent, en revanche, la capacité nutritive des forêts. On sait que le chevreuil broute volontiers les arbustes et consomme l'écorce des feuillus, riche en sels minéraux ; il contribue à faire disparaître les brins résiduels de ces essences sous les conifères et le manque de nourriture adéquate l'oblige à se rabattre sur les forêts de feuillus qui subsistent dans la région, provoquant d'importants dégâts aux jeunes plantations et aux semis naturels. C'est une cause fréquente qui fait obstacle, dans l'Ardenne belge, à la régénération naturelle des hêtraies et même à l'implantation de certains conifères, comme le sapin commun et le sapin de Douglas. De même, l'enrésinement des tourbières, des clairières humides et des découverts supprime les gagnages naturels du cerf, dont les dégâts se reportent sur les forêts de feuillus et les cultures (Burckhardt, 1959; Ueckermann, 1957; Melichar, 1960).

Cette situation se retrouve dans tous les pays où existe une protection législative du gibier et de la chasse. Burckhardt (1959) signale que le problème devient d'autant plus aigu que les populations de cervidés ont augmenté notablement depuis un demi-siècle. En Suisse, les cerfs sont 20 à 100 fois plus nombreux et les chevreuils 10 à 40 fois plus nombreux, selon les régions, qu'il y a 50 ans. En Allemagne, dans l'Eifel, il n'y avait pratiquement pas de cervidés en 1850; mais la charge atteignait, en 1953, environ 19 bêtes par 1000 ha de forêt, soit nettement plus que les normes acceptables pour l'équilibre et la régénération naturelle des forêts de feuillus.

Il existe donc aujourd'hui, dans divers pays d'Europe, spécialement en Suisse, en Allemagne et en Belgique, un déséquilibre forêt-gibier qui se solde par des dégâts alarmants dans diverses contrées et dont l'enrésinement de vastes surfaces est l'une des causes importantes. Il s'impose de concevoir d'urgence une politique forestière mieux adaptée aux exigences de la vie sauvage et des ressources cynégétiques et de promouvoir les recherches sur la biologie du gibier (Burckhardt, 1959; Ueckermann, 1957; Juon, 1963).

RÉSUMÉ

Divers griefs ont été formulés contre la culture intensive des conifères dans la zone des feuillus de l'Europe tempérée. Ils invoquent les dangers d'une dégradation des sols forestiers, d'une modification du bilan hydrologique et des ressources aquifères dans les bassins boisés, d'une stérilisation biologique du réseau hydrographique, d'une modification des flores et des faunes naturelles et d'une perturbation de l'équilibre gibier-forêt.

Ces griefs sont examinés à la lumière des recherches scientifiques effectuées durant les 10 dernières années dans les divers pays d'Europe occidentale. Les conclusions suivantes peuvent être dégagées :

1. La culture intensive des conifères provoque une régression de la biocénose du sol, une modification du type d'humus, un appauvrissement du sol en humus et une immobilisation minérale et azotée importante dans les litières. Cette régression biologique peut déclencher des processus de dégradation dans certains sols (podsolisation ou gleyisation) ; d'autres résistent, par contre, remarquablement à ces effets.

2. Les cultures pures de conifères ont une action défavorable sur le bilan hydrologique, dans les climats humides.

3. Leur effet stérilisant sur la capacité biogénique des eaux paraît établi, quand ces peuplements sont situés le long des ruisseaux et aux abords des sources.

4. L'appauvrissement de la flore du sous-bois est évident mais probablement réversible, sauf pour les espèces rares, en voie de disparition.

5. D'importants remaniements ont lieu pour ce qui concerne la faune entomologique (apparition d'insectes nuisibles), la faune aviaire et la possibilité nutritionnelle de la forêt pour le gibier.

SUMMARY

Various criticisms have been levelled from time to time against the intensive planting of conifers in the broad-leaved zone of temperate Europe. They have included the dangers of degrading forest soils, of upsetting the hydrological balance and water resources deriving from wooded watersheds, of the biological sterilization of the hydrological system, of modifying the natural fauna and flora and of breaking down the link between forests and stocks of game for sport-hunting.

These criticisms are examined in the light of the scientific research carried out during the last ten years in various countries of Western Europe. The conclusions reached can be summarised as follows:

1. Intensive conifer cultivation does encourage a progressive deterioration in the biocenosis of the soil, a change in the type of humus, a general impoverishment both of soil and humus and a severe decrease in the availability of minerals and nitrogen. This biological deterioration can in certain soils have the effect of finishing off the process of degradation, which has been set in train by other factors. On the other hand some soils have proved themselves remarkably resistant to such effects.

2. Pure stands of conifers do have an adverse effect on the hydrological balance in humid zones.

3. The effect of coniferous monoculture on the biological productivity of surface waters does seem to be established, in so far as the stands are situated along the banks of streams or in the neighbourhood of springs.

4. The resulting impoverishment of the undergrowth flora is obvious but can probably be reversed except in the case of rare species which are in the process of becoming extinct.

5. Important modifications take place in the invertebrate fauna (outbreaks of pest species for example), in the avifauna and in the nutritional potentiality of forest for game species.

REFERENCES

AMBROZ (1954). *Sborn. csl. Akad. zemed,* 27/5, p. 385-400.

BARNAT (1954). *Preslia,* 26/3, p. 277-284.

BECHER (1963). *Geob. Mitt. Giessen.*

BORNEBUSCH (1953). *Dansk. Skovfor. Tidskr.* 38/9, p. 557-559.

BROUWERS (1957). *Bull. Jnst. Agr. et St. Rech. Gembloux,* 25/1-2.

BUBUTZ (1959). *Forstarcb.* 30/6, p. 105-110.

BURCKHARDT (1959). *Schweiz. Zeitschr. f. Fortsw.* 110/1.

BOUILLENNE (1934). *Ann. Soc. Géol. Belg.* p. 54-55.

DUCHAUFOUR (1953, 1954, 1959). *Rev. For. Franç.* 5 (10), 6 (2), 9 (12).

DUCHAUFOUR et BONNEAU (1961). *Rev. For. Franç.* 13 (12).

EIDMANN (1959). *Ass. Int. Hydr. Sc, Publ.* 48, Gentbrugge.

EIDMANN (1962). *Proc. 13th Cong. Inst. Un. For. Res. Org.,* Vienne.
ENGLER (1919). *Mitt. Eid. Anstalt. forstl. Vers.* Bd. II
EGGELSMANN (1950). *Wasser Wirtscbaft,* 6.
FEHER (1933). *Unters. iiber die Mikrobiologie des Waldbodens,* Berlin.
FITTER (1960). *Nature,* 185 (4715), p. 731-2.
FRANZ (1950). *Bodensoziologie als Grundlage der Bodenpflege,* Akad. Verlag, Berlin.
GALOUX (1953). *St. Rech. Groenendael,* Serie A, 8.
GENSSLER (1959). *Diss. Hann. Miinden.*
HANDLEY (1954). *Bull. For. Comm. London,* 23.
HARTMANN (1960). *Cbl. Ges. Forstw.* 77/4.
HARTMANN (1952). *Forstökologie,* Fromme, Vienne.
HEMPEL (1956). *Z. Pfi. Ernähr. Düng.* 74/2, p. 139-143.
HOBER (1953). *Forstw. Centralbl.* 72 (9-10).
HUET (1951). *Proc. Int. Ass. Theor. appl. Limnology,* 11, Stuttgart.
HUET (1952). *Bull. Soc. Roy. For. Belgique,* 7.
JUON (1963). *Journ. for. suisse,* 114/3.
KORNEV (1952). *Lesn. Hoz.* 5/2, p. 65-70.
KRASILJNIKOV, KORENJAKO et MIRCENKO (1955). *Izv. Akad. Nauk. SSSR,* 3; p. 33-48.
LAATSCH (1954). *Dynamik der mitteleuropäiscben Mineralboden,* Leipzig.
LOHMEYER W. *Einige Beobachtungen über Scbädigungen künstlicb angebauter Fichte auf bestimmten Böden.* Rapport inedit.
LOHMEYER W. *Beispiele für Veränderungen der Bodenvegetation unter dem Einfiuss verscbiedener Nadelhölzer.* Rapport inedit.
LOHMEYER W. U. TRAUTMANN W. *Einige Beobachtungen iiber den Einfiuss des Ficbtenanbaus auf die Böden in Nordrhein-Westfalen.* Rapport inedit.
MARAN (1959). *Vestn. sel.-hoz. Nauki,* Moskva, 4/10.
MARAN et LHOTA (1954). *Shorn, csl. Akad. zemed* 27 B (4), p. 349-378.
MANIL et al. (1963). *Centre Et. Sols forest. Gembloux.*
MESMER U. FELDMANN (1953). *Forstarch.* 24 (11-12), p. 245-256.
MEYER (1960). *Arch. f. Mikrobiol.* 35.
MIKOLA (1954-1956). *Comm. Inst. for. Fenn.* 42 (7) - 43 (1) - 48 (2).
MOREAU (1959). *C. R. Acad. Sc. Paris,* 249 (12).
MUYLDERMANS L. *De avifauna van de naaldbossen.* Rapport inedit.
NATHLICH (1955). *Wasser und Boden,* 7, p. 337-341.
NEUHAUSL (1963). *Vegetatio,* 11/3.
NOIRFALISE (1959). *Bull. Soc. Roy. Forest. Belgique,* 10.
NOIRFALISE (1959). *La technique de l'eau,* 186.
NYS (1957). *Bull. Soc. Roy. For. Belg.,* 5.
OVINGTON (1954, 1955, 1958). *Journ Ecology,* 42 (1), 43 (1), 46 (1-2).
PAHAUT (1961). *Carte des sols de la Belgique,* 136 W.
POHITON (1958). *Pocvoved,* 6. Lesn. Hoz. 11 (4).
POLSTER (1950). *Bayer. Landw. Verlag,* München.
PSCHORN - WALKER (1958). *Mitt, forstl. Vers. Anst. Mariabrunn,* 48.
RABELER W. *Über die Tierwelt der norddeutschen Kieferforsten.* Rapport inedit.
RONDE (1953, 1954, 1957). *Forstw. Centralblatt* 72 (9-10), 73, 76 (3-4).
RUDNOV et ZLANNIKOVA (1960). *Soobsc. Lab. Lesored,* Moskva, 2.
SIMONART et HUYGH (1953). *Agricultura,* Louvain, 1 (1), p. 33-51 et 52-75.
SIZOVA et SUPRUN (1962). *Bjull. Mask. Obsc. Ipyt. Prir.* 67 (5).

SMIRNOVA et GROMASEVA (1955). *Pocvoved,* 6.
SKRYNNIKOVA (1958). *Pocvoved,* 4.
SONN (1960). *Einfluss des Waldes auf die Boden,* Fischer, Iena.
THILL A. *Influence des monocultures d'épiceas sur la flore forestière.* Rapport inédit.
UECKERMANN (1957). *Rehwild, Enting,* Neuwied Rhein.
UTENKOVA (1962). *Pocvoved,* 6.
VAJCIS (1958). *Pocvoved,* 5.
VALEK (1959). *Ass. Int. Hydr. Sc, Publ.* 48, Gentbrugge.
VAN BENEDEN (1963). *Protection des Hautes Fagnes,* Verviers.
VAN BENEDEN (1947). *Technique de l'eau,* 8 et 12; CEBEDEAU (1955, 1958), 28, 39.
VERIGINIA (1958). *Pocvoved,* 5.
WARTERESIEWICZ (1954). *Ekologia Polska,* 2/1.
WITTICH (1953). *Schr. Reihe Forstl. Fak. Univ. Göttingen,* 9.
WIND (1958). *Proc, and Inform. Committee on Hydr. Res.* T. N. O., 3.

INTRODUCTION AND SPREAD OF 'WEED' PLANTS IN EUROPE

by

H. GAMS

Dept. of Botany of the University of Innsbruck, Austria

a) *Water and swamp plants:*

The most famous " water pest " *Elodea canadensis* Rich, has been introduced (probably with Canadian timber) in Ireland 1836, observed in Scotland 1842, England 1847, Holland and Germany 1859/60, Denmark 1867, Sweden 1873, Finland 1884, Switzerland 1880, in the Alps 1894 (maps by Suessenguth in *Hegis Flora* 1939, Samuelsson 1934, Hulten 1940 a.o.), in most European localities only female plants, after invasion later often disappearing.

The introduction and diffusion of *Acorus calamus* L. has been studied in great detail by K. Wein (*Hercynia* I-III, Halle 1937/42), its cytology by H. D. Wulft (*Planta,* 31, 1940). The older records of " akoron ", " Calamus aromaticus " a.o., designate other plants, especially species of Iris. *Acorus calamus* var. *vulgaris* is a triploid, nearly sterile, derivate from diploid and tetraploid ancestors in the southern Himalayas, and has been introduced over Turkey by Busbe queto Vienna about 1560. It came to the gardens of Prague 1562, Wilna 1577, Paris 1587, etc. Naturalization (mostly by hydrochory) is mentioned from northern Germany since 1620, Holland 1633, Denmark and Sweden 1648, Poland 1651, England 1666, Italy 1719, Switzerland 1742. Since about 1800, *Acorus* has been common in nearly all European lowlands.

The cord-grass *Spartina tovmsendii* Groves 1870 is, according to Huskins (*Genetica* 12, 1930), a hybrid of the European *Sp. maritima* (Curt.) = *stricta* (Ait.) and the North American *Sp. alterniflora* Lois., first found in the Dovey estuary and transplanted since 1920 on the British coast, since 1924 on the French and Dutch, 1927 on the German and 1931 on the Danish coasts, where it soon became a rather dangerous pest (Oliver a.o. in *J. of Ecol.* 1922-25, Koenig in *Planta* 1948 a.o.).

b) *Terrestrial weeds:*

Oxalis pes-caprae L. (= *cernua* Thunberg) has got a nearly pantropical distribution, but came from southern Africa and invaded the whole Mediterranean only after 1800, likewise the Atlantic coast to the Channel and Scilly Isles. In Europe occur only short-styled, seed-sterile plants, often with filled corolla.

They are rapidly spreading by very hard bulbils and have already become a real pest in many countries, such as Macronesia, Bermuda and Australia (cf. D. P. Young in *Watsonia* 4, 1958).

A similar case is furnished by *Veronica filiformis* Sm. 1791, a pretty diploid plant closely related to the tetraploid *V. persica* Poiret (= *tournefortii* Gmel. non Schmidt), both native around the Caucasus and introduced into European gardens before 1800. The always fertile *Veronica* had spread by seeds already about 1830-1860 to gardens and fields of nearly the whole of Europe; the tender, nearly always sterile, *filiformis* only later: 1893 near Marseille, 1927 around Geneva, 1929 around Munich, 1930-1950 as a dangerous weed in the wet meadows around the Alps and to northern Europe (Bornmüller in *Beih. Fedd. Repert.* 1941, I. Thaler in *Phyton* 1951, Bangerter in *Proc. Bot. Soc. Brit. Isl.* 1957, 1962, 1965). *V. persica* flourishes nearly the whole year, *filiformis* only for 2-3 months and rarely (e.g. in Italy and Styria) with some fruits. Its rapid spreading in meadows is effected by very small axial bulbils.

Among the herbs spreading themselves actively by seeds, several annual species of *Impatiens* are of particular interest. Only /. *nolitangere* L. is really native in Europe. Several species producing and projecting a greater amount of seeds are now in competition: *I. parviflora* DC (cf. D. Coombe in *J. Ecol.* 1956 and *Veröff. Geobot. Inst.* Rübel 1959) from Central Asia, introduced in 1824 in the Botanical Garden of Geneva, 1831 in several other gardens, naturalized 1845 in England, 1850 in Denmark, 1866 in Scotland, since 1862 in many valleys of the Alps, where it is already more abundant than *nolitangere.* Later introduced is /. *glandulifera* Royle (= *roylei* Walp.) from the Himalaya, recorded since 1839 in European gardens, now naturalized from Russia to the Pyrenees, especially in wet valleys of the mountains. The North American /. *capensis* Meerb. is naturalized only around the Atlantic coasts, *I. balfaurii* Hooker (= *mathildae* Chiov.) in some valleys of the southern Alps.

Invading ruderal herbs of Asiatic origin are numerous among Crucifers, e.g. *Lepidium ruderale* L., *Cardaria draba* (L.) Desv. (in southern Germany since 1728, in northern Europe and in the Alps only after 1800, now common) and *Bunias orientalis* L. (native probably in Armenia, spread probably by gypsies around the Baltic 1750/1780, in France since 1814, in the Alps after 1900), perhaps also spread by soldiers during the wars (as " polemochore " *sensu* Mannerkorpi 1944 and H. Luther). A similar distribution along roads and railways, like *Lepidium ruderale,* has applied to *Matricaria matricarioides* (Less.) = *discoidea* DC, in western Europe only naturalized after 1850 (Berlin and Denmark 1852, Prague 1853, Konigsberg 1859, southern Germany and Switzerland 1874, Vienna 1889, Trieste 1896). The remarkable sage *Artemisia verlotorum* Lamotte (cf. Pampanini in *Bull. Soc. Bot. Ital.* 1923-25 and *N. Giorn. Bot. It.* 1926-30, Hulten in *Svensk Bot. Tidskr.* 1929) has first been distinguished from *A. vulgaris* and related species, in France 1873 (Grenoble and Clermont), in Italy 1909, Holland 1913, southern Germany 1920, in the eastern Alps 1924, later in northern Germany and England. It came probably from eastern Asia over North America and spread mostly only by stolons, as it flourishes very late and rarely bears fruits.

Many of the now commonest cultivated plants and also weeds are of American origin. The history of several has been described by K. Wein, e.g. *Oenothera biennis* (*Beih. Fedd. Repert.* 62, 1931), *Datura stramenium* (*ibid.* 66, 1932) and

Erigeron canadensis (*Bot. Arch.* 34, 1932). Some American species are now in competition with Eurasiatic ones, e.g. *Lepidium virginicum* and *densiflorum* with *L. ruderale, Juncus tennis* Willd. (in Europe : since 1824 in Holland, 1834 in southern and 1838 in northern Germany, 1883 in the Alps) with *J. compressus* Jacq., *Erigeron canadensis* and *annuus* with *E. acer.* There is also competition in Europe between several American species of *Erigeron, Aster, Solidago* (*canadensis* L. and *gigantea* Ait.), *Ambrosia* (*elatior* L. and *trifida* L.), *Galinsoga* (*parviflora* Cavan. and *ciliata* (Raf.) Blake) and other partly anemochorous, partly endozoochorous and epizoochorous Composites. Most active epizoochorous and also hydrochorous invaders are the annual species of *Bidens* and *Xanthium,* most of American origin (*Bidens frondosus* L., *bipinnatus* L. a.o., *Xanthium italicum* Moretti = *echinatum* auct. non Murr., *spinosum* L. a.o., cf. Schumacher in *Beih. Fedd. Repert.* 1941, D. Löve and Dansereau in *Canad. J. Bot.* 1959). It seems not impossible, that even the " Eurasiatic " species *Bidens cernuus* L. and *radiatus* Thuill., *Xanthium strumarium* L., *siciricum* Patrin a.o., from which fossil fruits and pollen are known from several quaternary deposits in various countries of Europe, could be originally of American origin and introduced through Asia attached to some now extinct mammals, e.g. elephants or rhinos. Together with *Xanthium italicum,* now very common in southern Europe, the bur-grass or hedgehog-grass *Cenchrus tribuloides* L. has been imported into Italy, perhaps as a " polemochore " by American soldiers. It was first observed in 1933 near Venice and is now a very troublesome pest on many Adriatic dunes.

c) *Invading trees and shrubs:*

Many trees extinct in Europe during the quaternary glaciations have been reintroduced from North America and East Asia, first in gardens and parks, some for reafforestation and fixation of dunes. The locust tree, false or white acacia, *Robinia pseudacacia* L. described in 1610 from Virginia, has been introduced 1630-1680 in western Europe, first by Robin to Paris, in 1683 to Edinburgh, 1710 to Vienna and then to Hungary, where it soon was considered as the national tree (" magyar fà ") and southern Russia, especially for fixation of dunes and shelter belts, often together with the " yellow acacia " *Caragana arborescens* Lam. from W. Siberia. In northern Italy, nearly pure *Robinieta* have been planted since 1785, often with undergrowth of other American plants (*Gleditschia triacanthos, Amorpha fruticosa, Phytolacca decandra, Asclepias syriaca*). Especially in the southern Alps, the locust tree is invading the indigenous oak-woods, often together with *Ailanthus peregrina* (Buc'hoz) Barkley (= *glandulosa* Desf., *cacodendron* (Ehrh.)), imported from China by d'Incarville in 1751 to London and then to France, Italy, etc., for feeding the *Ailanthus*-silk-moth. Both trees are already a rather troublesome pest in many sub-mediterranean woods.

In many Mediterranean and other sub-tropical countries, the destroyed macchia-woods have been replaced by artificial woods of exotic trees, especially *Eucalyptus globulus* Labill., introduced from Australia in 1854 by Ramel. Many other Australian trees, several other species of *Eucalyptus* and of *Acacia* (wattles) have been imported by Ch. Naudin, director of Villa Thuret on Cap d'Antibes, and several, e.g. *Acacia dealbata,* became naturalized. A great part of the Mediterranean and Atlantic shores is now covered by exotic plants from nearly all continents, especially many succulents now forming more or less stabilized biocenoses, e.g. the North American *Agave americana,* often with *Opuntia ficus-indica* (introduced from Mexico as early as 1731) and South African Mesembriantha-ceae, especially *Carpobrotus acinaciformis.*

d) *Fungal diseases:*

Many fungal diseases are spreading on indigenous and introduced trees and shrubs, e.g. *Cronartium ribicola* J. C. Fisch on introduced species of Pinus and Ribes, *Chrysomyxa rhododendri* (D.C.) de Bary on indiginous Picea, *Endothia parasitica* on indigenous and introduced species of Castanea (chestnut-disease) and *Ophiostoma ulmi* on various species of Ulmus (elm-disease).

COMMENTS

K. R. Ashby (U.K.) pointed out that not all alien plants which have become permanent members of the flora should be regarded as weeds; thus *Robinia* introduced in the southern Alps and the Appennines is important in checking soil erosion on degraded forest areas. *N. Polunin* (Nigeria) felt it well-nigh impossible to define a weed satisfactorily or to control unintentional importation of seeds and small fruits, since they were carried on clothes and viable spores (though not seeds) occur in the atmosphere even over the North Pole. *H. Zwölfer* (Switzerland) and *Polunin* suggested that the incidence of European weeds in North America is far greater than of North American weeds in Europe, but *Gams* did not agree although he suggested that European plants as weeds were more dangerous in N. America than in Europe.

PRATIQUE DE L'INTRODUCTION ET DE L'EMPLOI D'EXOTIQUES

par

H. GAUSSEN

Directeur de l'Institut de la Carte Internationale du Tapis Végétal,
Faculté des Sciences,
Toulouse, France

L'homme a beaucoup modifié la Nature qu'il a trouvée aux premiers âges de l'humanité. La Nature s'est d'ailleurs, de son côté, énormément modifiée durant les glaciations quaternaires.

Il n'est pas nécessaire de revenir sur le passé. La Terre a un état actuel, la question est de savoir ce qu'il faut faire car l'homme utilise actuellement des moyens très puissants pour modifier la Nature ; il en use et en abuse.

Il faut partir du principe moral que la Nature dans son état actuel est un capital légué par nos ancêtres, nous avons le devoir de le léguer à nos descendants, amélioré ou au moins égal à sa valeur actuelle.

Pour cela, pour notre usage, nous avons le droit d'utiliser le revenu du capital et il serait bon que nous augmentions le revenu et aussi le capital.

Je ne parle que du monde végétal. Le revenu c'est la récolte agricole, c'est la production forestière. On peut augmenter ce revenu par l'amélioration des rendements ou de la production forestière. On peut l'augmenter en augmentant le capital, c'est-à-dire en utilisant la surface cultivée ou la surface forestière sur des étendues plus grandes.

Les cultures et les forêts ont depuis longtemps utilisé des plantes exotiques. Y a-t-il lieu d'en chercher de nouvelles ; ont-elles été utiles ou nuisibles ? C'est la question à étudier ici.

L'INTRODUCTION DE VÉGÉTAUX EXOTIQUES DANS LES PAYS TEMPÉRÉS ET TEMPÉRÉS CHAUDS

A. *Les arbres forestiers*

1. *Augmentation de la production*

Ici on peut étudier comment augmenter la production forestière par l'emploi des exotiques. D'autre part, il faut se demander si les conséquences biologiques de ces introductions sont ou non sans danger pour la protection de la Nature. D'autre part, on peut augmenter la surface en forêts.

En chaque point P il faut connaître la production actuelle avec des arbres qui peuvent avoir plus d'un siècle.

Si on introduit des exotiques, il faut attendre au moins un demi-siècle avant qu'ils produisent un revenu. L'arbre qu'on plante sera exploité de nombreuses années plus tard. Les conditions économiques auront peut-être changé et l'arbre n'aura plus l'utilité qu'on prévoyait. Il aura pourtant toujours l'intérêt de fournir de la cellulose, matière première nécessaire à la chimie.

A l'heure actuelle on s'oriente vers la plantation d'exotiques à fort rendement : Résineux, Peupliers, Eucalyptus.

La méthode la plus capable de fournir le revenu maximum varie suivant les conditions.

— *En pays de plaine* c'est la monoculture de résineux, de peupliers ou d'eucalyptus sur de grandes surfaces et la coupe à blanc. Mais cela présente de graves dangers et en bien des contrées on fait preuve d'une grande imprévoyance.

Deux dangers sont essentiels: l'incendie et les maladies. L'incendie peut détruire des immensités forestières : en Colombie britannique, au NW des Etats-Unis, en Australie il y a eu de graves catastrophes.

Il faudrait s'astreindre à séparer les massifs résineux de dimensions raisonnables par des zones de pâturages ou de culture amenant de la population capable de lutter contre le feu. On peut aussi essayer de mélanger feuillus et résineux» l'exploitation est plus difficile mais le danger est moindre. Les maladies sont moins à redouter s'il y a mélange.

— *En pays de montagne* l'exploitation doit maintenir le couvert forestier pour éviter le danger d'érosion ; là aussi la méthode du mélange d'essences et l'exploitation par « jardinage » s'imposent. On peut améliorer la production de la forêt actuelle en introduidant des arbres d'un meilleur rendement en volume ou en qualité. Les « arbres + », les hybrides, la sélection, le choix des semences constituent l'essentiel de la sylviculture moderne.

Enfin on peut introduire de nouveaux exotiques. On en a déjà introduit beaucoup et la liste est longue de ceux qui ont fait leurs preuves. Si on veut en étudier d'autres il faut penser que les exotiques doivent être capables de vivre au lieu considéré P. La première question est de connaître la liste des arbres possibles. Evidemment si un exotique vit dans des conditions analogues à celles de P, il y a de fortes chances pour qu'il prospère en P. Cela implique une étude sérieuse des conditions dans lesquelles l'exotique vit dans son pays d'origine, et l'étude des conditions de P.

Pour cela les cartes du Tapis végétal donnent des indications précieuses qui seraient nécessaires dans tous les pays du monde.

Mais la plasticité de beaucoup d'arbres est grande et beaucoup peuvent vivre dans un autre milieu que celui que l'histoire géologique leur a assigné. *Pinus radiata* à aire restreinte au S. de la Californie a un succès étonnant dans bien des pays à conditions assez différentes.

Pour connaître les possibilités d'introduction, l'expérimentation en « phytotron » n'est guère possible que pour la résistance des jeunes semis car on ne peut pas laisser pousser un arbre pendant 20 ans dans un phytotron. L'étude des semis est pourtant utile car l'arbre commence par être jeune.

Heureusement depuis plus d'un siècle les forestiers ont fait des essais heureux ou malheureux et on connaît assez bien l'écologie d'un grand nombre d'exotiques. Mais beaucoup sont encore insuffisamment connus. Les possibilités des arbres chinois, des Pins du Mexique, si importants pour les pays subtropicaux, sont encore mal définies et il faut expérimenter. Près de Canberra une grande place d'expériences montre les réactions d'un grand nombre de Pins de Californie ou du Mexique : *Pinus radiata,* déjà cité, paraît le meilleur. C'est un exemple à répéter en de nombreux points du monde.

Dans la liste possible il faut choisir l'exotique ou les exotiques capables de vivre et de prospérer au point P et étudier leur rapidité de croissance, la qualité de leur bois, leur résistance aux maladies. Pour cela il faut introduire la notion d'écotypes souvent négligée et surveiller de très près la provenance des graines. Les « vergers à graines » doivent être multipliés et on obtiendra le meilleur rendement possible au lieu considéré.

Mais n'est-ce pas sans dangers?

Comme il a été dit plus haut il est normal d'utiliser le revenu du capital forestier mais il ne faut pas détériorer ce capital en voulant lui faire trop produire ! Il y a lieu d'étudier les conséquences biologiques.

2. *Conséquences biologiques*

La monoculture présente de graves dangers. Il a été parlé du feu et des maladies. En général elle appauvrit les ressources du sol en lui demandant toujours les mêmes éléments.

Beaucoup de résineux acidifient progressivement le sol et, si on n'y porte pas remède, le capital et le revenu diminuent. Dans la nature il y a des forêts d'une seule essence mais souvent il y a un mélange d'essences qui paraît constituer un meilleur équilibre. L'humus mixte de feuillus et de résineux est certainement le plus utile pour la conservation d'un bon équilibre édaphique. Mais il faut faire intervenir aussi la notion de concurrence et de « télétoxie ».

La concurrence fait que, par exemple, dans la forêt de Hêtre-Sapin pyrénéenne où il n'y a que ces deux essences, si l'homme n'intervient pas pour protéger le Hêtre, à la longue le Sapin le supplante et on obtient une forêt de Sapin pur. Celle-ci ne produit que de l'humus d'aiguilles de Sapin et déverse peut-être des produits toxiques dans le sol. Peu à peu, dans les sols siliceux tout au moins, la réussite des semis devient plus précaire et ils finissent par ne plus pouvoir germer. La forêt d'une seule espèce est destinée à disparaître, tout au moins si elle est dense et sur certains types de terrains.

S'il y a plus de deux espèces, ce qui est fréquent dans la nature, la forêt paraît éternelle.

Ces considérations sont importantes pour l'emploi des exotiques. Il faut donc veiller à éviter la détérioration du sol, qui ne se manifeste que progressivement et diminue peu à peu capital et revenu.

Pour l'éviter dans les cultures labourées on utilise les engrais avec plus ou moins de succès. La valeur de la récolte justifie la dépense. Dans les forêts de haut rapport la question doit être étudiée, et il est possible que l'emploi d'engrais appropriés soit rentable.

La lutte contre les parasites est particulièrement nécessaire dans les grands massifs forestiers où une essence est dominante. Plus on tend vers la monoculture, plus les parasites sont dangereux. La méthode d'aspersion en utilisant des hélicoptères a fait ses preuves mais il faut être prudent dans le choix du produit employé. Certains produits sont nocifs à d'autres êtres que les parasites et peuvent être dangereux pour l'homme.

Pour éviter les maladies, le contrôle sanitaire doit être sérieux mais l'expérience montre qu'il n'est pas toujours suffisant. Il faut remarquer aussi qu'un parasite peu actif dans son pays d'origine sur une espèce devient souvent très nuisible dans d'autres régions sur cette même espèce à l'occasion de son introduction.

On voit donc que l'emploi des exotiques exige des précautions et des études préliminaires.

Sous l'influence des études phytosociologiques certains forestiers préconisent le retour à la forêt climax, forêt mieux en rapport avec les conditions du milieu, donc plus stable que la forêt plus ou moins artificielle. Cette forêt se rapproche de la forêt naturelle avec ses arbres et son sous-bois. Des sylviculteurs s'appliquent à tâcher de réaliser peu à peu la forêt climax. Au point de vue de la protection des biotopes naturels c'est très sympathique mais l'économie n'y trouve pas nécessairement son compte. Les grandes pessières du Jura au rapport financier important devraient être des hêtraies pour les phytosociologues. Y a-t-il lieu de favoriser le développement ou même l'introduction du Hêtre peu productif en supprimant peu à peu l'Epicéa? Faut-il remplacer un champ où on cultive blé ou betterave par un bois de Chênes sous prétexte que le Chêne est le climax?

Il faut être raisonnable et modéré. Il est nécessaire de garder des exemples de végétation naturelle. Réserves et Parcs nationaux doivent être développés et là aussi il faut être prudent.

Si un biotope de la nature actuelle est en rapport avec une certaine action du bétail on ne le conservera pas si on supprime le bétail. Il faut donc, d'une part, réserver certains types pour les voir évoluer vers le climax, et en conserver d'autres dans les conditions d'utilisation actuelle.

L'un et l'autre permettront des études scientifiques et permettront de retrouver des asiles de nature loin des villes et des usines et de leur atmosphère empoisonnée.

Mais il faut aussi permettre l'introduction raisonnée d'exotiques s'ils rapportent en revenu ou en beauté plus que la végétation actuelle. Il faut le faire avec prévoyance et ne pas songer uniquement au revenu prochain. La détérioration progressive du milieu est à prévoir pour la forêt future.

B. *Les arbres fruitiers, arbrisseaux et plantes herbacées*

Ici il s'agit surtout de cultures pour lesquelles une longue expérience a établi les types pratiques.

Pour introduire de nouvelles cultures il faut aussi rechercher dans le monde les conditions analogues, il faut dresser les cartes de végétation, des climats, des sols. Il faut aussi expérimenter dans des phytotrons où on peut mettre les plantes à volonté dans les conditions normales et dans les conditions exceptionnelles au lieu considéré.

Ici aussi les études de sélection, les études de génétique provoquant la formation de polyploïdes ou de mutations sont à réaliser et peuvent amener à des résultats intéressants pour augmenter le revenu des cultures.

Mais l'introduction d'exotiques peut modifier profondément le type d'exploitation. Qu'on compare les plantes cultivées dans nos régions sous l'Empire romain aux cultures actuelles. Beaucoup d'arbres fruitiers ont été introduits de l'Orient. La culture de la Pomme de terre, des Haricots venus d'Amérique a transformé l'alimentation. Les Mais hybrides américains ont eu le plus grand succès chez les cultivateurs des climats atlantiques. Mais là aussi il faut être modéré.

La standardisation chez les arbres fruitiers a ses inconvénients. Pour une bonne pollinisation il est préférable d'avoir des variétés différentes dans un verger. Il faut manier les insecticides avec prudence et pour tuer le parasite éviter aussi de tuer l'insecte pollinisateur.

En fait on a introduit avec succès dans nos pays beaucoup de cultures exotiques et dans les climats tempérés d'Amérique du Sud, d'Afrique du Sud, d'Australie, des montagnes des pays tropicaux, bien des plantes ou animaux venus de l'hémisphère boréal ont eu un grand succès.

Il s'est souvent manifesté le pullulement de l'exotique qui est un phénomène curieux. Le Lapin en Australie, l'Eichornia dans les fleuves d'Afrique en sont des exemples célèbres.

Tout cela bouleverse les équilibres naturels et l'homme doit veiller à ne pas devenir un apprenti sorcier.

Il faut employer raisonnablement des exotiques quand leur introduction augmente sans danger le capital.

Il faut garder et développer réserves et parcs nationaux pour conserver des exemples d'équilibres naturels.

C. *Augmentation des surfaces utilisées*

On peut aussi augmenter la production par le boisement ou la culture de terres nouvelles où il faudra nécessairement utiliser des exotiques.

C'est un très vaste problème dont dépend peut-être l'avenir d'une humanité qui pullule de façon catastrophique.

Là aussi il faut une étude cartographique des surfaces possibles, des conditions de milieu naturel, des possibilités de les modifier dans un sens favorable par irrigation, par drainage, par des façons culturales.

Tout cela est fondamental et urgent et l'emploi des exotiques est donc un des problèmes majeurs qu'ait à résoudre la science contemporaine.

RÉSUMÉ

Il faut partir de l'état actuel. L'homme a des moyens puissants de modifier la nature, mais il doit utiliser le revenu du capital actuel ou augmenter le capital. Cultures et forêts ont utilisé des exotiques ; doit-on en introduire de nouveaux ? Rétablir le climax originel est considéré par certains comme l'idéal. Dans ces

conditions, il faudrait supprimer les cultures et, au Jura, remplacer l'Epicéa qui rapporte beaucoup par le Hêtre qui rapporte peu. Il faut être modéré. Garder des réserves pour voir évoluer la végétation, laisser d'autres parties dans l'état actuel et créer des parcs nationaux avec des législations variées.

Il faut être prudent dans l'emploi des exotiques qui parfois détériorent le sol, donc diminuent le capital. Il faut connaître les possibilités d'augmenter la production par le boisement ou la culture de terres nouvelles. Une étude cartographique des espaces possibles et des conditions écologiques est nécessaire.

Summary

The starting-point should always be the existing situation. Man now possesses powerful means for modifying nature, but he still has either to utilise the income from nature's capital or to build up the capital itself. Agriculture and forestry have made much use of exotic species. Ought one to introduce further new ones ? Some people consider that the ideal to aim at is to re-establish the original climax. This would mean suppressing introduced species and, for example, in the Jura replacing spruce, which is very productive, with beech which gives little return. Compromise is necessary. Reserves must be established where the natural evolution of the vegetation can be studied, while other areas are left in their existing state, and national parks are created under varying regimes.

It is necessary to be careful when using exotic species which can sometimes lead to degradation of the soil and hence reduce the capital assets. A proper understanding of the possibilities of increasing production whether by afforestation or by bringing new land into cultivation is essential. Cartographic analysis and study of available land surfaces and the ecological factors are therefore equally essential.

Comments

M. van der Goes van Naters (Netherlands) commented that monoculture of conifers may be uneconomic if account is taken of recreational use of forests. In Holland for instance the government gives a subsidy of 40 Sw. fr. per hectare if the forest is used for recreation. Thus beautiful but so called unproductive woods become " profitable ".

G. M. Wachtmeister (Sweden) contrasted natural forests of hardwoods, with their attractive ground flora, with coniferous plantation where the understorey vegetation may be absent. *J. D. Ovington* (Australia) referred to problems arising in Australia where the wood production of some second rotation plantations of *Pinus radiata* is significantly less than that of the first crop, and suggested that any evaluation of different systems of land use must take into account long term effects. *H. Gaussen,* whilst accepting the dangers associated with monocultures and the threat to native species, emphasised the economic aspects of forestry and the very marked increases in production and financial returns that are possible with economic forestry.

THE NATURALIZATION OF ALIEN PLANTS IN AUSTRALIA

by

R. M. MOORE

Cunningham Laboratory,
C.S.I.R.O.
St. Lucia, Queensland, Australia

I. INTRODUCTION

Australian plants and plant communities evolved in virtual isolation from those of the other large continents and as far as is known it was not until European settlement in the late 18th Century that indigenous plants came into contact with alien species. Prior to white settlement the number of herbivorous animals was relatively small and the principal factor affecting plants, other than climate and soils, was probably fire.

European settlement and the introduction of sheep, cattle and rabbits disturbed existing equilibria within plant communities; trees were killed and, as a consequence of the establishment of a sedentary pastoral system, grazing pressures on the herbaceous vegetation were increased several fold.

From the middle of the 19th Century the pastoral occupation of Australia proceeded rapidly and by 1890 sheep numbers had reached 100 million. Wool is admirably adapted to the carrying and spreading of seeds and fruits, and sheep are largely responsible for the rapidity with which plants intentionally and accidentally introduced by Europeans spread throughout the southern part of the continent. Native species declined in density or disappeared entirely on grazed areas which were then occupied by alien species pre-adapted to such environments by long association with man in Europe, Asia and North Africa.

II. FACTORS AFFECTING THE ESTABLISHMENT OF ALIEN PLANTS

The evidence in Australia is that man and his domestic animals have played predominant roles in distributing alien species and in creating environments for them. It will be seen that the plants best adapted to environments modified by man are those of the old centres of civilization, the pioneer and the weedy species. Hartley and Williams (1956) estimated that of the 10,000 or so species of grasses in the world, only about 40 were important in cultivated pastures and of these 24 were from Europe, Asia or the Mediterranean; 8 were from East Africa and 4 from sub-tropical south America. Hartley (1963) observed further that the important cultivated grass species were from forest margins rather than from the great grasslands of the world and that the regions to which they were native were those in which the important groups of grazing animals originated. The climax dominants of the grasslands of other countries do not occur adventitiously in Australia and repeated attempts have failed to establish *Buchloe dactyloides* (Nutt) Engelm., a dominant of the short grass plains of the United States.

The success of alien species is due to their greater adaptability to environments altered by disturbance rather than to greater aggressiveness in unmodified climax communities. In fact field evidence suggests that aliens do not establish in stable native plant communities without prior disturbance and modification of the environment. An example is given in Table I which shows the botanical compositions of three contiguous areas near Goulburn N.S.W. The climax community is a *Themeda australis* - *Poa caespitosa* - *Stipa aristiglumis* grassland.

TABLE I

Effect of disturbance on numbers of individuals per square link of native and introduced species in a *Themeda australis* - *Poa caespitosa*-*Stipa aristiglumis* grassland.

Species	Type of Disturbance		
	Cultivation	Heavy grazing	None
Themeda australis (R.Br.) Stapf.	0	0	1.68
Poa caespitosa auctt. austral.	0	0	0.23
Stipa aristiglumis F. Muell	0	0	0.07
Stipa falcata Hughes	0	1.91	0.24
Danthonia spp	0	4.30	0.13
Introduced annuals	8.17	5.97	0

Unless severe erosion has occurred the cessation of disturbance such as the exclusion of grazing animals normally results in elimination of alien species, and re-establishment of the climax community. However, in regions devoted to farming and pastoral activities disturbance is a permanent factor of the environment. Moreover in much of southern Australia, especially the more humid zones, superphosphate has been applied more or less regularly. This has made environments more favourable for aliens than for native species adapted to soils low in plant nutrients particularly phosphorus and nitrogen.

The modification of a woodland community and the changes in species composition resulting from clearing, grazing and application of superphosphate are shown in Table II. The data are from an *Eucalyptus melliodora* A. Cunn. —*E. blakelyi* Maiden community on the Southern Tablelands of N.S.W. and are typical of the effects of " pasture improvement " on the most important sheep raising areas of southern Australia (Moore, 1959 b, 1962,1964). In this community levels of available nitrogen are always low under the climax dominants, the tall warm season perennials. As a consequence of the elimination of these species by grazing there is an increase in nitrate nitrogen in the top soil in autumn, the beginning of the growing season for cool season species. Nitrate-nitrogen levels are further increased by superphosphate and resultant greater production by introduced legumes (see Fig. 1). The higher levels of plant nutrients such as nitrate nitrogen, phosphorus, sulphur and calcium create a soil environment

TABLE II

Species and soil changes resulting from grazing herbaceous communities of *Eucalyptus melliodora* - *E. blakelyi* woodlands. Soil nitrate-nitrogen 0-4 inches autumn 1960.

Soils: Red yellow podsols pH. 5.9 (1: 5 suspension)
Rainfall: 23 inches per annum - distribution uniform.
Locality : Southern Tablelands, New South Wales.
Altitude: 2,000 feet above sea-level.

CLEARING

Themeda australis - Stipa aristiglumis - Poa caespitosa
N03-N o.7ppm.
(Tall (3-4 ft) warm season perennial tussock grasses)

GRAZING

Stipa aristiglumis - Poa caespitosa - Stipa falcata
No_3-N 1.7ppm.

Stipa falcata - Danthonia carphoides - Danthonia auriculata
N03-N 3.6oppm.
(Short perennial (2"-6") cool season grasses)

Danthonia carphoides - Danthonia auriculata

Native species from more arid communities. { Enneapogon nigricans, Chloris truncata, Tripogon loliiformis, Panicum effusum, Vittadinia triloba, Euphorbia drummondii, Convolvulus erubescens.
(Short warm season species)

GRAZING

Danthonia carphoides - Danthonia auriculata

Mediterranean annuals.

Trifolium glomeratum, Vulpia bromoides,
Bromus spp., Hordeum leporinum,
Composites, Erodium cicutarium,
Aira caryophyllea.
(Exotic cool season annuals)

Enneapogon nigricans, Chloris truncata, Panicum effusum, Vittadinia triloba, Eragrostis brownii.
(Short warm season perennials)

Vulpia bromoides, Bromus spp.,
Trifolium glomeratum, Cirsium vulgare.
(Exotic cool season annuals)

Chloris truncata, Eragrostis cilianensis,
Chenopodium carinatum, Polygonum aviculare.
N03-N 36.2ppm.
(Warm season species)

GRAZING, PHOSPHATE & SUB. CLOVER

Trifolium subterraneum, Vulpia bromoides,
Hordeum leporinum, Lolium rigidum, Erodium spp.,
Cirsium vulgare, Onopordum acanthium, Carduus pycnocephalus.
(Exotic cool season annuals or biennials)

Eragrostis cilianensis, Chenopodium carinatum.
No_3-N 118.2ppm.
(Warm season annuals)

which is more fully exploited by introduced annuals than by short native perennials which in time are eliminated. The change to annuals is accelerated by surface broadcasting subterranean clover (*Trifolium subterraneum* L.) which is more productive and more efficient in fixing nitrogen than the other annual *Trifolium* species which have established spontaneously in southern Australia.

In southern and eastern Australia the 20 inch isohyet roughly divides pedocals and podsols. The naturalized annual legumes on the former belong to the genus *Medicago* whilst on the latter, as has been shown, species of *Trifolium* predominate. Annual species of *Medicago* are common on red-brown earths and grey-brown soils of heavy texture, and on these soils the change under grazing from native warm-season perennials to introduced cool season annuals occurs rapidly even in the absence of superphosphate. Species commonly associated with *Medicago* spp. are the introduced annuals, *Hordeum leporinum* Link, *Vulpia bromoides,* S.F. Gray, *Carthamus lanatus* L. and the native, *Erodium cygnorum* Nees. Changes in species composition as a result of clearing and grazing a *Eucalyptus woollsiana* R.T. Baker, woodland are illustrated in Table III.

There is evidence of convergence towards communities of similar or related introduced annuals as available soil nutrients increase and levels of a particular nutrient or combination of nutrients may determine which species predominates. For example, introduced annual grasses are favoured by high levels of both nitrogen and phosphorus, annual legumes by high levels of phosphorus alone and other annual dicotyledons, notably composites such as *Cryptostemma calendula* (L.) Druce, by high levels of nitrogen. Among nitrophilous species soil calcium levels may be a determining factor in the presence or absence of a particular species of Mediterranean origin. It has been shown in greenhouse experiments that levels of nitrogen and calcium determine the outcome of competition between the two closely related introduced species *Carduus pycnocephalus* L. and *C. tenuiflorus* L. The spread on red-yellow podsols of the introduced annual grass, *Hordeum leporinum,* a dominant on red-brown earths and grey-brown soils of heavy texture, is a direct consequence of the accretion of nitrogen, phosphorus and calcium on podsolic soils following applications of superphosphate and the sowing of subterranean clover. The same appears true of *Carthamus lanatus.* As a consequence of rising levels of soil fertility, communities of annuals on podsols are becoming nearer in composition to those on the less leached red-brown earths and grey-brown soils of heavy texture.

III. Characteristics of naturalized plants

High seed production, efficient seed dispersal mechanisms, rapidity of establishment and persistency under defoliation are characteristics of pioneer plants which as a class include the worst weeds and the best pasture plants.

The world wide distribution of many weeds and pasture plants and the similarities among species of unstable and denuded sites in different countries suggest that further genetic adaptation may not always be necessary for the naturalization of a pioneer species in a new country.

Climatic factors such as temperature vary widely both diurnally and seasonally on sites which are sparsely covered or entirely denuded of vegetation, and

Fig. 1. Seasonal fluctuations in nitrate-nitrogen levels in soils under climax and disdlimax communities in a *Eucalyptus melliodora-Eucalyptus Makelyi* woodland. Canberra, A.C.T. 1960.

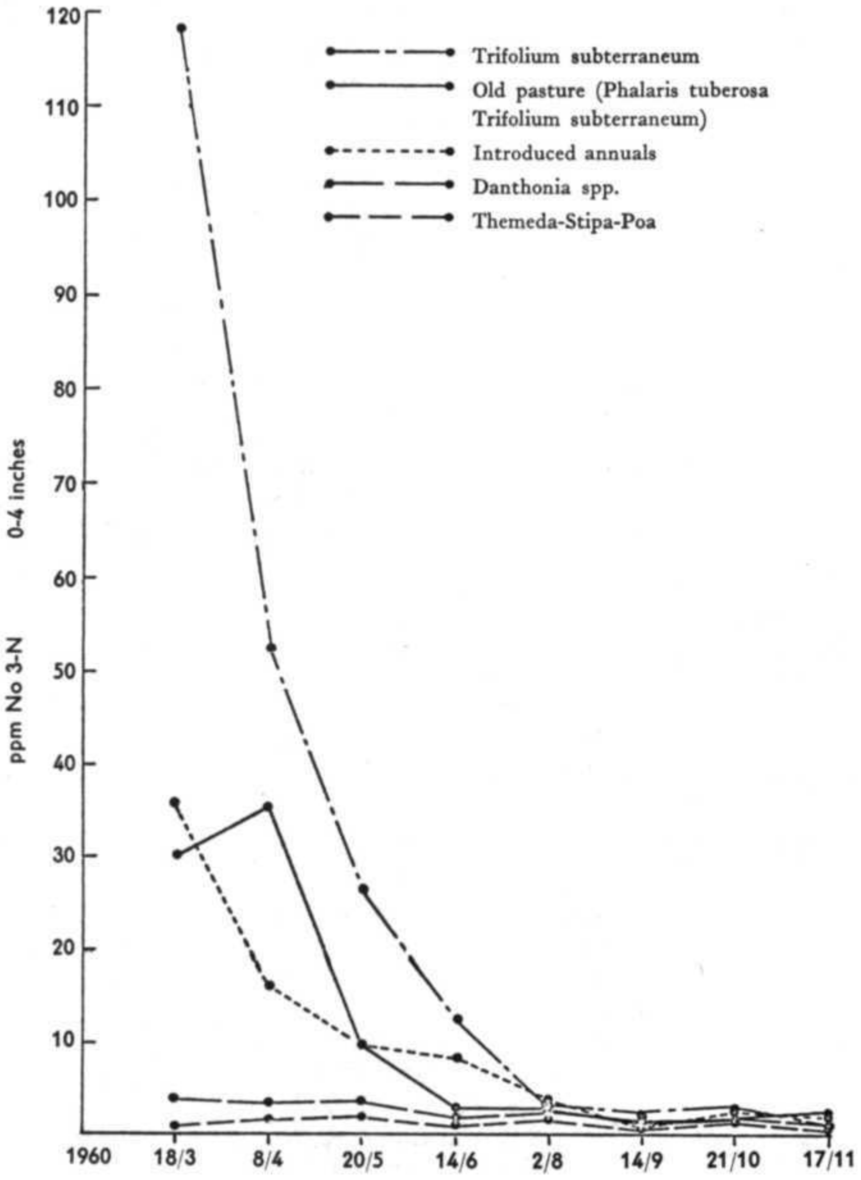

TABLE III

Species changes resulting from grazing herbaceous communities of *Eucalyptus woollsiana* woodlands.

Soils: Red-brown earths pH 6.9 (1: 5 suspension)
Rainfall: 20 inches per annum - distribution uniform.
Locality : South-western slopes, New South Wales.

Themeda australis - Stipa aristiglumis - Poa caespitosa
(Tall warm season perennials)

GRAZING
↓

Stipa aristiglumis - Poa caespitosa - Stipa falcata

↓
Stipa falcata - Danthonia caespitosa
(Mid-grasses, cool season)

↓
Stipa falcata

Enneapogon nigricans, Chloris truncata,
Sida corrugata, Wahlenbergia gracilis,
Vittadinia triloba, Euphorbia drummondii,
Convolvulus erubescens, Helichrysum apiculatum.
(Short warm season perennials)

Mediterranean annuals. { Hordeum leporinum, Medicago minima, M. denticulata, Trifolium glomeratum Erodium cygnorum, Vulpia bromoides, Aira caryophyllea, Moenchia erecta, Cryptostemma calendula, Carthamus lanatus.
(Mainly exotic cool season annuals)

GRAZING
↓

Hordeum leporinum, Medicago minima,
M. denticulata, Erodium cygnorum,
Vulpia bromoides, Carthamus lanatus,
Aira caryophyllea, Salvia verbenacea.
(Mainly exotic cool season annuals)

Chloris truncata, Enneapogon nigricans,
Wahlenbergia gracilis, Sida corrugata.
(Warm season perennials)

Euphorbia drummondii,
Eragrostis cilianensis,
Xanthium spinosum.
(Warm season annuals)

---

of necessity, plants which establish on these sites have wide climatic tolerances. Repeated selection on areas subject to continual disturbance and to wide diurnal and annual ranges of temperature may result in what has been called " a general purpose genotype ". Certainly the evidence suggests that pioneer plants are pre-adapted to a wide range of climatic factors and this is sufficient to account for the rapid naturalization of many species in countries other than those to which they are native.

IV. Case histories of some Australian introductions

The densities, growth and sometimes the climatic ranges of many introduced plants, trees, pasture plants and weeds appear to be greater in Australia than in countries to which they are native. This has been ascribed variously to genetic modification, to absence of insect enemies, and less frequently to fewer other species with similar requirements for establishment and growth.

It is difficult to make accurate comparisons of climatic ranges of plants in Australia and abroad. Not only is it hard to obtain adequate and comparable climatic data but few density records are available so that casual and sporadic occurrences of a species overseas may be weighted equally with high degrees of abundance in Australia and vice versa. Nevertheless some comparisons are interesting and instructive.

a) Skeleton Weed (*Chondrilla juncea* L.). This species, a deep rooted perennial composite native to the Mediterranean regions of Europe is believed to have been accidentally introduced into Australia at Marrar, N.S.W. in 1914. *Chondrilla* does not appear to have been modified genetically since its introduction to Australia. It is known to be an obligate apomict and the Australian population extending from Kingaroy, Queensland to just south of Geraldton W.A. is uniform both morphologically and physiologically. All the evidence suggests that it arose from a single introduction (McVean 1965).

Chondrilla is found in localities with annual rainfalls from 9 to 60 inches and is adapted to a wide range of environments. It is abundant in areas well beyond those with Mediterranean type climates and is an excellent example of a plant which has spread widely in spite of efforts to eradicate it. Cultivation and the application of phosphate fertilizers for wheat and pasture production appear to have influenced the distribution and density of *Chondrilla* in Australia (see Fig. 2).

b) *Phalaris tuberosa* L., a cross-pollinated perennial grass of Mediterranean origin, introduced at Toowoomba, Queensland in 1884. Although it shows some tendency to spread without sowing or cultivation it is not yet fully naturalized in Australia. It is sown in pastures from southern Queensland to the south-west of Western Australia in areas receiving from 16-30 inches of rain annually. Although Australian population shows some variation there is no evidence of ecotypic differentiation. This cool season species is interesting in that without genetic modification it has been more persistent under heavy grazing in regions of eastern Australia receiving rain in both winter and summer, than either in the south-west of Western Australia or in California, U.S.A. where the summers

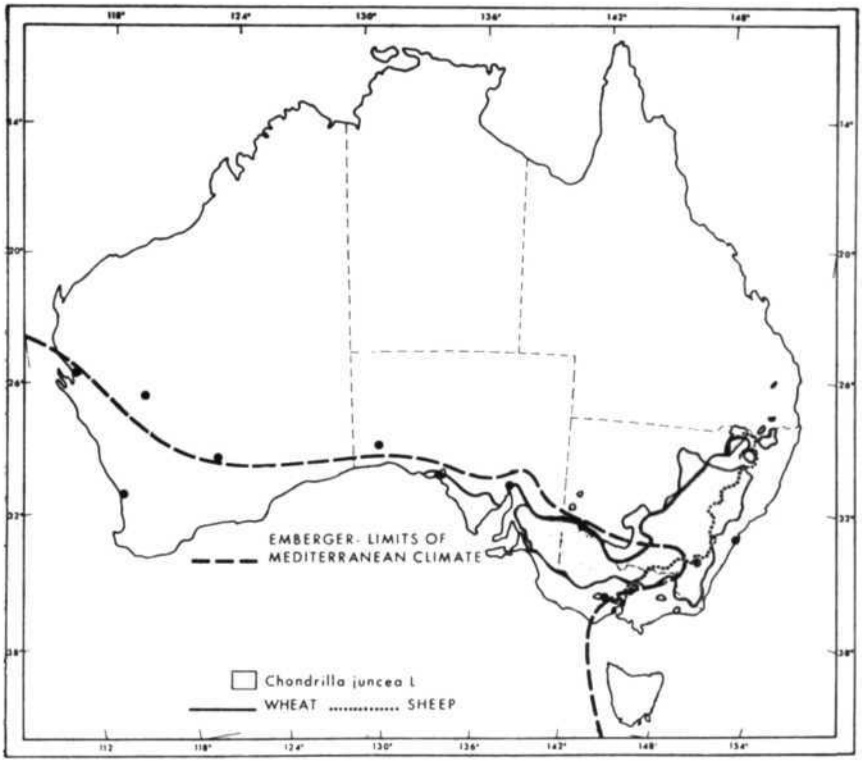

Fig. 2.

are hot and dry, and the climates more typically Mediterranean. The inland limits of the Australian commercial cultivar is at a higher annual rainfall in Western Australia than in New South Wales which has a higher summer rainfall component (Fig. 3).

c) Subterranean clover (*Trifolium subterraneum* L.). A self-pollinated annual of Mediterranean origin, accidentally introduced and first reported as naturalized in Victoria in 1887. Today there are more than fifty strains of subterranean clover in Australia. The origins of these strains are unknown. The Australian strains have been shown to have about the same spread of flowering times as collections from the Mediterranean. Few characters present in the Australian strains are absent in the Mediterranean collections suggesting that except for one or two known mutations there has been little genetic change since the species established in Australia. The large number of varieties in Australia could be the result of a number of accidental introductions. The *T. subterraneum* complex in Australia extends far beyond the limits of a true Mediterranean climate as defined by Emberger (1959). See Fig. 4.

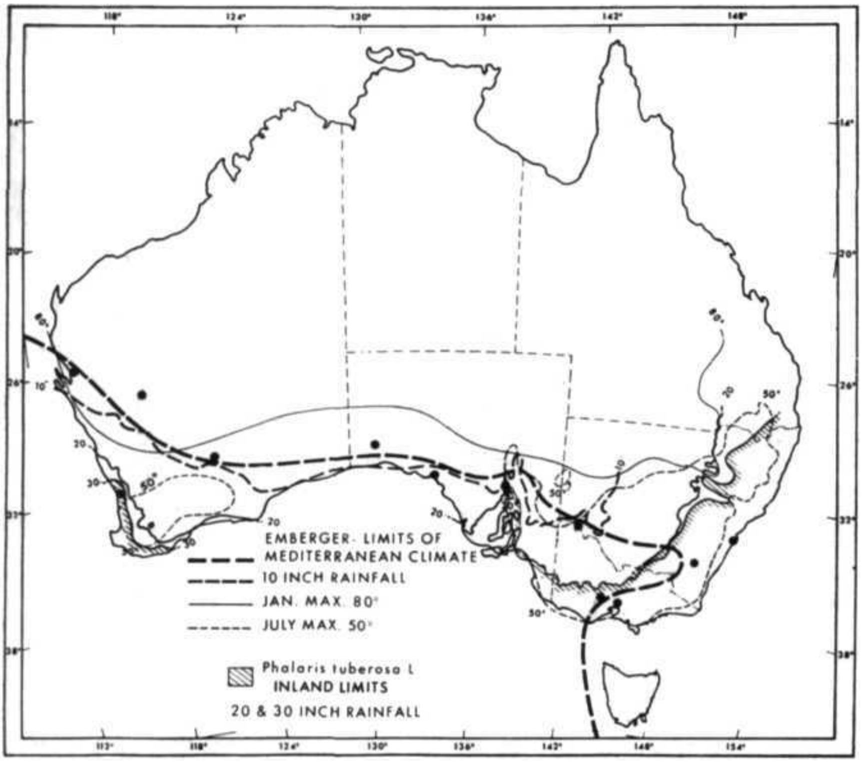

Fig. 3. Inland limits of *Pbalaris tuberosa* in Australia.

d) Patterson's Curse (*Echium plantagineum* L.). This annual and sometimes biennial species, a native of the Mediterranean and Atlantic coasts of Europe was introduced accidentally into South Australia in 1875. It is now widely distributed through southern Australia and in places is the most abundant species along roadsides and in fields.

W. Straatmans and R. M. Moore (unpublished data) found that dense stands of *Echium plantagineum* in Australia occur under the following climatic conditions :

Rainfall warmest month	> 2.5"
	70-80°F
Daily temperature range warmest month . . .	25-35°F
Rainfall coldest month	> 1"
Mean temperature coldest month	40-50°F
Daily temperature range coldest month . . .	15-25°F
Annual rainfall	< 50"

A critical factor appears to be the diurnal temperature range which is correlated with the annual range of temperature (difference between the mean maximum

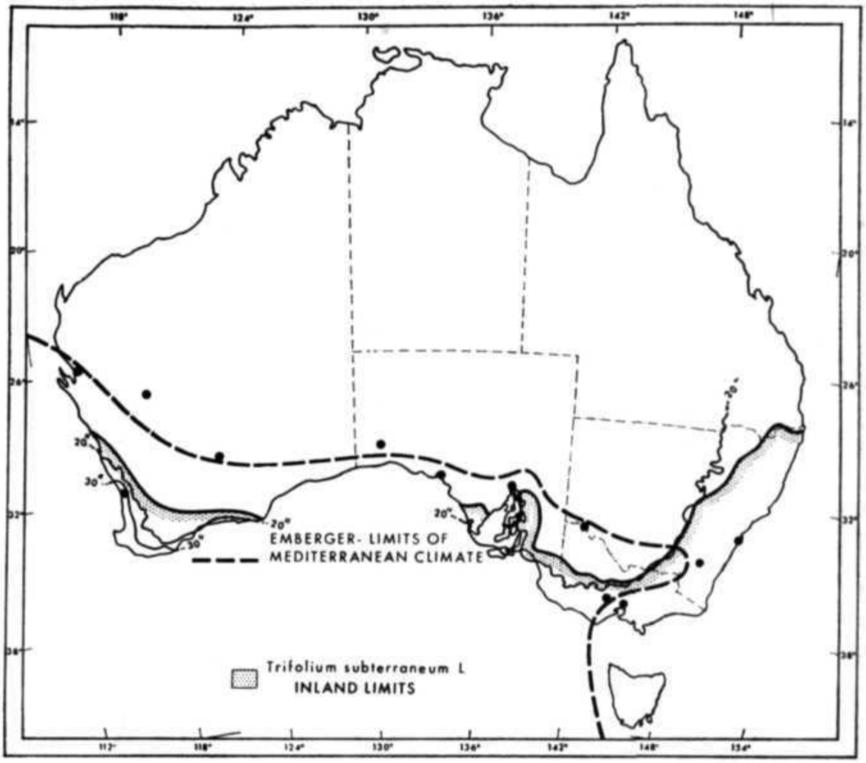

Fig. 4. Inland limits of *Trifolium subterraneum* L. in Australia.

temperature January and the mean minimum temperature July) and with the temperature amplitudes of Prescott (1942). The annual temperature range of *E. plantagineum* in Australia is 50-60°F (temperature amplitude 15-20°F) with a summer (January) maximum of 8s°F and a winter (July) maximum exceeding 55°F. Rainfall, at least the amount received annually, seems of little significance but seasonal rainfall is important in its effect on temperature. Rain in winter raises, and in summer lowers the mean temperatures so that rain in both summer and winter narrows the annual temperature range.

The distribution of *Echium plantagineum* extends well beyond the limits of Mediterranean climates in Australia and is most abundant in N.S.W. which is not truly mediterranean in climate (Fig. 5). The annual, *Echium vulgare* L. however, occurs mostly within Emberger's limits.

Echium is less abundant than expected in much of northern Victoria, but this is due to land use practices and to a rigorous campaign of eradication rather than to climatic unsuitability. The occurrence of *E. plantagineum* in lower latitudes in Australia than in the northern hemisphere is due possibly to the smaller area of North Africa with both favourable temperature amplitudes and summer maxima. The Mediterranean distribution of *Echium plantagineum* is shown in Fig. 6.

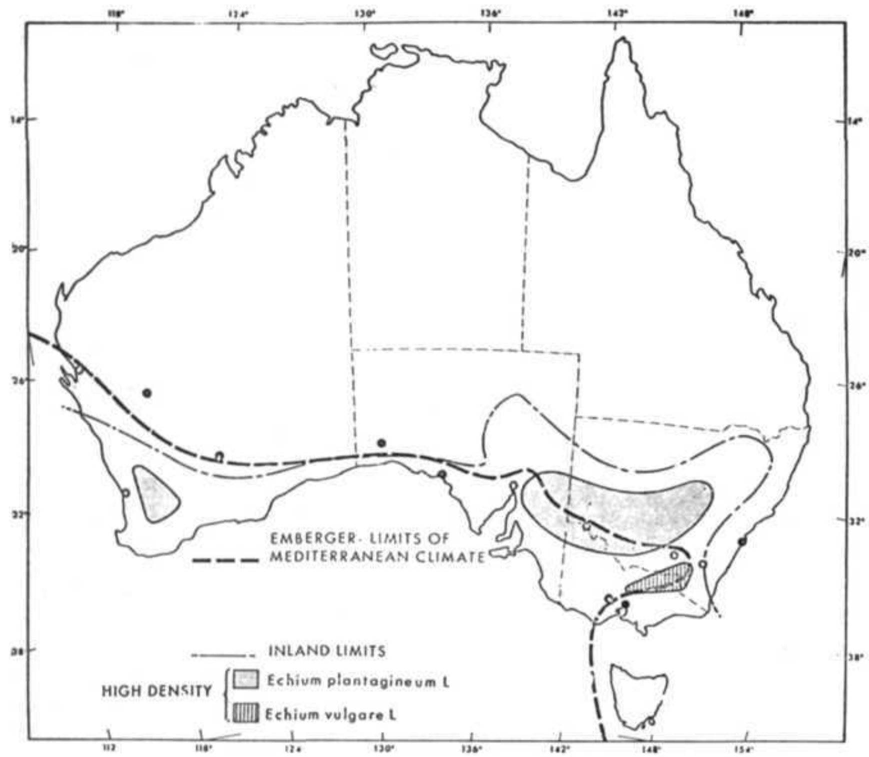

Fig. 5.

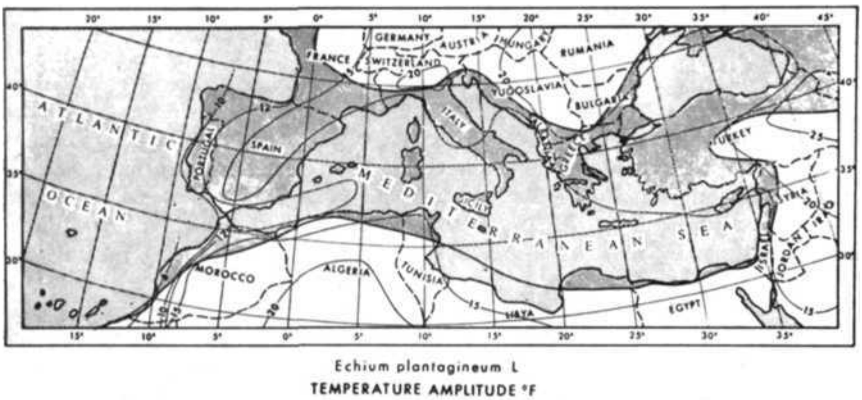

Fig. 6. Latitudinal distribution of *Ecbium plantagineum* in the Mediterranean.

DISCUSSION

The continentality of inland climates in southern Australia and the continual denudation of plant communities by farming and pastoral activities provide environments suitable for alien pioneer plants of Mediterranean origins. Many of these species appear pre-adapted to disturbed sites by an evolutionary history in areas constantly disturbed by the activities of man and his domestic animals.

Because of their adaptation to environments with wide diurnal and seasonal fluctuations in climatic and edaphic factors, pioneer plants of the Northern Hemisphere might be expected to have wide climatic tolerances. A further reason for the wide geographical ranges and high densities of many species naturalized in Australia may be the fewer competitors compared with their native countries. It is well known for example, that the macro-climatic ranges of plants under cultivation are wider than in the wild state. Prescott and Lane-Poole (1947) have commented on the wider climatic spread of plantations of *Pinus radiata* D. Don. in Australia than might have been expected from the restricted range of the species in its native California. Part of the explanation is the deliberate reduction of competition by agricultural and silvicultural practices. Most crop plants too, are genetically modified by selection and breeding. However few of the common pasture plants in Australia have been bred or purposefully selected.

Phalaris tuberosa was quoted as an example of an introduced plant which without genetic modification has been cultivated successfully in parts of Australia differing climatically. The greater persistence under grazing of the common Australian cultivar in areas with some summer rain raises a question as to whether the climate for survival under yearlong grazing may be necessarily the same as that which is optimal in the absence of regular grazing. That is, the climate optimal for maximum production and capacity to compete with other species with similar growth characteristics may differ from that for survival under repeated defoliation in pasture communities of few species. The reduction of the root system of *Phalaris* as a result of sustained grazing may lower its capacity to survive the hot dry summers of the more Mediterranean type climates. Also the further vegetative growth often possible after flowering and seed-setting in areas receiving some summer rain may enhance the formation of buds on rhizomes and thus capacity for survival and regeneration.

Chondrilla juncea too, seems well adapted to temperate climates other than the more extreme Mediterranean types, at least under the land use practices prevailing in southern Australia. It is not regarded as a weed of any significance in the Mediterranean nor does it achieve the population densities that it does in eastern and southern Australia where it is the most important weed of cereals. In Europe *Chondrilla juncea* is commonly classed as a biennial. It is seemingly much more perennial under cultivation in Australia than in Spain, possibly the source of origin of the Australian population. The apparently greater persistence of *Chondrilla* in Australia may be due to the same factors which enable *Phalaris tuberosa* to withstand heavy grazing in an environment not completely homologous with that of the Mediterranean areas to which it is native.

Dependence on seed production for survival restricts the ranges of annual species but many pioneer species are remarkably plastic. For example, seed maturation time in a single strain of *Medicago denticulata* Willd. varies widely with soil moisture and with nutrient supply.

Although many alien species can grow as well or even better in regions of Australia with climates seemingly differing in some degree from those of their places of origin, in general the common naturalized aliens of southern Australia are European and North African and those of northern Australia are sub-tropical and tropical in origins. However, many temperate European plants have become naturalized in sub-tropical areas. Everist (1959) observed that of the plants naturalized in Queensland 40 % were from Europe, West Asia and North Africa, 3 % from East Asia, 13 % from the Old World Tropics, 3 % from South Africa, 8 % from extra tropical North America, 20 % from the New World Tropics, 9 % from extra Tropical South America and 3 % were cosmopolitan or of uncertain origins. The large proportion of European plants in a State which is largely tropical and sub-tropical is thought to be due to the fact that Australia is settled by Europeans and its communications are largely with the European continent. The inference is that the naturalization of exotic plants in Australia is influenced by history as well as by climate and other factors.

Opportunity too, plays an important part. Michael (1965) found that the pentaploid variety of *Oxalis pes-caprae* L. was more widely distributed in Australia but less widely in its native South Africa than the tetraploid. On the basis of bulb production at different moisture levels, Michael concluded that the tetraploid had a greater potential for spread and survival than the pentaploid. The greater range of the latter in Australia is believed to be due to the showiness of its flowers and its more frequent use in gardens which provide focal points for spread and naturalization.

SUMMARY

Before European settlement Australia was sparsely occupied and the impact of man and of native animals on vegetation was seemingly slight. This and the low fertility of many of the soils restricted opportunities for the evolution of species adapted to disturbed sites and to soils high in plant nutrients.

The introduction of domestic animals and the establishment of a sedentary pastoral system by Europeans modified and frequently destroyed native plant communities. The environments so created are less suited to native species than to those alien species which evolved in association with man in the older centres of civilization. The alien species most likely to become naturalized are the so-called pioneer species characteristic of the early and less stable stages of secondary succession.

The progressive changes resulting from grazing and other pastoral activities are described in two woodland communities of south-eastern Australia. Soil nitrate nitrogen levels accompanying changes in species composition are shown for one of these communities.

Brief case histories are given of five alien species which have become naturalized to some degree in south-eastern Australia.

From the evidence available it would seem that the climatic ranges of some alien species in Australia may be greater than in the countries in which they are

natives. Some perennial species considered to be of Mediterranean origins appear better adapted to parts of Australia receiving both summer and winter rains than to areas with more typically Mediterranean-type climates.

Environmental modification rather than genetic change appears to have been of most significance in the naturalization of alien plants with wide distributions in Australia.

RÉSUMÉ

Avant la colonisation européenne, l'Australie n'était occupée que de façon parsemée et l'impact de l'homme et des animaux indigènes sur la végétation était apparemment peu considérable. Ce fait et la faible fertilité d'une grande partie des sols réduisirent les possibilités d'évolution d'espèces adaptées à des sites perturbés et à des sols riches en substances nutritives.

L'introduction d'animaux domestiques et l'établissement d'un système pastoral sédentaire par les Européens modifièrent et, souvent, détruisirent les groupements de plantes indigènes. Les milieux ainsi créés conviennent moins aux espèces indigènes qu'aux espèces exotiques qui se développent en association avec l'homme dans les centres plus anciens de civilisation. Les espèces exotiques les plus susceptibles de s'acclimater sont celles qu'on appelle les espèces pionnières, caractéristiques des premiers stades moins stables de succession secondaire.

Les changements progressifs résultant du pâturage et autres activités pastorales sont décrites dans deux associations de savane forestière de l'Australie du sud-est. Les fluctuations des niveaux d'azote de nitrate du sol accompagnant les changements dans la composition des espèces sont montrées pour l'une de ces associations.

Un bref historique est donné dans le cas de cinq espèces exotiques ayant atteint un certain degré de naturalisation en Australie du sud-est.

Selon les données dont on dispose, il semblerait que certaines espèces exotiques en Australie sont exposées à une plus grande gamme de variations climatiques que dans les pays dont elles sont originaires. Quelques espèces pérennes considérées comme étant d'origine méditerranéenne paraissent mieux adaptées à certaines parties de l'Australie recevant à la fois des précipitations estivales et hivernales qu'aux régions ayant un climat plus typiquement méditerranéen.

Le facteur le plus significatif dans la naturalisation des plantes exotiques largement répandues en Australie semble avoir été la modification du milieu plutôt qu'un changement génétique.

REFERENCES

EMBERGER, L. (1959). La place de l'Australie méditerranéenne dans l'ensemble des pays méditerranéens du Vieux Monde. *Monogr. Biolog.* VIII, 259-273.

EVERIST S. L. (1959). Strangers within the Gates. *The Queensland Naturalist.* 16: 49-60.

HARTLEY, W., and WILLIAMS, R. J. (1956). Centres of Distribution of Cultivated Pasture Grasses and their Significance for Plant Introduction. *Proc, 7th Inter. Grassl. Cong.* 190-201.

HARTLEY, W. (1963). The Distribution of the Grasses. In *Grasses and Grasslands,* Ed. C. Barnard. 19-45.

McVean, D. (1965). Skeleton Weed in Australia. *New Scientist* 23: 764-766.

Michael, P. W. (1965). Physiological Comparisons between the Pentaploid and Tetraploid Varieties of *Oxalis Pes-caprae. Proc. Aust. Weeds Conj.* Vol. 1.

Moore, R. M. (1959a). Some Ecological Aspects of the Weeds Problem in Australia. *Proc. IVth Inter. Congr. Crop Prot. Hamburg.* 447-449.

Moore, R. M. (1959 b). Ecological Observations on Plant Communities Grazed by Sheep in Australia. *Monog. Biolog.* 8: 500-513.

Moore, R. M. (1962). The Effect of Sheep Grazing on Australian Vegetation. In *The Simple Fleece-Studies on the Australian Wool Industry.* Ed. A. Barnard. Melb. Univ. Press and A.N.U.

Moore, R. M. (1964). Ecological Effects of Grazing on Grasslands in southeastern Australia. *Proc. IXth Inter. Grass. Cong. Brazil.*

Prescott, J. A. (1942). The Phase and Amplitude of Australian mean monthly temperatures.

Prescott, J. A., and C. E. LANE-POOLE (1947). The Climatology of the Introduction of Pines of the mediterranean Environment to Australia. *Trans. Roy. Soc. S. Aust.* 71 (1): 67-90.

Comments

D. Hey (S. Africa) did not accept that an exotic plant cannot invade a climax plant community and pointed out that the Wacchia vegetation of the mountains of the Western Cape has been invaded and sometimes completely dominated by Hachea and Cluster Pine. This spread cannot be attributed to human agencies but is due to natural fires and the distribution of seeds in the droppings of birds. This latter factor is particularly important in relation to the distribution of *Acacia cyclops* in the coastal area of South Africa. *C. L. Boyle* (U. K.) asked if the dictum that species cannot invade climax communities applied to parasites and pointed out that species such as mistletoe established themselves on the indigenous flora.

R. M. Moore was not certain of the position with regard to parasites, but said he knew of no instance where invasion had not been preceded by disturbance. Most Australian vegetation was fire resistant but plants from South Africa were often successful invaders in Australia. The invasion of Prickly Pear into the Brigalow area in Australia might be cited as an instance of invasion without disturbance, but in fact the area was subjected to cattle grazing.

SOME ECOLOGICAL EFFECTS OF WILD AND SEMI-WILD EXOTIC SPECIES OF VASCULAR PLANTS

by

F. R. FOSBERG

Smithsonian Institution
Washington D.C. 20560

INTRODUCTION

Throughout his history, especially since he began to live by agriculture, man has exerted a profoundly disturbing effect on the ecosystems in which he has lived. With the rise of pastoralism this effect tended to increase, especially in the extent of area affected; with the development of modern agriculture, cities, and vastly stepped-up mobility of people, the increase in disturbance has been exponential. Not the least of the processes of disturbance and change has been the carrying about of plants and their establishment in places that they had not yet been able to reach by natural (non-human) means.

Of course, agriculture usually involves a complete substitution of one or more cultivated species for the entire plant community that previously occupied the land. Forest plantations also tend to replace the natural plant communities almost completely by one or several introduced species. This paper will not deal further with these planted species, except as they may be involved as part of habitats invaded by other exotic species. The exotics dealt with here are those either introduced unintentionally by man or escaping from his cultivation or forest planting, and maintaining themselves spontaneously.

It is not always easy to tell whether a species is indigenous or brought by man, if it has a wide or disjunct range. Many mistaken assumptions have been made—both ways. Species have been regarded as indigenous—even described as new and endemic—only to have their identity with species from elsewhere become obvious (e.g. a number of supposed endemics in Guam) and historical evidence turn up bearing on their introduction. Even so, it is frequently difficult to prove conclusively that a species was brought by man in the absence of documentary evidence directly involving the introduction.

An example (told to me many years ago by Carl Epling) of a fairly clear case was the discovery of a disjunct station in a lake in the state of Idaho (U.S.A.), of an Asiatic water lily. It was assumed that here was a remarkable instance of a wide disjunction in range until someone pointed out that some years earlier there had been a Chinese laundry on the shore of this lake. Less certain is the status of *Cordia lutea* in the Marquesas Islands. *Cordia marchionica,* described as an endemic, was recently shown to be indistinguishable from the above species of the west coast of South America.

Viola rafinesquei, of the eastern half of the United States, on the other hand, was first described as an Eastern American endemic, then relegated to the synonymy of the European *V. kitaibeliana,* later fairly conclusively shown to be a native American plant after all.

These doubtful cases, however, are only a small minority. The greater part of the naturalized species in all areas are clearly known to be such. Ecological considerations may likely help us determine the status of certain others, and also may contribute to our confusion if not accompanied by very careful and critical historical studies.

The subject of the ecological effects of introduced species is a very complex one, and our understanding is limited by our very scanty knowledge of how even simple ecosystems work. Several types of models have recently been formulated, by necessity highly generalized. Some of them enable us to classify species according to their major ecological roles. However, there have been few attempts to arrange the species of particular ecosystems according to such classifications and even fewer attempts to determine whether species may not have one or more secondary roles, or exert more than one effect. A simple and obvious example is provided by *Pinus sylvestris,* which is a dominant in certain natural (as well as planted) European forests. In addition to its major role as a primary producer of organic matter, it shades out many other species, or eliminates or prevents their establishment by root competition. It breaks the fall of rain as well as spreading a blanket of needles over the ground surface, reducing soil erosion. It is the major agent in recycling of mineral nutrients, which it also stores for a time in the blanket of needles. These needles provide the substrate for fungi and bacteria which decompose them. Their decomposition products, percolating through the soil, bring about podzolization and acid conditions, which in turn exert a limiting effect on the establishment of many potential colonist species, and by this reduction in competition, may permit or favor the establishment of acid-tolerant or acid-requiring ones. Species that are parasites or epiphytes on the pine are provided with a habitat. Animal species that prey on parasites or species sheltered by the pine are provided with their requirements. Others are provided with shelter and nesting places. The effects of the pine on accumulation and persistence of snow, as well as on the percolation into the ground of rain and snow water are profound. This in turn affects height of the water table and the flow of springs and streams, and consequently *the populations of* aquatic plants and animals in and downstream from the pine forest. The fallen, rotting trunks, after the trees are dead, shelter and provide sustenance for a complex community of reducing organisms, both plant and animal, and their parasites and predators. And, in a minor way, even the dark color of the trees serves to absorb, rather than reflect, the sun's rays, raising slightly the energy content of the system.

The fact that, in any major natural ecosystem, there are hundreds or even thousands of species with similar but extremely diverse relationships, interlocking with each other, may give a hint of the infinite complexity with which we are dealing. The most intricate model or description could only at best be a drastic oversimplification.

Granting these limitations to any possible understanding, we may attempt to discuss the role of exotic species of vascular plants in the natural scene.

A. Two critical considerations

Before any discussion of a plant species introduced into an ecosystem can be of tangible interest, or have any measure of reality, two factors must be established, or at least taken into account.

1. *The ecological status of the habitat*

A bare, open pioneer type of habitat will favor the establishment of many pioneer species, while completely discouraging species that require the shelter or other effects of mature vegetation. A " closed " vegetation will be invaded by very few exotic species unless it is disturbed, and " open " conditions created. The amount of available moisture, also, is an important limiting factor, as is temperature. In other words, conditions have to be right for any particular species to become naturalized.

2. *The ecological characteristics of the introduced species*

A pioneer species will not establish itself in closed vegetation. An epiphyte will seldom grow without a host plant for substratum. An aquatic will not grow on dry stony ground. But a sun-loving, intolerant species may become abundant where forest is cleared or opened up by grazing. A parasite may increase enormously if introduced in an area where suitable hosts are growing—for example, *Striga lutea* in the maize fields of North Carolina, or *Cuscuta arvensis* in California alfalfa fields.

Likewise, the growth habit of an exotic plant may either adapt it to establishment in a particular community or habitat, or preclude its naturalization. Growth habit may also have a profound effect on the ecological effects it exerts. For example, certain trees will provide dense shade, precluding or shading out sun-inhabiting species. Plants with vigorous and rapidly growing rhizome systems may completely dominate an area in a short time—as *Aster macrophyllus* did in my wooded yard within a very few years of its introduction.

Perhaps the most important generalization in this area is that the vast majority of the most successful exotics are plants occupying relatively early stages in vegetational succession and hence able to benefit from the disturbance that is increasingly the rule in most regions.

B. Habitats, from viewpoint of receptivity to additional species

It is axiomatic that unless a seed or other propagule falls in a suitable habitat the plant will not become established. Unsuitability either may be due to unfavorable factors in the physical or biological environment, or to the fact that the spot is already fully occupied. Recent work, by Egler and others, on the stability of certain managed vegetation types shows that the particular species already occupying a site have a tremendous effect on what others are able to gain a foothold. Unfortunately, however, the fact that vegetation of certain combinations of species seems indefinitely stable has given rise to the idea that the concept of vegetational succession is unsound, which seems a step backward.

1. *Over-all suitability of habitat*

The numbers of species in floras of areas equivalent in size, at least on continents with large floras available, seem related to habitat diversity, temperature, and abundance of resources utilized by plants. Thus a mountainous area in the same temperature belt may have more species than a flat one, a warm area more than a cold one of similar other characteristics, and an eutrophic area more than an otherwise similar oligotrophic one. Since species differ in their means of tapping the resource pool, as well as in their requirements, an area of abundant and diverse resources usually supports a large flora and provides more favorable circumstances for new colonists to become established if there is any disturbance to give them a foothold. Extreme habitats, in terms of temperature, dryness, salinity, or alkalinity, acidity, or fluctuation in conditions are generally occupied by small native floras. They are likely to be receptive to relatively few exotics, also.

2. *Unoccupied niches*

Generally, in a situation that is reasonably favorable and not isolated from continental areas with large floras, most of the environmental niches open to vascular plants are occupied. On islands, where a certain degree of isolation prevails, there may be open niches. This is certainly true for young islands where adequate time has not elapsed for either extensive colonization or adaptive radiation or speciation. Part of the paucity of the floras of coral atolls may be explained in this way. On such islands there are usually unoccupied niches which provide opportunities for easy establishment of exotics with appropriate requirements.

3. *Disturbance and creation of new niches*

The existence of an abundant and diverse exotic flora, however, is not necessarily an indication of diversity of naturally unoccupied niches for them to move into. It more likely indicates a great amount of disturbance of the habitat, which creates new niches. I remember seeing in southern New Mexico a flourishing stand of *Portulaca oleracea,* a plant not seen elsewhere in the entire desert area, in a shallow artificial pit, in a very uniform desert area of sparse *Larrea-Flourensia* vegetation with certain native annual herbs. The fine soil exposed by the digging was very different from the " desert pavement " of pebbles surrounding it and general in the area. This creation of new niches by disturbance of all sorts seems to be one of the most potent factors in encouraging the establishment of exotics. Once established they may or may not be able to spread and encroach on native vegetation in less disturbed ground. Once a species is established the competitive relations in the community are likely to be altered, and its potency to spread may be enhanced. It may, in some cases, itself contribute to the increase of niches favorable to its own seedlings, or to those of other exotics.

4. *Classification of habitats*

This is a vexing subject, and has occupied the attention of many able ecologists, but without the appearance of any single universally satisfactory classification. Various classifications of particular components of habitats are available—climate, vegetation, soils, physiography, lithology, and drainage. It is likely that the possibility of a universal classification of habitats—situations involving all of these features—is an illusion. Classifications will be created and suitable for particular purposes.

For understanding the behavior of exotics it seems that the primary division of habitats should be into currently undisturbed and disturbed habitats. That the undisturbed ones have been disturbed in the past is likely. They may perhaps be grouped according to how far succession has gone from a pioneer stage toward one of relative stability. Another significant breakdown would be on the ecological characteristics of the habitats—wet vs. dry, salt vs. fresh, cold vs. warm, eutrophic vs. oligotrophic. The number of categories on each of these gradients would be a matter of choice or expediency. The currently disturbed habitats could be grouped according to the original type of habitat and the degree of disturbance. This subject is too big to deal with in detail here; this would require a separate paper, or even a separate symposium. Suffice it to say that with such a classification it would be far more possible to predict the behavior of an exotic species whose original habitat was known.

C. THE ABILITY OF SPECIES TO ESTABLISH THEMSELVES AND SPREAD IN NEW HABITATS

Clearly enough, some species become established more readily than others, and, once established, some will spread very rapidly and aggressively, while others will not. We have seen *Halogeton* become established in the Great Basin region of the United States and occupy large areas of semi-arid and irrigated land. *Salsola kali* var. *tenuifolia* is an even more extreme example. On the other hand, *Setaria sphacelata,* from the same general region, has been established in central California for forty years that I can remember and has never been more than very locally common. The most extreme type of restricted establishment is that of a dioecious or self-sterile perennial species with no means of vegetative propagation, which may persist for years as one individual but never spread.

1. *Ecological amplitude or range of tolerance*

This is a complex subject, but a critical one in the establishment, persistence and spread of exotics. For example, the inability to survive frost eliminates the vast majority of tropical plants and, hence, a majority of all plants from any possibility of invading temperate or cold habitats. Plants that cannot tolerate water-logged soil around their roots cannot invade marshes or swamps. Obligate oxylophytes do not prosper in neutral, much less in alkaline soils. Plants with no means of controlling water loss seldom invade deserts unless they have extremely deep root systems (phreatophytes). It scarcely needs saying that it is the tolerance of the least tolerant stage in the life history of the plant that is most critical.

2. *Competitive ability*

Ecological amplitude is not at all as obvious a characteristic as it might seem. More and more species that are restricted in their ranges are found to be so not because of an unfavorable factor in the physical environment, but simply because of inability to compete with other species except in some extreme habitats to which they are adapted. Mangroves are inhabitants of saline swamps; Egler, however, has shown (*Carib. Forester* 9: 299-320, 1948) that they grow perfectly well in fresh water, but apparently there are other plants that grow better there and crowd them out.

Many characteristics contribute to competitive ability, in addition to generally vigorous growth. Among these are abundant seed production, effective means of vegetative reproduction, rhizome formation, selective conditions for seed germination, effective dispersal mechanisms, production of antibiotic substances, and a growth habit that assures access to such resources as light and water. Competitive ability is essentially the capacity of a species to secure and hold a sufficient share of the needed space and other essential resources to maintain itself and to spread at the expense of its competitors for these resources. The successful exotics are those with high competitive ability.

3. *Heterozygosity and diversity of biotypes*

It is commonly observed that weeds and other successful species are exceedingly variable. Segregating as well as self-perpetuating strains are numerous. The production of an assortment of strains and individuals with differing ecological requirements and morphological features enables a species to occupy many niches and to take advantage of diversity and disturbance in the habitat. The environment shows a great multiplicity of gradients and local sets of conditions. The species that produces variations capable of filling many of these niches increases enormously its chances of success.

4. *Ecological equivalence of species*

Under similar combinations of environmental conditions in different areas, species with similar requirements and adaptations have frequently arisen and may be to some extent interchangeable. Such equivalent species, even though they may not be at all related systematically, may replace each other when they are introduced as exotics—even without much disturbance of the habitat. Usually exotics are introduced without their normal parasites, diseases, and other natural enemies. This may give them a great competitive advantage over their indigenous counterparts, even though physiologically and in other respects they may have no advantage at all. An understanding of the ecological characteristics of a species may provide means of predicting its probable behavior if introduced into a similarly well-understood habitat or community.

E. Dynamics of invasion and naturalization

Any discussion of the processes involved in invasion and naturalization must be based on the characteristics of habitats and species brought out in the above remarks. The dynamics observed are a result of the interaction between introduced species, with their particular characteristics, habitats with their properties, the plants and communities already occupying the habitat, and animals including man which may exert a disturbing or modifying influence. The infinite range of possibilities resulting from interaction of such a large number of variables in an enormous variety of situations makes effective generalization, except on the broadest scale, impossible. All one can do is discuss some of the kinds of dynamic processes involved and certain factors that influence them.

1. *Establishment the first requisite*

As brought out above, an invader must succeed in establishing itself in order to be of any consequence in the ecological picture. The germination of a seed, spore or vegetative propagule, and growth of the first plant to reproductive maturity is the essential first step that any potential exotic must make before it becomes a member of a flora or forms a significant part of the vegetation in an area where it has not been before. Requirements for this vary with the species. Many require a spot of bare mineral soil. Others start in peat or humus. Many require sunlight, others shade. Some start on the bark of other trees, others in sand, still others in rock crevices. Most have rather specific temperature and moisture requirements for germination.

2. *Ability to utilize environmental resources*

Once a plant has gained a foothold, its further progress in invading its new territory depends on its means and ability to secure a good share of the available resources in its environment—water, light, mineral nutrients, and " lebensraum ". As noted above, this is difficult to do in a community that is stable and well integrated, where the available niches are already occupied—where there are not many resources to spare. It has been estimated, for example, that in a tropical rain-forest 70 percent of the total available mineral nutrient supply is, at any one time, actually tied up in plant tissues. The layered structure and the abundance of epiphytes assure that no sunlight and little space are unused. Only water is available in greater abundance than is actually used.

The tropical forest is the extreme example, but any closed vegetation is to some extent saturated with plants and difficult to invade. Here natural forces such as wind, floods, landslides, lightning, create occasional disturbances that may allow the entrance of an occasional new plant. Animals, especially man, are, however, the primary causes of the disturbance that makes invasion by exotic plants such a tremendous phenomenon that a symposium paper should be written about it. Rather than a rare event successful invasion has become the dominant force in shaping most land plant communities and landscapes.

The continual " churning " up of the natural environment by man, livestock, and fire, at the same time permits exotics to spread and is detrimental to many native species. The most favored newcomers are generally pioneer plants or so-called " weeds ". Their capability for rapid multiplication and their effective dispersal mechanisms enable them to fill the available space very quickly, so that they are soon in competition even among themselves. Usually these plants soon lose out to more effective species often of larger stature, which cut off their sunlight and reduce the available water. More and more shade-tolerant species enter the community. The species that can reproduce in their own shade and overtop the neighboring trees are the ones that will eventually dominate a community. They, of course, may either be indigenous or exotic species.

Not enough is known of the actual mechanisms that enable different species to compete effectively for resources. There are obvious things such as tall stature, deep root systems, ability to use efficiently light of low intensity, capacity to store water and growth habits that enable plants to reach the light by climbing on others. There certainly are more subtle features that make up what is known as " aggressiveness ", the quality that makes one species a successful weed, and another, to all appearances similar in the obvious characters, remain a rare plant. I know of no general statement of these features, and am not enough of a physiologist to have one to offer.

3. *Hybridization of closely related species*

This topic is only peripherally important here, but should be mentioned because invasion has been accomplished by genomes, even though the exotic species that contributed them may not have been successful. One merely has to mention × *Spartina townsendii,* as an example where an American genome became very successful in a European environment as a component of this hybrid.

There probably are many cases of contributions to variability and diversity of biotopes resulting from casual hybridization where an exotic has been literally absorbed into a local population. H. H. Allan once mentioned something of this sort among New Zealand *Acaena* species, contaminated by crossing with an introduced Australian one.

4. *Tendency of local species to prevail*

Some cases have been observed where native species have been able to reassert themselves and crowd out exotics after the pressure of disturbance has been lowered—when an area has been fenced, or livestock or feral grazing animals

Temoved. This is likely only where the environment is merely superficially changed. If the vegetation alone has been degraded, recovery is likely, but if the soil has been removed, any recovery will be on a geologic time scale, if it happens at all. Exotics and native pioneers able to survive in rock crevices or on raw subsoil "will prevail.

5. *Effects of continued disturbance*

Continued disturbance will gradually eliminate many species, which will be usually replaced by exotics, except perhaps in a few regions with a very long history of disturbance, where many of the plants well adapted to man and hit activities and widely introduced elsewhere may have evolved. Some of these may have been unwittingly brought into existence by man and have been his camp-followers ever since. A modern example is the above-mentioned *Spartina townsendii.* We do not have documented histories of many other aliens which have come out of the Mediterranean region or south Asia, but which show a remarkable ability to take advantage of man's influence, in spite of his efforts to destroy them.

One need not look far for examples of landscapes completely occupied by alien species. The outskirts of cities, as well as pastures and even certain range lands, furnish many such. On a recent visit to Argentina for several days I did not see a single native species, until I was taken to a garden where a few were maintained under protection, and to a tiny relict scrap of the riverine forest that once lined the Rio de La Plata. All else was dominated by European weeds, pasture plants, and cultivated species. This process of long-continued disturbance has doubtless vastly changed the flora of Europe, also, but much of it was so remote in time that the plants are now frequently regarded as native.

E. THE ECOLOGICAL EFFECTS OF INTRODUCED SPECIES

These effects are certainly innumerable and they vary from species to species. Only a few generalizations will be attempted here in the way of a summary. As will be seen, the effects are not all bad. However, it is almost a truism that the niche occupied by an exotic is practically always one from which one or more native species have been partially or completely displaced. The most difficult problem in indicating this and other ecological effects of introduction of an exotic is to determine whether the species caused an effect or was merely able to invade and survive in a habitat because of alteration of the environment by other agents. This latter possibility very severely limits the number of effects that can be safely ascribed to introduced species of vascular plants. The following suggestions are offered, with qualifications where necessary, but with full knowledge that such clear-cut effects only scratch the surface of a very complex problem.

1. *Increase of effects of fire on the ecosystem*

Even under the same climatic conditions vegetation made up of certain species of plants may be much more subject to fire then that composed of other types of plants. An example that comes to mind is pine introduced into certain French forests (Fontainebleau, Landes, etc.). Forest fires became much more frequent and serious than in the previous hardwood forests. Annual grasses introduced into certain sparsely vegetated arid areas in the southwestern United States are able to make sufficient growth in the very short rainy season to provide fuel for fires after they have matured and dried, though there were no fires before. In New Zealand, the introduced *Ulex* is quite fire susceptible, but the fire brings about germination of quantities of dormant *Ulex* seeds, so that the species tends to become much more abundant and to dominate the vegetation.

2. *Replacement of species of low ecological amplitude*

In most floras there are species of low ecological amplitude or restricted genetic variability (heterozygosity). Opinions may differ as to their importance in vegetation, but in many systems of phytosociology they may be regarded as of great consequence. Where they are growing near the limits of their tolerance, at least, they are very liable to being displaced by exotic " weeds " with more variability and adaptability. This may greatly alter the composition, and even the physiognomy of the vegetation.

3. *The replacement of complex plant communities*

When a mixed community is affected by human influences, fire or heavy grazing, its tendency is to recover, gradually, its original composition and physiognomy, if the disturbance lessens. However, if well-adapted exotic species are present they may be able to move into the niches opened up by the disturbance and one or a few broadly tolerant species may occupy the places of a range of narrowly adapted native ones. This was seen in the Hawaiian Island of Molokai, where native montane forest vegetation was damaged and opened up by grazing. Several introduced grasses and the " pamakani ", *Eupatorium adenophorum,* invaded the area and soon the rich native forest was replaced by a dense scrub of *Eupatorium,* with the grasses choking any openings. The complex community was replaced by a much simpler one made up of a very few exotics, and with an entirely different physiognomy and structure. There are innumerable examples of this phenomenon, mostly attendant on serious disturbance, rather than due solely to the presence of exotic species. The formation of blankets of creepers and vines, as *Lonicera japonica* in disturbed places in the eastern United States, brings about the smothering out of many native species, even trees in time, and a profound change in structure.

4. *Protection of badly disturbed habitats and reduction of erosion*

On the other side of the coin is the role of " weeds " in covering bare soil after disturbance and in reducing erosion. The fact that so many exotics are aggressive pioneers makes them very effective in this function. A glance at the flora of an abandoned field will show a great proportion of exotics in the plant cover that establishes itself on the raw soil. Soil conservationists have not been slow in taking advantage of this feature. Exotic grasses and legumes are encouraged and planted on road-cuts and embankments. Proposals to introduce the natural enemies of *Lonicera japonica* to reduce its effect on native vegetation have been opposed by road and railroad engineers who value this plant for its ability to cover and cut down the erosion of their embankments.

5. " *Nurse-plant " effect in saving species that cannot survive open conditions*

Most of the species that make up mature vegetation are ill adapted to growing in the open, even in their seedling stages. When forest vegetation is destroyed and open conditions prevail, the forest plants tend to disappear. Where aggressive " tree-weeds " or even shrubs or tall herbs occupy such an area, the seedlings of native plants may be given a chance to establish themselves and to persist, possibly eventually replacing the pioneer " nurse-plant " that protected them in their early stages. An example of this was pointed out by Egler (*Empire For. Jour.* 18 : 9. 1939) on Oahu, Hawaiian Islands, where *Psidium cattleyanum* var. *littorale* was able to colonize areas where erosion had removed the top soil. In its shade many native forest plants were able to survive which would have had a hard time in the open on such a poor substratum.

6. *Establishment of new communities of different floristic composition*

Vast areas of the earth are occupied by plant communities that are very different from what was there when man entered the scene. In most of these, exotic plants are important components. It is hard to say without prolonged study which of these communities are relatively stable. In the United States we are accustomed to see rapid change and very little order in our disturbed landscapes. Chance seems very important.

An American visitor to Europe sees the same or similar communities repeated in many situations. A greater impression of order and stability is gained than at home. He, of course, is likely to assume that the plants he sees are the natives—he knows the same ones from America, where he has been taught they are " European weeds ". If he goes about with European botanists he finds that at least some of these species are known to have been brought, perhaps in very early times, from other parts of Europe, or even from Asia, and that they are exotics here, just as in America. He hears debates on whether or not the beech, yew, and box are native in England, is assured that the Scots Pine is not native in France, and finds that only a very few tree species survived the glaciation in central and northern Europe. He even sees familiar American plants, as *Robinia pseudoacacia, Quercus rubra,* and *Oenothera biennis* very much at home and members of apparently stable communities. Many of the exotics in Europe have been around long enough to have acquired a normal coterie of diseases, parasites, and other natural enemies, so as not to have a tremendous advantage. They are behaving like native species even though known to have survived the glaciation only in refugia in the Mediterranean region or to have originated in Asia or America.

Of course, no one knows what species may have disappeared from the flora or may have had their ranges greatly restricted, in the process of establishment of new communities of exotic or partly exotic plants.

7. The effect of exotic species and especially of new communities formed by them on the physical environment must not be overlooked. Podzolization by coniferous forests, building up of humus horizons in the soil, and changing soil moisture relations are only a few examples. Microclimates are certainly altered, and there have been suggestions of greater climatic changes, at least on a local scale, brought about by changes in vegetation.

Perhaps the most important general effect of plant introduction and naturalization is that of progressive impoverishment of the world's flora. Local plants tend to become rare and disappear as they are replaced by exotics. Occasionally in any one place this may not result in a lessened total flora. In Islands with very small floras it may even result in an increase. However, taking the world as a whole, the same relatively few species tend to be introduced in the same climatic regions. *Rumex acetosella* may replace one set of species in Virginia, another in California, another in Hawaii, and still another in the Andes. The " cosmopolitan flora " discussed by Aubert de La Rüe (*Proc. gth Pac. Sci. Congr.* 20 : 89, 1958) exhibits a monotony as one goes around in the tropics—it is exciting to the visitor from the Temperate Zone, but to the person familiar with the Tropics it is the same whether he sees it in Hawaii, Singapore, West Africa, or Venezuela. He has a feeling of sadness that he has not had an opportunity to see the plants that originally made up these landscapes.

With impoverishment in any of its components an ecosystem is likely to lose some of its stability. It becomes more vulnerable to change, and the reestablishment of equilibrium more difficult. Perhaps in the long run, impoverishment of the biota is the most serious ecological effect of the transport of plants or animals from their native habitats to places that they had not been able to reach under their own power.

COMMENTS

N. Soyrinki (Finland) reported that Finnish experience supported the view that introduced plant species are only able to intrude into natural vegetation if disturbance occurs. Exotics cannot invade the virgin vegetation of Finnish forests and peat bogs, but where there is no natural balance invasion occurs e.g. *Glyceria maxima* invasion on lake shores and the northerly spread of *Thlaspi alpestre* in semi-natural meadow vegetation. He suggested that to be successful against native species, an exotic must possess some ecological advantage and in the case of the last named species this is early flowering so that the fruit ripens earlier. *N. Polunin* (Nigeria) pointed out that ecesis does not necessarily involve seed germination. Thus temperate cruciferous weeds and other aliens in high-arctic Spitsbergen and many exotics in West Greenland persist commonly by vegetative means. He did not find it surprising that the water chestnut had spread aggressively in North America since introduction, as it was widespread there before the Pleistocene glaciations. *F. R. Fosberg* suggested there were more European weed species in N. America than *vice versa* because culture went from Europe to N. America. He again urged the need for more research to provide a better understanding of plant ecosystems.

SECTION II

Ecological effects of introduced animal species

Effets écologiques de l'introduction d'espèces animales

PREFACE

by

Professor GEORGE A. PETRIDES

Department of Fisheries and Wildlife, Michigan State University
Rapporteur général

The values of non-native plants and animals have been obvious to man ever since he cultivated food plants and domesticated birds, mammals, and other animals. In his wanderings and at his new settlements, it has been his usual practice to establish the species which had been important resources to him and which had been tamed, often with genetic modification, at other localities.

As time went on, such organisms as wheat, pines, roses, lawngrasses, lucerne, cows, goldfishes, honey bees, and house cats, became spread around the world. And since they were useful additions to native resource-organisms, people cast around for still other helpful plants and animals to aid man in combating nature (which, until quite recent times, was viewed as mainly malevolent).

In connection with man's activities and movements, and as a result of both deliberation and accident, species of plants and animals which later became known as weeds and pests also were transferred to new lands where they harbored diseases, preyed upon or competed with native life, or otherwise became nuisances.

Both the values and the dangers of exotic species are becoming well-known to biologists. Since the mechanics of population control and the possible effects of species interactions are still largely a mystery to the layman, thoughtless introductions continue to take place. The matter of exotic introductions is of importance from many practical viewpoints, including that of the protection of natural areas.

It was the effort of these Technical Sessions to provide background information upon which to base a policy acceptable to IUCN, governing the introduction of exotic species. Professor Ovington has prepared the fine statement which prefaces the Section 1 Papers of this Volume, on Plant Introductions. Since the natural laws which govern animal populations are essentially those which control plant populations, there would seem to be no need to modify Dr. Ovington's presentation. If in every place that he uses the word " plant", the word " species " is substituted, his comments equally suitably preface the joint topic of animal introductions.

BIOLOGICAL EFFECTS CAUSED BY TERRESTRIAL VERTEBRATES INTRODUCED INTO NON-NATIVE ENVIRONMENTS

by
ANTOON DE VOS
University of Waterloo
Waterloo, Ontario, Canada
and
GEORGE A. PETRIDES
Michigan State University
East Lansing, Michigan, U.S.A.

One of the ways by which man has modified his environment is through the introduction and transplanting of species, either willingly or unintentionally. Ever since human history began, man has moved around plants and animals, but large-scale introductions were tried only recently. In 1953, not less than 21,000 animals were released in the U.S.S.R. (Niethammer, 1963). Hungary, between 1930 and 1940 yearly exported on the average 40,000 living hares (*Lepus europaeus*), 50,000 gray partridges (*Perdix perdix*), and 35,000 pheasants (*Phasianus colchicus*) (Niethammer, *op. cit.*). From 1927-1953 inclusive, 117,000 muskrats (*Ondatra zibethica*) were introduced in 500 localities throughout the U.S.S.R. (Hall, 1963).

The successful introduction of animals can be explained in three ways, although usually many complex factors intervene contemporaneously:

1. In case of a vacant and suitable ecological niche, the introduced species will occupy it to become well established. It may even proliferate to pest proportions.

2. Where a closely related autochthonous species is present in an ecological niche, an introduced species may be more aggressive and successful in competition so that the native species is gradually reduced in numbers and may be eliminated.

3. Also the introduction of predatory species may threaten a predator-prey balance, and modify this to the detriment of native species (Dorst, 1963).

Ecological effects include the hybridization of introduced species with related native forms, the disappearance of native species through competition and the bringing of diseases and parasites with them which may do considerable damage to the native fauna.

Prior to and during the early stages of human settlement in many parts of the world, most animals were moved around unintentionally, for example as stowaways on ships. Intentional introductions of animals, however, have been practiced. These reached a peak during the nineteenth century.

The majority of introductions of animals have failed and many successful introductions have proved detrimental to man or existing natural communities. Introductions frequently initiate chain reactions, and the consequences of these ecological sequences are mostly unpredictable. An exotic species will not usually fit into the specific niche which the introducer expects it to fill. By and large it seems impossible to introduce animals under completely " scientifically controlled " conditions, because of our lack of knowledge of ecological conditions both at home and abroad and because of the difficulty and artificiality of experimentally controlled conditions.

Overly-successful introductions usually lead to a need for control. It is difficult and extremely costly to exterminate well-established introductions. The only known case of the successful eradication of an introduced mammal that was well-established over a large area is that of the muskrat in England (Warwick, 1934).

In general, the more generalized the characteristics of a vertebrate species, particularly in its food habits, the better are its chances of establishment.

On oceanic islands the lack of competition with indigenous species has generally favoured the establishment of introductions.

An analysis of the mechanism of introductions shows that there are internal factors of the immigrant species such as genetic variation and differences in the means of reproduction, and external factors of the physical and biotic environment (Elton, 1958).

TERMINOLOGY OF SPECIES INTRODUCTION

Since there are differences in the national or regional usages of terms regarding introductions, an effort at clarification is desirable and the following definitions are proposed:

Introduction (introduce) — the movement by man of live organisms to a new location outside their recent natural geographic range. This word may be used as a verb, referring to the combined activities of movement and release, or as a noun, with reference to the introduced species itself. Deliberate (intentional) and accidental (unplanned) introductions may occur. Synonym (noun): imported species.

Re-introduction — the act of returning a species to an area within its original geographic range from which it has disappeared. The term is also used as a noun. (Since species have evolved in their original ranges, it is likely that a re-introduced species will be adapted to live there unless the environment, either physical or biotic, has been altered critically. In such an original environment, it is probable, too, that the species will not increase to pest proportions.) Synonym (noun): restored species.

Transplantation — the introduction of a breeding population into a new area, either within or whithout its natural geographic range.

Stocking — a term identical to transplantation, but sometimes used without the requirement of a reproducing unit.

Successful Introduction or successful Transplantation — has reference to a population which has survived and increased in its new environment. Objectionable qualities of a species may make a successful introduction an undesirable one, but they do not affect the success of transplantation. Synonym: established species.

Establishment — the result of a successful transplantation, as evidenced by a sustained or increasing breeding population. It is suggested that the term

" settlement " be dropped because it does not imply continued breeding. The process of becoming established has two related terms, of which *acclimatization* should be avoided, because climate is only one of the environment factors which determine survival and reproduction. *Naturalization,* perhaps, may be used synonymously.

Native — an individual or population which is a member of the natural biotic community. Synonym: indigenous.

Exotic — a species native to an area located outside of, or foreign to, the area under review. An exotic species established in a new area is an introduced species.

Feral — an adjective synonymous with wild, referring to a native wild animal or to one which, even though once tamed or domesticated, has reverted to living in the wild.

Adapted species — a species which is successful in maintaining and increasing its numbers. For introductions, this term is given preference over " aggressive species ", which emphasizes behavioral adaptations over anatomical or physiological ones, and " preadapted species " which implies conscious direction toward a suitable evolution. The term " adapted " merely recognizes the evidence that an " established " (successful) species obviously is adapted.

Niche — a portion (or aspect) of the environment which is particularly suited to support a certain species; that aspect of the environment which especially fits the structural, functional, and behavioral characteristics (requirements) of the organism.

BIOLOGICAL EFFECTS OF INTRODUCED ANIMALS

Evidence is accumulating suggesting that among several species of introduced animals rapid genetic changes may take place which induce changes in morphological structures and food habits. These are influenced by the new environment.

Among mammals, e.g. the alpine hare (*Lepus timidus*), introduced from Norway to the Faroe Islands in 1854-55, has developed into the subspecies *seclusus* which retains its brown colour the year-round (Bourliere, 1954). A new race of mouflon (*Ovis musimori*) has developed in Slovakia since about 1910 (Allen, 1954). Fallow deer (*Dama dama*) in Europe, originally introduced from Asia Minor, differ considerably from the few remaining representatives of the species in Mesopotamia. The house mouse (*Mus musculus*) has developed new subspecies in several parts of the world. On the Faroe Islands, e.g., four distinct subspecies exist today (Bourlière, 1954).

In case of several species of birds, e.g. Canada geese, *Branta canadensis,* and mandarin ducks, *Dendronessa galereculata* (Niethammer *et al.,* 1963), migration behaviour has been disrupted in some areas of introduction.

In some cases man purposely has tried to induce genetic changes. In Russia, e.g., attempts have been made to produce a strain of coypu or nutria (*Myocastor coypus*) which is " frost-resistant " (Davis, 1964).

Often, introduced species change their food habits in their new environment, or, at least, they do damage not known in their native range. In the Caucasus, the raccoon-dog (*Nyctereutes procyonoides*) reportedly changed its foods from the fish and crabs, which were eaten in its native Japanese habitat, to game birds, hares and poultry. The introduction of the North American muskrat into Eurasia resulted in a serious threat to the local economy by damage to dikes, by eating fish and also damaging nets in freshwater ponds, and by raiding field and garden crops (de Vos *et al.,* 1956). The edible dormouse (*Glis glis* L.), introduced from eastern Europe, has damaged planted trees in the U.K. by eating the bark (Thompson and Platt, 1964).

There are several known cases of genetic changes in the local population of a species caused by the introduction of another form. Crosses of the Siberian race of roe deer (*Capreolus capreolus pygargus*) with the native race in Czechoslovakia are still perceptible in abnormally tall and thick antlers. The transplantation of German red deer (*Cervus elaphus*) into Norway has apparently resulted in the virtual extermination of the entire species there, probably because the German strain is less hardy. Siberian weasels (*Mustela sibirica coreana*), imported to Japan in 1930, have hybridized with the native weasels (*M. s. itatsi,* de Vos *et al.,* 1956). The Kamchatkan sable (*Martes zibellina kamshadalica*), introduced into Western Siberia, has interbred with the native form to produce hybrids with heavier furs (Lindemann, 1956). The introduction of red foxes (*Vulpes vulpes*) from England to Sweden may have been responsible for the appearance of numerous " Samson foxes ", animals with an inherited deficiency of guard hairs. Alaskan silver foxes (*Vulpes fulva alascensis*), released in Finland in 1938, are apparently interbreeding with the native red fox (de Vos *et al.,* 1956).

Rate of spread of introduced mammals

Unfortunately the rate of spread of introduced species has been inadequately documented. Probably, this is seldom a steady rate.

The most rapid spread recorded for any introduced mammal is that of the muskrat (*Ondatra zibethica*) after its introduction in Europe. The spread in Finland was 18-25 miles per year (de Vos *et al.,* 1956). The rate of spread of the grey squirrel in Britain during the period since it was successfully established has been in the order of about five miles per year (Taylor, 1964).

The spread of ungulates does not appear to be as rapid, with the possible exception of the chamois (*Rupicapra rupicapra*), whose rate of spread in New Zealand was estimated at 5.3 miles per year (Caughley, 1963). After its introduction into Newfoundland, the moose (*Alces americana*) spread at 2 miles per year (Pimlott, 1953). In New Zealand, fallow deer, whitetailed deer (*Odocoileus virginiana*), rusa deer (*Cervus timorensis russa*), sambar deer (*Cervus unicolor*), and wapiti (*Cervus e. canadensis*) spread at the rate of 0.5 miles per year; sika deer (*Cervus nippon*), thar (*Hemitragus jemlahicus*) and red deer at 1 mile per year (Caughley, 1963).

Introduction of diseases and parasites

The consequences of the importation of diseases and parasites with exotics as hosts are not fully appreciated. Most diseases are more dangerous to hosts which have not been previously exposed to them, since such hosts have not had the opportunity to develop immunity. It may be impossible to eradicate introduced diseases in their new hosts and they may be particularly destructive. Examples of epizootics introduced from one continent to another include rinderpest, foot-and-mouth disease, and swine fever. Blackhead among turkeys in North America originated from Old World chickens.

Although natural selection tends to reduce the severity of the effect of a pathogen on a wild host (as in case of myxomatosis among European rabbits in Australia), the new host may be exterminated by the disease before it has been able to build up adequate resistance, or at least it may become rare. In the case of species competing for the same niche, the original host with which the disease was introduced may take over completely or partially from the native species. Various introduced pathogenic agents have been responsible for rarity in certain endemic birds.

There are few data on introduced parasites and their possible influence on native hosts. Parasites do get introduced, however, sometimes several species in one host. It seems likely that the tick *Trombicula akamushii,* which harbors the rickettsial disease, scrub typhus, has been spread widely with rats and other rodents. The Indian rat flea (*Xenopsylla cheopis*), which transmits bubonic plague, has also been spread with rats from ships in many parts of the world (de Vos *et al.,* 1956). Three nematodes and two cestodes were introduced to New Zealand with the European rabbit. At least two parasites, a cestode and a trematode, were introduced with muskrats to Great Britain. The more complicated the life cycle of the introduced parasite, the less likely are the chances of its survival (de Vos *et al.,* 1958).

DAMAGE TO MAN'S FOOD SOURCES

Outstanding examples where damage has been done to human food resources by introduced animals involve the European rabbit (*Oryctolagus cuniculus*) in Australia and New Zealand, the European hare in Ontario and Argentina, the brown rat (*Rattus norvegicus*) in many parts of the world, and the gray squirrel (*Sciurus carolinensis*) in South Africa. Other damaging pests are European starlings (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*) in North America, and the Chinese mitten crab (*Eriocheir sinensis*) in western Europe.

COMPETITION BETWEEN INTRODUCED AND INDIGENOUS SPECIES

The introduction of a species may result in competition, particularly with closely related indigenous species. Such competition may include competition for food, cover, nesting or denning space. In some cases, diseases seem to play an important role in affecting competition.

Some cases have been well documented. These include competition between the American gray and red squirrels (*Sciurus vulgaris*) in England (Middleton, 1930; Shorten, 1960), and between European hare (*Lepus e. europaeus*) and alpine hares in Sweden. Introduced rats are blamed for diminishing small insectivores (*Nesophontes*) and native rice rats and spring rats on the Caribbean Islands (Westermann, 1953). In North America, the European starling has effectively reduced the population of other hole-nesting birds, such as the eastern bluebird (*Sialia sialis*). The mynah (*Acridotheres tristis*), originally from southeast Asia, has been introduced into several other warm countries, from South Africa to Oceania. Wherever it has been introduced, it has contributed to the reduction of native birds by occupying their nests, and chasing ecologically comparable species from their territories (Dorst, 1963).

WHAT ARE " USEFUL " INTRODUCTIONS?

The problems discussed and the principles elucidated in this paper are based on limited data. There is a need for more research on introduced species everywhere in the world.

Introductions offer both advantage and dangers. Many cultivated crops and domesticated livestock species, strictly speaking, are exotic to many areas of the world and yet are essential to human welfare there. Among wild animals, too, such introductions as the moose in Newfoundland can hardly be viewed except as useful. Possibilities for further introduced species exist wherever unoccupied habitats occur, but the greatest care must be taken to import species which not only are capable of biological success but also are certain to be wholly desirable.

We cannot adequately and completely foresee the implications of our actions when we introduce another species. Introductions should be made only when the mentioned limitations are carefully considered. Estimates should be made of the possible side-effects of an introduction. Efforts should be made to make the public aware that unexpected side-effects may occur at any time.

There is considerable need for more research on the biology and ecological requirements of a species that is scheduled for introduction and of the ecological conditions that prevail in the environment into which the introduction of such a species is planned. But even the most carefully executed research does not eliminate the possibility of changes in the habits of species after introduction. Extreme care must be taken where further introductions are undertaken.

REFERENCES

ALLEN, D. L. *Our wildlife legacy,* Funk & Wagnalls Co., New York, 422 p., 1954.

BOURLIÈRE, F. *The natural history of mammals,* A. A. Knopf, New York, 1954.

CAUGHLEY, GRAEME. Dispersal rates of several ungulates introduced into New Zealand. *Nature* 200 (4903): 280-281, 1963.

DAVIS, R. A. The coypu on the continent and in Britain. *Bull. Mammal Soc. of the Br. Isles,* no. 21, p. 627, 1964.

DE VOS, A., MANVILLE, R. H. & VAN GELDER, R. G. Introduced mammals and their influence on native biota, *Zoologica* 41(4): 163-194, 1956.

DORST, JEAN. L'introduction d'especes animales et leur impact sur l'environnement tropical, p. 245-253, in : *The ecology of man in the tropical environment.* IUCN Publ., new series, No. 4. Proc. & Papers of the Ninth Tech. meeting, Morges, Switzerland, 1964.

ELTON, C. S. *The ecology of invasions by antmals and plants.* London, Methuen, 1958.

HALL, E. R. Introduction of exotic species of mammals. *Proc. XVI Int. Congr. of Zool.,* vol. 1, p. 267, Washington, 1963.

LINDEMANN, W. Transplantation of game in Europe and Asia. *Trans. N. Amer. Wildlife Conf.* 8: 62-66, 1956.

MIDDLETON, A. D. The ecology of the American grey squirrel (*Sciurus carolinensis* Gmelin) in the British Isles. *Proc. Zool. Soc. London, paper* 38 : 809-849, 1930.

NIETHAMMER, G., *et al. Die Einbürgerung von Saugetieren und Vo'geln in Europa.* Paul Parey, Hamburg, 1963.

PIMLOTT, D. H. Newfoundland moose. *Trans. N. Amer. Wildlife Conf.* 18: 563-581, 1963.

SHORTEN, M. Introduced menace. *Nat. Hist. magazine* LXXIII (10) : 42-54, 1960.

TAYLOR, J. C. Implications from the gray squirrel experience. *Bull. Mammal Soc. Br. Isles,* No. 21, p. 728, 1964.

THOMPSON, H. V. and PLATT, F. B. W. The present status of *Glis* in England, in : *Bull. Mammal Soc. Br. Isles,* No. 21, p. 5, 1964.

WARWICK, T. The distribution of the muskrat (*Fiber zibethicus)* in the British Isles. *Jour. Anim. Ecol.* 3 : 250-267, 1934.

WESTERMANN, J. H. Nature preservation in the Caribbean. *Publ. Found. Sci. Res. in Surinam and Netherlands Antilles* 9: 1-106, 1953.

COMMENTS

F. O'Gorman (Ireland) asked whether any ecological effects had been noted as a result of the moose introduction into Newfoundland. *A. de Vos* replies that since the introduction 20 years ago, moose had spread rapidly; despite some local damage to forests, careful management of moose including adequate hunting should however enable control of damage and recreational benefits to be achieved.

F. K. von Eggeling (Germany): the German Shooting and Wildlife Protection Society believes it is better to protect native habitats and wildlife than to introduce any species, unless it is certain that no adverse results will ensue. *J. C. M. Carvalho* (Brazil) contrasted the rapid spread of the European house sparrow throughout South America and the unsuccessful introduction of the camel into Brazil.

CAUSE AND EFFECT IN THE INTRODUCTION OF EXOTIC SPECIES

by

PETER SCOTT

The Wildfowl Trust,
Slimbridge, Gloucestershire, U.K.

Successful species are constantly trying to extend their range ... to colonise new areas. They are limited by the scope of their adaptability to a new environment, by their methods of locomotion, or by behavioural tradition. Thus seasonal food supply or winter temperature may limit the range of, say, the Common Chameleon in Europe; a narrow strait may prevent mice from colonising a new island ; the family bond in wild geese may prevent them from resorting to pastures new because their parents did not lead them there. Some of these limitations have been overcome by the deliberate or accidental intervention of man. On the other hand, many species have extended their range by entirely natural accidents against which the odds must be very long indeed. How many iguanas, lizards, geckos, tortoises, and snakes must have drifted down the Pacific rivers of South America on floating islands of weed before breeding stocks of each could establish themselves 600 miles out from shore on the volcanic Galapagos Islands newly risen from the sea ? How many plant seeds had to drift out ? How many land birds like finches and mocking birds and hawks had to be blown out to sea by off-shore winds ? These accidental natural introductions of animals to a group of originally lifeless volcanic islands helped Darwin to formulate his theory of evolution by natural selection, and led to an understanding of the principles of adaptive radiation.

The animals I have mentioned were introduced, so far as we know, without man's assistance. But the same islands are now also over-run with wild populations of donkeys, pigs, goats, dogs, cats, rats and mice, all introduced on purpose or by accident by man himself. The list has been described as " the wrecking crew ", because of their effect on the natural ecosystem.

Introduced species have in many cases caused the extinction of indigenous species, because the native animals were not evolved to withstand the onslaught of new predators or to defeat new competitors for food, and cannot adapt themselves quickly enough to survive. In other cases, like the rabbits in Australia and the Red Deer in New Zealand, populations of introduced species have reached pest proportions with serious economic consequences.

These examples have led to a general conclusion among ecologists and conservationists that the deliberate or accidental introduction of any exotic species is highly dangerous and basically to be condemned as ignorant, careless and irresponsible. And yet every year thousands of animals are being translocated by a large number of people for the express purpose of releasing them into a new environment. Nowadays this is usually done in the name of sport — more precisely as part of the economics of sport-hunting and fishing. Less frequently it is done with the intention of providing biological control of some pest. In former times simpler motivations were at work — the desire of colonists to have familiar creatures, especially song birds, around them, or even just the desire to enrich a poor local fauna by making some colourful or attractive additions.

In the past, too, pigs, goats and rabbits were deliberately released on uninhabited islands to provide a source of food for castaways. The pigs and goats on the Galapagos Islands are probably attributable to this source, and the feral pigs in particular are still a staple item of diet for the 3000 people living on the islands.

Accidental introductions have been no less disastrous than deliberate ones. Man cannot settle anywhere without bringing the rat which has probably caused more extinctions of bird species than any other single factor attributable to him. When his two principal predator pets, dogs and cats, are added and become feral, as they almost always do in a habitat rich in native prey species, the position soon becomes critical for birds, small mammals and small reptiles. The cats on Ascension Island, for example, are currently threatening the seabird colonies. Pigs have more often become feral accidentally than by deliberate human intention and are particularly damaging to ground nesting birds. They were certainly a major factor in the extinction of the Dodo in Mauritius about the year 1681. Pigs also eat the eggs of the various forms of Giant Tortoises in Galapagos and have been a major contributory cause of the extinction of at least two forms.

It is on the oceanic islands, which have so often evolved animal communities of particular variety and interest, that introduced animals have wrought so much havoc; and undoubtedly mammalian introductions have had the most serious consequences. In a very few cases bird introductions have been significantly inimical to man's interests; more often the effects of competition have been damaging to indigenous bird species, occasionally causing extinction. In the light of all these dire consequences, what should the attitude of responsible people be to the introduction by human agency of any exotic species of animals ?

The conclusion must surely be that the unknown dangers of tampering with ecosystems in this way make *any* introduction hazardous and basically undesirable. This is particularly true of small discrete ecosystems such as those of oceanic islands or isolated montane biotopes. Introduction of any mammals, and especially predatory species, is the most dangerous to the native fauna, insects probably the next most dangerous (with the possible exception of butterflies), then fish. Birds, which for sporting and aesthetic reasons are among the most popular animals for introduction, only rarely have a sweeping effect on the environment. It must be borne in mind that flight, combined with strong winds, has led constantly to the " accidental " natural colonisation of new areas by birds. The recent spread of the Cattle Egret *Ardeola ibis,* into the New World and the arrival of the Collared Dove *Streptopelia decaocto* in Britain, are cases in point. A similar unsuccessful example was the presence in New Zealand of a small population of the Australian White-eyed Pochard *Aythya australis australis,* for a limited period in the early part of this century.

The successful introduction into Britain of such birds as the Little Owl, the Canada Goose, the Mandarin Duck, the Pheasant, the Red-legged Partridge and most recently the Ruddy Duck *Oxyura jamaicensis,* do not so far seem to have adversely affected the environment or the indigenous avifauna. In other areas introduced species have been less welcome — for example the Starling in N. America and elsewhere, the Indian Mynah in Hawaii and other Pacific Islands, the House Sparrow, etc.

In New Zealand the desire of colonists for familiar creatures from the homeland led to the establishment of a network of Acclimatisation Societies, vying with each other to introduce exotic species. This has had a very significant effect on the endemic avifaune. Deer of a number of species have greatly altered the nature of the forests; European stoats and ferrets, and Australian Possums have decimated the native birds. The wetland ecology has been changed by the addition of Australian Black Swans and Canada Geese, both now present in tens of thousands. The northern hemisphere Mallard has crossed extensively with the New Zealand Grey Duck *Anas superciliosa superciliosa,* producing a rather ugly hybrid which is now widespread.

Although these results are to be deplored, it is still open to argument that justification may exist on aesthetic grounds for the introduction of colourful or melodious birds into a dull native avifauna. Such argument might be extended to include butterflies and perhaps some small reptiles and amphibia. A second justification might be established for the introduction of biological controls for pests as an alternative to chemical pesticides, though it should not be forgotten that the introduction of the mongoose to control rats has been unsuccessful and singularly disastrous in many places, notably in Hawaii.

Introduction for biological control might consist of predatory or parasitic invertebrates though even then the results may well turn out to be unexpected and embarassing, and clearly the technique should only be used sparingly, and then only when it offers a promising alternative to significant human hardship or suffering. A third possible justification might be found for translocating a species seriously and irrevocably threatened in its own range to a new area outside its own range. This was the intention (at least in part) for the introduction 57 years ago of the Greater Bird of Paradise *Paradisaea apoda* into Little Tobago.

Another aspect of the subject is the re-introduction of animals into areas which they formerly inhabited, but from which they have been exterminated. A recent proposal suggests that the wolf and the bear might be reintroduced to Britain to control over-population of deer in some areas. This is only practical if the original causes of extermination have been removed. In this case conflict with man over depredations of domestic livestock was probably the principal original cause, and it seems likely that the same conflict would bring the re-introduction experiment to nought. It is questionable whether a state of opinion has yet been reached in which man will be ready to accept material loss by depredation for the advantages of ecological balance and an enriched fauna for his aesthetic enjoyment, although in the long run such a state of affairs might well be attained in developed countries. The idea that some small financial sacrifice may be necessary and desirable in the name of aesthetic enlightenment and civilisation is gaining ground in some countries quite rapidly.

When a form has become totally extinct it could be worth considering the introduction of a closely related form which might be adaptable enough to become established. For example, another race of the Prairie Chicken might be introduced into the former range of the now extinct Heath Hen, *Tympanuchus cupido cupido,* provided that a viable amount of suitable habitat could be set aside for the purpose.

The tendency of man to wish to interfere with the natural distribution of animals is not always associated with practical or material motivation. There seems to be an element of curiosity to see whether an artificial introduction " will work " and a sense of challenge to make the attempt a success.

We may regret man's tendency to " play God " in this way and we may feel that the purist approach which deplores any introduction whatever is the more responsible view. We should not forget that whichever attitude finally prevails, man has already greatly modified the distribution of animals across the earth, and will certainly continue to do so. We should also remember that man and his attitudes are more than ever an essential ingredient of natural evolution, because man is still an integral part of nature. The evolution of the conservationist will in the long run play its part in man's total impact on the biosphere, which makes our deliberations at technical meetings of the kind now being held at Lucerne more important than perhaps many of us realise.

Comments

G. A. Petrides (USA): it can perhaps be accepted as a general principle that the reintroduction of an animal into its native area tends to hold fewer ecological dangers than the introduction of a foreign species. P. *W. Joslin* (Canada): attention should be given to the reintroduction of large predators into North American national parks where there has been a history of predator decimation. Many of these species are facing extinction and furthermore could be beneficial in regulating the abundance of ungulates.

F. R. Fosberg (United States) asked whether information is available concerning the transmission of bird diseases by introduced species. P. *Scott* replied that he knew of no case where such diseases had been reported, but New Zealand biologists must certainly have learned if such a problem existed as a result of introductions there. *R. A. Falla* (New Zealand): there is no evidence of diseases transmitted to native birds by species introduced into New Zealand. Several native species did decline rapidly, however, shortly after the introduction of other birds. This has been often ascribed to the transmission of diseases but little investigation has been undertaken except to detect forms of avian malaria in some of the native species. Research into the virology of wild bird populations is being carried out currently under Dr. J. A. R. Miles of the University of Otago.

M. Jones (U.K.) called attention to the importance of public education in ecological matters, both with respect to introduced species and to all resource matters.

THE INTRODUCTION OF EXOTIC ANIMALS INTO THE UNITED STATES

by

JOHN S. GOTTSCHALK

Director, Bureau of Sport Fisheries and Wildlife, U.S. Department of the Interior, Washington, D.C., U.S.A.

Since the earliest days of its history, the United States has served as the testing ground for the intentional and accidental stocking of literally thousands of animals from abroad. Fortunately perhaps, most of the arrivals failed to establish themselves. Some, such as the Norway rat, starling and house sparrow have become our most pernicious pests. Yet, several deliberate introductions have proved to be valuable additions to the native American fauna, and support substantial recreation-oriented economies.

After the War of Independence, the United States rapidly developed a great interest in the close examination and description of its wildlife. During the end of the eighteenth and the beginning of the nineteenth centuries, the Atlantic seaboard was the center of this scientific inquiry, the land west of the Appalachians being largely unexplored and poorly known. It attracted men whose one great ambition was to explore and describe the flora and fauna of that region.

One eighteenth century investigator was the Swedish naturalist, Pehr Kalm (1716-1779). He expressed his feelings saying, " I everywhere found such plants as I had never seen before. When I saw a tree, I was forced to stop and ask those who accompanied me how it was called. I was seized with terror at the thought of ranging so many new and unknown parts of natural history ". He was followed by the Scotsman, Alexander Wilson, who became known as the " Father of American Ornithology ", and later by the great Audubon. All found in this new country pristine flora and fauna. The land these men, and many more of their kind, must have seen was virgin wilderness—exposing to their amazed eyes the species of the new world—spectacular and different in color, habit, and habitat.

The European scientific world was eager for examples of the American fauna and flora, and in the early nineteenth century, John Bartram, the Pennsylvania naturalist, initiated what was probably the first exchange of living material between this country and the rest of the world. He was employed by various English noblemen to collect and gather native American plants and trees, and these he shipped for naturalization to England. His efforts alone resulted in the successful export to Europe of 150 American plants. He corresponded with the great Linnaeus, various Scottish, French and Russian scientists—all eager to share in this first beginning exchange between the new and old worlds.

Since the days of these early naturalists, there has been an ever increasing exchange of animals between the United States and other countries. Over the years this activity has grown from the importation of a few specimens to operations involving thousands of animals. Prior to our Foreign Game Introduction Program, which started in 1948, the efforts were largely unplanned. Since the formal Program has been initiated, we have attempted to enhance the American biota in a small but highly sensitive manner, matching relatively unpopulated ecological niches with game birds, mammals and a few fishes from other countries. The plan is to stock our vacant habitat with suitable exotics.

The Foreign Game Introduction Program is a cooperative venture involving the United States Department of the Interior through the Bureau of Sport Fisheries and Wildlife and the various State fish and game departments. The program has also involved many foreign governments and various private organizations, particularly the Wildlife Management Institute of Washington, D. C.

HISTORY OF THE ANIMAL INTRODUCTION PROGRAM

The history of the introduction of foreign species into the United States can be separated into two phases:

1. The early unplanned, uncontrolled introductions which have usually resulted in species being brought in, disappearing completely, or establishing themselves as residents to become pests causing untold millions of dollars in damage to habitations and crops.
2. Recent introductions based on scientific principles and practices to insure a relative measure of success with a minimum of hazard to the ecology of the receiving area or to its resident species.

According to Phillips (1928), birds apparently were the first interest of early colonists for introduction, although the history of species and introduction to this country is mostly clothed in darkness. However, it seems apparent that even though early America had a wealth of animals and plants there was still a longing for living souvenirs of the old country among the people who came here from the other parts of the world. In addition, the colonists were intensely practical men who recognized that wildlife could help feed and clothe them.

For example, ten years after the Declaration of Independence, George Washington was the recipient of a shipment of foreign game birds. In 1786, his friend, the Marquis de Lafayette, sent him several kinds of pheasants and a pair of French or red-legged partridges, *Alectoris rufa.* Also, Richard Bache, a son-in-law of Benjamin Franklin, introduced English pheasants, *Phasianus colchicus* and gray partridges, *Perdix perdix,* to his estate in New Jersey in 1790. There is no evidence that any spread from these early trials.

Until recently, the introduction of foreign fauna has been haphazard, without attention to the ecological requirements of the species or of their possible adverse effects. As a result, few species have persisted which are desirable. Among those which have become established, some have produced disastrous effects on the existing environment and the economy of the people. A regrettable feature, until very recently, has been a neglect to record the facts, with the result that much of the significance of these introduction experiments has been lost to the scientific record.

Birds

According to Phillips (1928), periods of activity in introduction of foreign birds began in the late 1860's. Since then, limited information is available on what was attempted. For a period of 15 or 20 years, unsuccessful efforts were made to introduce species of European song birds, largely through the enthusiasm of German-American bird fanciers and various cage-bird clubs.

In the late 1870's the migratory *Coturnix* quail was the subject of a virtual introduction craze; all attempts were unsuccessful. Little attention was paid to foreign game birds from then until after the successful introduction of Chinese ring-necked pheasants, *Phasianus colchicus torquatus,* into Oregon in 1881. This event triggered great enthusiasm for pheasants, and ring-necks of various origins—including Chinese, Mongolian and English—were set out indiscriminately all over the country. From these plantings, large Chinese pheasant populations have built up in the central, northern and northwestern farmland. At the present time, the species has an extensive range in these parts of the United States (Aldrich and Duvall, 1955).

The gray or Hungarian or European partridge came next and has also enjoyed great success from large shipments liberated just before World War I. These have succeeded in the drier, grain-producing farmland of the extreme north central part of the country after failures elsewhere (Aldrich, 1947).

Fifteen great tinamous, *Tinamus major,* were brought privately from Guatemala in 1923 and placed on Sapelo Island on the coast of Georgia (Phillips, 1928). Additional ones were taken unsuccessfully to Louisiana. In the first locality, during the same period (Phillips, 1928), curassows and chachalacas were transplanted from Mexico. The chachalacas have persisted to the present time, but the other two species disappeared. New efforts with several species of tinamous native to southern South America are now planned under the present Foreign Game Introduction Program described beyond.

The mute swan, *Cygnus olor,* an ornamental species imported frequently for city parks and estates, has gone wild from time to time. One colony which seems to be prospering at present is near Newport, Rhode Island. The little European land rail, *Crex crex,* known as the corncrake, was set free by the Cincinnati Acclimatization Society between 1874 and 1877, but was never found again. Guineafowl were liberated in Georgia and California and achieved temporary success in the latter State about 25 years ago (Phillips, 1928). There are none today.

Black grouse, *Lyrurus tetrix,* and capercaillie, *Tetrao urogallus,* two famous birds of northern Europe, have received considerable attention. A large shipment of black grouse was liberated in 1904 and 1905 on Grand Island in Lake Superior. Others were set out in the Adirondack Mountains of New York State about 1900. Capercaillie were released at New Sweden, Maine, in 1895; on Grand

Island, Michigan, in 1904 and 1905 ; in the Adirondacks of New York in 1906 (Phillips, 1929).

Experimental releases of both species were made on Outer Island, Wisconsin, in 1949 and 1950, as a part of the Foreign Game Introduction Program. They did not succeed (Bump, 1963). Hazel grouse, *Tetrastes bonasia,* were also set out on Grand Island, Lake Superior, in the early 1900's. None of these grouse introductions showed any indication of success.

Interest in the chukar partridge, one of the three foreign game species to become established in the United States, was late in getting started, although five pairs were liberated in Illinois as early as 1893. After 1928, however, interest increased rapidly with numerous trials all over the country until the species became well established in the arid Great Basin foothills in the late 1930's (Aldrich, 1947 and Christiansen, 1954).

The red-legged partridge has received little attention in this country since Lafayette sent the first ones to George Washington at Mount Vernon, Virginia. A few pairs were imported into Illinois in 1896 but vanished the following spring. Recently, the Foreign Game Introduction Program has included this species for extensive trial in the southern parts of the United States.

The black francolin, *Francolinus francolinus,* was imported unsuccessfully into Illinois in 1891. In recent years the Foreign Game Introduction Program has given much attention to this species and the gray francolin, *Francolinus pondicerianus,* and considers them candidates for successful introduction for some areas in central southern parts of this country (Bump and Bump, 1964).

Bamboo partridges, *Bambusicola thoracica,* have been introduced on a large scale in the arid interior sections of this country beginning in 1904, and have been given a fair trial recently under the Foreign Game Introduction Program. All efforts have been unsuccessful.

Reeve's pheasant, *Syrmaticus reevesii,* recently was given a thorough trial by the State Conservation Department in Ohio. The results were not encouraging. The silver pheasant, *Gennaeus nycthemerus,* has been tried unsuccessfully on a small scale in the State of Washington. Kalij pheasants, *Lophura leucomelana,* have been the subject of considerable study, and as a result are recommended for trial introductions under the Foreign Game Introduction Program. Likewise, the red junglefowl, *Gallus gallus,* another forest-inhabiting pheasant, studied intensively in India, has been considered a likely candidate for establishment in game-deficient wooded sections of the southeastern United States (Bump and Bohl, 1961).

Golden pheasants, *Chrysolophus pictus,* have been liberated many times in the country starting with a pair sent to George Washington by Lafayette in 1786. In addition to Virginia, liberation has been in such widely separated places as California, Washington State and Illinois. No success is indicated.

Both the copper pheasant, *Syrmaticus soemmerringii* and the green pheasant, *Phasianus versicolor,* of Japan have had limited trials starting in the Northwest about 1885. Recently, the Foreign Game Introduction Program has given attention to both of these species and the green pheasant has shown signs of becoming established in coastal Virginia.

Sand grouse, *Pterocles exustus,* have been liberated from time to time starting in Washington and Oregon in 1881. Recently, more extensive efforts, under the

Foreign Game Introduction Program, have been made but are not encouraging.

Among the doves, the bleeding heart dove, *Gallicolumba luzonica,* was released around 1924 in the State of Washington, and the European woodpigeon, *Columba palumbus,* between 1910 and 1913 in a park in New York, both without success. The common domestic pigeon or rock dove has, of course, gone wild in many places even outside cities. The Chinese spotted dove, *Streptopelia chinensis,* and ringed turtledove, *Streptopelia decaocto,* have become established in a limited area in southern California, and the latter also in southern Florida.

Among song birds, many attempts at introduction of numerous species have been made mostly for sentimental reasons. The house sparrow, *Passer domesticus* and starling, *Sturnus vulgaris,* have been notorious successes. The European tree sparrow, *Passer montanus,* a close relative of the house sparrow, persists in a small area about St. Louis, Missouri. The skylark, *Alauda arvensis,* and European goldfinch, *Carduelis carduelis,* have been liberated in many places in the United States and have always disappeared. Very recently the spotted-breasted oriole, *Icterus pectoralis,* blue-gray tanager, *Thraupis virens,* and red-whiskered bulbul, *Pycnonotus jocosus,* have apparently become acclimated in the vicinity of Miami, Florida, after escaping from aviaries.

Mammals

Probably none of the terrestrial mammals (except domesticated forms) have been as generally successful as certain game birds and fish. Most introduced mammal species have failed to survive. Of those which did, the majority became destructive and undesirable, such as the house rat, *Rattus norvegicus,* and mouse, *Mus musculus,* the mongoose, *Herpestes* sp. and the nutria, *Myocaster coypus.* As early as 1889, Dr. T. S. Palmer called attention to the risks involved in introducing such species.

When Captain Cook discovered Hawaii, only one terrestrial mammal was present—the Hawaiian rat, presumably introduced by the Polynesians at an earlier date. Today, at least 15 species of land mammals are living in a wild state on the Hawaiian Islands. These include pests such as the black and Norway rats, and house mouse; feral domestic species including the cat, dog, pig, goat and sheep; and wild exotic species, such as the rock wallaby, *Petrogale* sp., the European rabbit, *Oryctolagus cuniculus,* the mongoose, axis deer, *Axis axis,* Columbian black-tailed deer, *Odocoileus hermionus,* pronghorn, *Columbianus antilocapra americana,* and the mouflon sheep, *Ovis musimon.*

Introductions on the King Ranch in Texas have been summarized by Lehmann (1948). On this and other extensive Texas ranches, various exotic game species have been released on the open range in hopes of their becoming established in the wild. Besides several American species from further north, these introductions have included fallow deer, *Dama datna,* blackbuck, *Antilope cervicapra,* nilghai, *Boselaphus tragocamelus,* mouflon, serow, *Capricornis* sp., aoudad, *Ammotragus lervia,* roe deer, *Capreolus capreolus,* sambar, *Rusa unicolor,* and axis deer, These efforts are currently being evaluated by the Texas Wildlife and Parks Department.

One of the earliest game reservations in the United States was the 26,000-acre preserve in New Hampshire established by Austin Corbin in 1880 (Manville, 1964), which is still maintained as a game area. Both native and non-native mammals were introduced. Among the non-native mammals introduced there in the early years were European wild boar, *Sus scrofa,* red deer, roe deer and Himalayan tahr, *Hemitragus jemlahicus.* Today, only the descendants of the boar and elk, *Cervus canadensis,* remain.

Conversely, we have furnished muskrats for introduction to Europe, and gray squirrels, *Sciurus carolinensis,* to England and South Africa, where both have become established and are now regarded as pests. Further, American beaver, *Castor canadensis,* and mink, *Mustela vison,* have gone to Scandinavia; raccoons, *Procyon lotor*, and skunks, *Mephitis* sp., to Russia; and elk to Austria and New Zealand (de Vos *et al.,* 1956).

None of the mammals introduced to North America has proven completely successful and desirable from the viewpoint of our present human population. Some have been more destructive and undesirable than others (Manville, 1962).

The brown rat, *R. norvegicus,* is thought to have originated in Central or Southeastern Asia. This rodent was introduced into the American colonies in 1775 and has since spread to every State. Rats eat millions of bushels of grain each year and carry many diseases.

At the time of the colonization of North America by Europeans, the native red fox, *Vulpes fulva,* apparently occurred only in what is now Canada, Alaska, and the United States roughly north of Pennsylvania. Between 1650 and 1750 red foxes, for hunting purposes, were introduced from England into Virginia and the country further south. They survived, spread, and apparently crossed with the native red foxes to the north. Foxes are occasional destroyers of poultry and are reservoirs of rabies and other diseases (de Vos, *et al.,* 1956).

The European and Russian races of wild boar were introduced into New Hampshire in 1889, and into North Carolina in 1912. They have since spread from these original sites. Some of the Carolina stock were later transplanted to California (1924), and to Hawaii, where a total population of 80,000 was estimated in 1964 (Anon, 1965). As game animals they are favored by some sportsmen. However, they do compete with native species, may do considerable damage to local crops, and are subject to cholera and other diseases.

During our Civil War, a number of camels were introduced for possible use by the Army as draft animals. Several attempts were made to establish them in Texas, Cuba, Jamaica and South America; all were unsuccessful (Goodwin, 1925). The camels introduced into our country survived for many years in our southwestern deserts before finally disappearing.

Between 1891 and 1902, the semi-domesticated Old World reindeer, *Rangifer tarandus,* was introduced from Siberia to Alaska in an attempt to improve the economy of the native Eskimos. At first they thrived and increased, but then declined. Their history in Alaska has been erratic owing largely to a lack of knowledge of proper management procedures. In 1929 a herd of 2400 was sold to Canada, and the offspring of this herd still persist, providing food for the native peoples and thus aiding in the economy of our northern areas. They also have competed with, and tended to hybridize with, the native caribou. Disadvantageously, they damage the delicate Arctic range considerably by overgrazing.

In 1930, 34 musk ox, *Ovibos moschatus,* from Greenland were brought to Alaska. In 1935 these animals were moved to Nunivak Island of the Aleutian archipelago. The herd has grown to more than 400 head. Also, blue fox, *Alopex lagopus,* was introduced into the Aleutians from Siberia and the Kommandorskie Islands many years ago. The foxes now constitute an abnormal source of predation on ground-dwelling birds.

Fishes

With the exception of aquarium fishes, very few exotic species of fish have been brought into the United States. About 1,200 to 1,500 aquarium species have been imported from Africa, Ceylon, China, Germany, Japan, Malaysia, and Central and South America. Only a few of these species have become established in our natural waters (Swingle, 1957).

Deliberate fish introductions for the purpose of improving our fishery can be divided into three different periods:

1. *Before 1887.* During the 1870's, prior to the organization of a Federal agency and various State fish commissions, fish were brought into the United States by private individuals. Although many native species of fishes were transplanted to other sections of our country during this early period, only a few non-native species were imported. These probably included the European carp and the goldfish. Note of these introductions were particularly successful.

2. *1877—1900.* During this period, introductions of foreign fishes were mostly the results of cooperative ventures of Federal and State fishery agencies. During the first few years of operation the U.S. Fish Commission encouraged and assisted the States in organizing State fish commissions. Early efforts of Federal and State fish commissions were concerned with transplanting native species and developed fish culture facilities. Around 1875, attention was given to the possibilities of foreign fish introductions. During the following 25 years, several species of fish were imported including the European carp and the brown trout.

3. *1954—Present.* As a result of the overwhelming success—with rather disastrous results—of the planned introduction of the European carp during the period from 1879 to 1896, Americans developed a great apprehension concerning foreign fish introductions. This feeling persists even today. Within the past 10 years, however, fishery biologists and some sportsmen have considered the importation of foreign fishes which might improve our sport and commercial fisheries. A few species, such as some of the tilapia, have been successfully introduced in selected waters. The early fear still exists and elaborate precautions are taken before any foreign fishes are deliberately released in natural or impounded waters.

The following is a brief account of most of the foreign fish introductions into the United States:

The two most successful introductions were the European carp and the brown trout.

The carp (*Cyprinus carpio*). It is uncertain when the first carp were brought to the United States. It was reported (Cole, 1905), that Captain Henry Robinson, Newburgh, New York, brought carp from France in 1831 and 1832, and that he stocked some in the Hudson River.

Mr. J. A. Poppe, Sonoma, California, brought carp from Germany to California in 1872. Professor Spencer F. Baird, Commissioner of the United States Fish Commission (Cole, 1905), questioned whether or not these were true carp.

Mr. Rudolph Hessel shipped 345 carp to New York on May 26, 1877, and these were taken to ponds in Druid Hill Parks, Baltimore, Maryland. During the spring of 1878, 113 carp were transferred from Baltimore to ponds on the Washington Monument lot in Washington, D. C. During 1879, 12,265 carp were distributed to over 300 persons in 25 States and territories. During 1883, 260,000 carp were distributed to 9,872 applicants in 1,478 counties. By 1897, carp culture was discontinued by national fish hatcheries.

The primary purpose of importing the carp was to provide a food fish for our growing population. Some of the advantages of the carp were reported to be:

1. Their high fecundity and adaptability to artificial propagation.
2. They lived largely on a vegetable diet.
3. They were hardy.
4. They were highly adaptable.
5. They grew very rapidly.
6. They were harmless in relation to other fishes.
7. They populated waters to the fullest extent.
8. They were an excellent table fish.

Carp lived up to some of these expectations. Their fecundity and ability to populate waters was demonstrated in Lake Erie. A few carp were stocked in western Lake Erie in 1883. By 1889, comercial fishermen took 3,633,679 pounds. The carp sold for about one and a half cents per pound. Coincidentally, there was a major decline in aquatic vegetation, particularly *Vallisineria, Sagitteria* and *Zizania.* There was also a decline in the canvasback duck (*Aythya valisineria*) population in western Lake Erie. By 1900, most of the desirable aquatic vegetation was gone as were the canvasbacks. Similar reports were received by the U.S. Fish Commission from duck clubs throughout the United States. There were also reports of serious declines in game and commercial fishes. Although glowing reports on the high food value of the carp were received by the U.S. Bureau of Fisheries from carp recipients, the American public did not accept the carp as a table fish.

The European carp, whether good or bad, had found a home in America. By 1904, it was found in great abundance throughout the country. Thousands, perhaps millions, of dollars have been spent in attempting to eliminate this species from certain waters. Except for small ponds, these attempts have been only temporarily successful.

During the past few years, the Israeli strain of the European carp has been used successfully in controlling vegetation in some farm ponds in the southeastern United States (Neely *et al.,* 1965). It is reported that this strain does not reproduce in ponds nor does it compete with largemouth bass, *Micropterus salmoides* and bluegill, *Lepomis macrochirus.*

During 1962, commercial fishermen took over 30 million pounds of carp. The average wholesale price was about 3 ½ cents - per pound.

The brown trout (*Salmo trutta*). In many American trout waters the brown trout is highly prized as a game fish. It is also highly regarded as a table fish.

The first brown trout were reared in the United States by Mr. Seth Green of the New York State Fish Commission in 1883. About 30,000 trout were hatched from eggs received from Herr von Behr of Germany. The following year, Loch Leven eggs were received from Scotland (Marston, 1896). By 1900, brown trout had been widely distributed in American trout waters through efforts of State and national fish hatcheries. The various subspecies of European brown trout have lost their identity in America and they are all considered to be one species. Although brown trout propagate naturally in many American waters, much of the fishery is maintained through artificial propagation and stocking. Over 1,000,000 pounds of brown trout are reared annually by State and national fish hatcheries.

The major complaint received from sport fishermen concerning the brown trout is that they are more difficult to catch than the native trout. The main advantage of the brown trout is that they can tolerate warmer waters than most native trouts.

In addition to the carp and brown trout, several other species were brought into the United States during the 19th century. These include:

1. Danube salmon (Danube trout), *Salmo hucho:* Mr. Thaddeus Norris, a New York fish culturist, obtained *Salmo hucho* eggs in 1864. Although the eggs hatched, the liberated fry did not survive (Baird, 1874). We are interested in the possibilities of this species. However, its habitat requirements and disease characteristics must be established and determined before further introductions into this country can be accomplished.

2. Goldfish (*Carassius auratus*). Captain Henry Robinson of Newburgh, New York, stocked goldfish in the Hudson River in 1843. During the past 100 years almost every American household has had one or more goldfish as pets at one time or another. These are usually kept in bowls, aquaria and outside garden pools. Many goldfish have found their way to natural waters via kitchen sink drains or by the overflow of garden pools. They are found in natural waters throughout the United States, but are rarely found in large numbers. They are commonly cultured as bait minnows. This species rarely reproduces in farm ponds and is the only recommended bait minnow for farm pond use in some of the States. Nevertheless, several hundred thousand pounds are taken annually by Lake Erie commercial fishermen.

3. Tench, *Tinca tinca.* The tench was introduced from Europe late in the 19th century as forage fish. Although it has been widely stocked it has only survived in a few waters, without any noticeable ill effects on the native fish fauna or habitats to the present time.

4. Golden orf, *Idus idus.* This species was also introduced from Europe around 1894, and although it was widely stocked, it has never done well in our natural waters.

5. Bitterling, *Rhodeus sericeus.* The bitterling was introduced into the United States around 1925 and is apparently established in one stream, Sawmill River, in New York (Moore, 1957). No ill effects have been noted, although the fish may have established a form of commensal relationship with molluscs in the stream.

In addition to the preceding, during the 20th century several species of fish were brought into the United States for experimental purposes. These include several species of *Tilapia. Tilapia mossambica* were brought to Hawaii from Singapore in 1951. This species is well established in ponds and reservoirs on the major islands of the Hawaiian group where they are utilized as food fish. *Tilapia* are also used in the Island area as a bait fish for the skipjack tuna, *Euthynnuspelamis* (Hida *et al.,* 1962). Although *Tilapia* were previously brought into our country as aquarium fishes it was not until 1954 (Swingle, 1960), that experiments in using members of this genus as pond fish in the Southern States were begun at Auburn University in Alabama. *Tilapia* are usually overwintered inside hatchery buildings. The fry are stocked in the spring when water temperatures reach about 60 degrees Fahrenheit. Excellent success has been obtained in the production of *Tilapia* as a pond fish. The most common species used are *Tilapia mossambica, T. nilotica,* and the Malacca hybrid of Tilapia. In southern Florida, *Tilapia* have overwintered out-of-doors. One African species, *T. heudeloti* (Synonym *T. macrocephala*), apparently escaped from captivity and is well established in the Hillsborough Bay area on the west coast of Florida (Springer and Finucane, 1963). At present it is a rather aggressive, but not destructive, addition to the aquatic fauna of the area.

Other species which were recently imported for experimental pond and lake use include the grass carp, *Ctenopharyngodon idellus,* obtained from Southeast Asia, the peacock bass, *Cichla ocellaris,* from South America, and the Ohrid trout, *Salmo ohrid,* from Yugoslavia.

The South American suckermouth armored catfish, *Plecostomus* sp., was found in the San Antonio River, San Antonio, Texas, in 1964 (Barron, 1964). They apparently escaped from a pool in the San Antonio Zoo where they were stocked in 1956 to control filamentous algae. This area of the river is fed by warm springs, and winter water temperatures are slightly above the 62^0 F. limit for this fish. The piquito, a poecilid, *Belonesox belizanus,* a native of Central America, is also found in the same section of the San Antonio River.

Several imported aquarium and bait fishes have become established in limited areas. These include the Oriental weatherfish (dojo), *Misgurnus anguillicaudatus,* which was found in a Michigan pond (Schultz, 1960). It was reported (Deacon, *et al.,* 1964) that convict cichlids, *Cichlasoma nigrofasciatum,* were established in Lake Mead and other areas in Nevada. Other foreign species recently found in Nevada are guppies, *Lebistes reticulatus,* shortfin mollies, *Mollinesia mexicana,* and platys, *Xiphophorus maculatus.* Mollies have also become established in parts of Florida.

For the most part, these introduced species are limited in their distribution by finding their required habitats only in scattered, isolated areas. Within these confines, the exotics have restricted their diets to small aquatic organisms and have not been overly destructive or competitive to the present time.

Amphibians and reptiles

In addition to the introductions of birds, mammals and fish described in this paper, there have also been introductions of amphibians and reptiles. These have probably been accidental and none can be said to have been the result of biological study. Many go unnoticed and perish. Some may exist for a time, but few have survived to become a part of the animal community in which they were released. Snakes and lizards often escape from travelling zoos and animal shows. Tropical varieties usually do not survive the first winter in a temperate or cold climate. Also, chances of the two sexes meeting in the strange environment are even more remote. Possibilities of exotic species surviving are much better in southern latitudes and a number of amphibians and lizards are reported as occurring in the State of Florida resulting from chance introductions.

Consultation with specialists of the United States National Museum, reveals that some 14 species and subspecies of lizards have found their way to Florida's mainland and now seem to be established there. Several of these were originally found in the Caribbean area. Also, four amphibians, principal of which is *Bufo marinus,* the marine toad, have become established in Florida. This species is giving herpetologists some concern because it is highly competive with our native frogs and toads and appears to be reducing the number of some beneficial species.

THE MODERN PROGRAM

Recent and current programs have been designed primarily to augment the natural stocks of game animals in the United States, particularly birds. Although America has always had a rich outdoor legacy, originating in early colonial days, the demand for recreation through fishing and hunting has grown tremendously.

Nationwide surveys of hunting and fishing conducted in 1955 and 1960, show the scope and magnitude of fishing and hunting in America:

« A detailed study of participation in these sports, including types of fishing and hunting, expenditures, mileage traveled and the like, was made of the more active sport fishermen and hunters, who for the most part, were licensed or, if unlicensed, either took part in these sports on several occasions or reported at least a modest expenditure for these activities. This study—the *National Survey of Fishing and Hunting*—revealed an estimated 30 million sport fishermen or hunters in 1960, some 23 percent of the population 12 years old and over. These more substantial participants reported around 650 million recreation days of fishing and hunting and an expenditure of close to 4 billion dollars on these pastimes. As compared with a similar survey conducted in 1955, the number of these sportsmen had increased by over 5 million and their expenditures by 1 billion dollars. »

The preceding illustrates the interest in these sports by the American public and also shows the role they play both personally and economically in the lives of a large portion of the population.

As the responsible federal agency, the Department of the Interior, Bureau of Sport Fisheries and Wildlife, is vitally concerned with introductions of foreign fauna for several reasons. We are obligated to protect our citizens against harmful effects on existing natural resources by unplanned foreign introductions, and on the other hand, to supplement these resources with desirable additions from abroad. We recognize the fact that this is a difficult ecological problem.

A growing awareness is developing that attention must be paid to all aspects of proposed actions affecting natural resources, particularly those involving subtle biological effects.

This awareness was slow in starting. Unfortunately, in the economic and intellectual growth to our present status there were many mistakes involving exploitation of plants and animals. Since the colonists first arrived, our country lost the passenger pigeon, the heath hen, the Carolina parakeet, the sea mink and many others—all bitter commentaries on a failure to understand the importance of conservation practices.

Today, the conservation movement is stronger in our country. Once again, we can see the bison, the whooping crane, the trumpeter swan, the sea otter, the fur seal and other species that were brought to the verge of extinction—but saved. For them, conservation consciousness came in time and they survive through good management and understanding of their ecological requirements.

We must contend with many factors resulting from constantly changing land use. Our population is increasing very rapidly and land, formerly providing habitat for certain species, is being converted into great urban areas. The so-called « clean farming » with new types of farm equipment, heavy grazing, and chemical control of weeds all cause changes which may not meet the needs of the native fauna. Thus, species which thrived under one set of environmental conditions may not survive when these are changed. Consequently, there is a decrease in game abundance and, in some instances, of the species withdrawn from the former range. One example is the prairie chicken, formerly resident over a large area from the North Central States south to Texas. Initially responding favorably to very limited and primitive farming which first invaded its native grasslands environment, it declined drastically after overgrazing and use of its range for modern agricultural purposes, and occasional over-hunting.

There are large areas in the United States which have never been occupied by more than one or two species of game birds and, in some cases, none at all. We have focused our attention on these regions. One example is a large part of the arid West that was sparsely stocked with native game birds until the chukar partridge was introduced. Now in this region, excellent upland game hunting is available since the chukar has survived as a successful resident in some of the arid rim rock and foothill country.

In general (McAtee, 1929), it appears that the wildlife of the Old World has shown far greater ability than that of the New to survive despite man's occupation of the land. It is logical, therefore, when seeking species for transplanting to a well populated country to utilize those species that have been tested and tempered by countless centuries of close association with man.

We recognize the hazards in introductions and have attempted to avoid them while also trying to meet the demands for additional wildlife resources in certain areas. We have established certain criteria that must be considered before a candidate species is released into the wild. Questions which must be satisfied, include:

1. Does a niche occur in a particular environment that is devoid of a native species?

2. Is there a habitat type in which native species are not sufficiently abundant to provide desired harvests?

3. Do habitats exist which have been modified by agriculture and other human activities to the point that they can no longer support native species?

4. Will a species threatened with extinction in its native range find a similar and suitable habitat in a different geographic area without posing a threat to native species already occupying that habitat in the new area?

In the past, candidate species for introduction have been sought and their characteristics assessed for value in supplying additional hunting recreation. Another conceivable objective has received some attention: use of the Introduction Program to assist in the preservation of rare and endangered species. The great upsurge of the public's consciousness over its responsibility for preventing any more species from becoming extinct gives greater emphasis to this objective.

A special concern is the effects of introductions on the ecology of various environments in which the new species are to be tried. We evaluate ecological-niche relationships of both existing and candidate species to determine their similarities and differences, and to provide a basis for estimating the effects of introductions on the native fauna. We are aware that a new species may serve as a reservoir for new diseases or parasites detrimental to native species, and that it may offer serious competition to native species or possibly be a predator in the new environment. Lastly, and not the least important, will it, because of possible close genetic relationship, interbreed with a native species, thus upsetting the genetic adaptation to its environment acquired through many generations of natural selection?

Economic implications must be carefully considered. The exotic starling and house sparrow do millions of dollars worth of crop damage each year, and the domestic pigeon or rock dove, has gone feral and become a pest. In our cities, all three birds foul public buildings, and their droppings are loci for diseases which affect humans.

Game production habitat in the United States is decreasing under the impact of human activities such as clean farming, scientific forestry, overgrazing, drainage, pesticides, declining soil fertility, and urbanisation. All contribute to a decline in the abundance of native game birds and limit their distribution.

We conducted a survey (1955), through game departments in the fifty States who reported on the amount, distribution, types and characteristics of understocked habitats. The results indicated that over one-fifth of the land area of the United States is understocked with game species. Some areas had no native game birds. In others, game bird populations were very low.

For the Foreign Game Introduction Program these are the target areas. They afford the possibility of locating and introducing an adaptable exotic game bird that might thrive without creating serious problems for man or the resident wildlife. There are limited risks involved, but there are also very substantial rewards. For example, in a normal year our hunters harvest 5° million game birds, including 10-12 million pheasants, 4 million gray (Hungarian) partridges, and 1 million chukars. These provide nearly thirty percent of the total game bird harvest. As far as has been determined, none of the three are incompatible with native species. Also, the first two are tolerant of agricultural practices and the third inhabits an area where only a scattering of native game birds is found. Without them, there would be substantially less recreational hunting in the United States.

Our program is particularly concerned with birds. It is known as the Foreign Game Introduction Program. It originated in 1948 and has two objectives:

1. To discourage unwise game bird introductions by making careful biological evaluations in advance of any importations.
2. To meet a real recreational need by filling vacant niches with attractive, adaptable game species.

This program is a cooperative effort between the various State game departments, the Federal government, and a private concern, The Wildlife Management Institute.

Studies are made to define world analogues for continental United States areas, and candidate game species are selected. We perform on-the-spot study of habitats, characteristics and requirements of candidate species, and coordinate this with State game departments for trial consideration. Biologists are assigned overseas to select the candidate species. We require intensive study in the foreign country to define the habits, habitats, hazards and potential of the species, particularly with regard to its chances of survival in the United States without competing unduly with existing native species or becoming a pest. Finally, it is necessary to secure, ship and quarantine adequate numbers of birds for field release with cooperating States in habitats believed to be suitable.

Since 1950, more than 100 varieties of foreign game birds have been considered. Of these, 18 have been selected for intensive study before trial release in 45 States.

Thus far in the appraisal of overall program results, there have been indications of both success and failure. In addition to the two Iranian pheasants already mentioned, black and gray francolins have demonstrated an ability to survive, reproduce and increase in release areas. Conversely, the Indian sandgrouse, *Pterocles exustus hindustan*, and Reeve's pheasants have not succeeded. Six other species are holding their own sufficiently to justify guarded optimism.

Progress in the studies of the candidate species in their native lands, the gathering of stock of promising exotics, and the propagation and liberation of stock of the chosen species by the cooperating States has been described by Bump and Bohl (1964), Bump and Bump (1964), and Christensen and Bohl (1964).

The unplanned, hit-or-miss character of almost all of the early introductions was the prime reason for their failure. The people who desired to acclimatize the foreign species to our shores did not have the scientific acumen to fully evaluate differences in climate and habitat between their old and new countries. Many species were introduced into areas completely different from their original homes, with the result that they failed to " take " and disappeared. Also, the long periods required for sea transit without necessary fresh foods and proper caging caused animals and birds to arrive in a weakened physical condition, thus reducing their chances of survival.

Recently, an additional facet became apparent in foreign introductions. There exists within a species variant populations or subspecies which have differing transplant capabilities. For example, the subspecies of ring-necked pheasant from northern China, which was so successful in the northern United States, failed in our southern States despite numerous attempts; however, the subspecies from Iran has been tried in Virginia and gives strong indication of being successfull.

Dr. Gardiner Bump, biologist in charge of our introduction program, has listed reasons for the possible failures of promising candidate species. These can be summarized as follows:

1. Failure to liberate in the proper habitat or failure to use proper methods in liberations.
2. Poor physical condition of the liberated game precluded survival.
3. Failure to properly condition game farm raised birds before liberation.
4. Failure to release sufficient numbers of specimens to ensure a breeding potential over a period of time.
5. Failure to ensure protection from losses resulting from predators or hunting pressure.

In addition, the time that is required to assess the success or failure of an introduction activity is often not realized. Thus, success of a program may entail as much as five to twenty years before an evaluation can be made regarding any specific species. We know the ring-necked pheasant required years and many tries before it finally " took ". For this reason, we have, perforce, been guarded in our statements regarding our efforts.

The program has been successful in that many of the fears of critics have been proven to be groundless. None of the candidates released have usurped the normal ranges or habitats of native species, nor have our releases brought into the country game diseases which were disastrous to native species. Further, there has not been any widespread hybridizing with resident game to the disadvantage of native populations. Ecological dovetailing into the prospective habitat has been the major factor in success of our activities.

From its start the program has been controversial. Some look on efforts with exotics as unnecessary and unwise. Also, there is the aesthetic objection to mixing foreign and native faunae. And, in addition, there is the more practical concern about adding foreign forms of life without knowing the biological and economic consequences.

On the other hand, many parts of our country have changed irreversibly as a result of human population movement and consequent agriculture and industry. In these, resident native species have become extirpated because they were intolerant of habitat changes. The foreign introduction program takes cognizance of this and seeks to bring in species that can survive in such areas and become established.

REFERENCES

ALDRICH, J. W. (1947). *The Hungarian and Chukar Partridges in America* U.S. Department of the Interior, Wildlife Leaflet 292, p. 1-10.

ALDRICH, J. W. and DUVALL, A. J. (1955). *Distribution of American Gallinaceous Game Birds.* U.S. Fish and Wildlife Service, Circular 34, 30 p.

ANONYMOUS (1965). *Big Game Inventory for 1964.* Wildlife Leaflet 470, Bureau of Sport Fisheries and Wildlife. U.S. Department of the Interior.

BAIRD, SPENCER F. (1874). *Report of the Commissioner of Fish and Fisheries for 1872 and 1873.* U.S. Department of Commerce, 808 p.

BUMP, G. (1963). History and Analysis of Tetraonid Introductions into North America. *J. Wildlife Management* 27, p. 855-866.

BUMP, G. and BOHL, W. H. (1961). *Red Junglefowl and Kalij Pheasants.* U.S. Fish and Wildlife Service. Special Scientific Report - Wildlife No. 62, 41 p.

— — (1964). *Summary of Foreign Game Bird Propagation and Liberation, 1960 to 1963.* U.S. Fish and Wildlife Service, Special Scientific Report - Wildlife No. 80, 48 p.

BUMP, G. and BUMP, J. (1964). *A study and Review of the Black Francolin and the Gray Francolin.* U.S. Fish and Wildlife Service, Special Scientific Report - Wildlife No. 81, 86 p.

CHRISTENSEN, G. C. (1954). *The Chukar Partridge in Nevada.* Nevada Fish and Game Commission, Biol. Bull., 1, 77 p.

CHRISTENSEN, G. C. and BOHL, W. H. (1964). *A Study and Review of the Common Indian Sandgrouse and the Imperial Sandgrouse.* U.S. Fish and Wildlife Service, Special Scientific Report - Wildlife 84, 71 p.

COLE, LEON J. (1905). *The German Carp in the United States.* Report, Bureau of Fisheries, 1904. U.S. Department of Commerce, p. 523-641.

DEACON, J. E., CLARK HUBBS and ZAHURANEC, B. J. (1964). Some of the Effects of Introduced Fishes on the Native Fauna of Southern Nevada. *Copeia,* No. 2 (June), p. 384-388.

GOODWIN, G. G. (1925). The First Living Elephant in America. *J. Mamm.,* Vol. 6, No. 4, p. 256-263.

GRINNELL, J. (1925). Dangers of Introduction. *Science* No. 1590, p. 621-623.

GULLION, G. W. (1965). A Critique Concerning Foreign Game Bird Introductions. *Wilson Bull.* 77, p. 409-414.

HIDA, T. S., HARADA, J. R. and KING, J. E. (1962). *Rearing Tilapia for Tuna Bait.* U.S. Fish and Wildlife Service. Fishery Bulletin 198, 20 p.

LEHMANN, V. W. (1948). Restocking on King Ranch. *Trans. N. Amer. Wildl. Conf.,* Vol. 13, p. 236-242.

MCATEE, W. L. (1929). *Game Birds Suitable for Naturalization in the United States.* U. S. Department of Agric, Circular 96, p. 1-24.

MANVILLE, RICHARD H. (1962). *The Nutria in the United States.* Wildlife Leaflet 445, Bureau of Sport Fisheries and Wildlife, U.S. Department of the Interior, 4 p.

— (1964). *History of Corbin Preserve.* Smithsonian Report for 1963, p. 427-446.

MANVILLE, RICHARD H. and STANLEY P. YOUNG (1965). *Distribution of Alaskan Mammals.* Circular 211, Bureau of Sport Fisheries and Wildlife, U.S. Dept. of the Interior.

MARSTON, R. B. (1896). *The Brown Trout* (*Salmo fario*). 1st Annual Report, Commissioners of Fisheries, Game and Forests, New York, p. 141-144.

MOORE, G. A. (1957). Fishes. Part II of *Vertebrates of the United States.* McGraw-Hill Book Co., N. Y., p. 31-210.

NEELEY, W. W., DAVISON, V. E. and COMPTON, L. V. (1965). *Warm-water Ponds for Fishing.* U.S. Department of Agriculture, Farmer's Bulletin 2210, 16 p.

NEWSOM, WILLIAM MONYPENY, (1937). Mammals on Anticosti Island. *J. Mamm.,* Vol. 18, No. 4, P. 435-44-2.

PALMER, T. S. (1899). *The Danger of Introducing Noxious Animals and Birds.* U.S. Department of Agriculture, Yearbook for 1898, p. 87-110.

PERRY, JOHN (1966). *The Management of Exotic Mammals on Texas and Mexican Ranches.* National Zoological Park, Washington, D.C. Staff Document (Private Communication).

PHILLIPS, J. C. (1928). *Wild Birds Introduced or Transplanted in North America.* U.S. Department of Agriculture, Tech. Bull. 61, p. 1-64.

SCHULTZ, EDWARD E. (1960). Establishment and Early Dispersal of a Loach, *Misgurnus anguillicaudatus,* (Cantor), in Michigan. *Trans. Am. Fish Soc,* Vol. 89, No. 4, p. 376-377.

SPRINGER, V. G. and FINUCANE, J. H. (1963). The African Cichlid. *Tilapia heudeloti* Dumeril, in the Commercial Fish Catch of Florida. *Trans. Am. Fish Soc.* Vol. 92, No. 3, p. 317-318.

SWINGLE, H. S. (1957). Report of Committee on Importation of Fish and Fish Eggs. *Trans. Am. Fish Soc,* Vol. 85 (1955), p. 309-312.

— (1960). Comparative Evaluation of Two Tilapias as Pond Fishes in Ala., *Trans. Am. Fish Soc,* Vol. 89, No. 2, p. 142-148.

U.S. Bureau of Land Management. *Public Land Statistics,* 1962, Washington, G.P.O.; 1964, P. 3.

University of Michigan, Department of Conservation, *Hunting in the United States: Its Present and Future Role.* Report to the Outdoor Resources Review Commission. Washington, G.P.O., 117 p. (ORRRC Study Report 6).

DE VOS, ANTOON, RICHARD H. MANVILLE, and RICHARD G. VAN GELDER (1956). Introduced Mammals and their Influence on Native Biota. *Zoologica,* Vol. 41, part 4, p. 163-194.

COMMENTS

J. Berry (U.K.) expressed surprise that the European brown trout can tolerate warmer waters in the United States than can American species. In his experience, admittedly limited, the American rainbow trout in Scotland was more tolerant of high temperatures and of pollution.

D. Hey (South Africa) reported that experience in South Africa would tend to confirm the observations of Dr. Berry, though the brown trout often did better in the peat-stained streams of the western Cape Province. *J. S. Gottschalk,* replying, suggested that part of the explanation could be that there were undoubtedly different genetic strains involved in the representatives of the species which had been introduced in various parts of the world.

INSECT INTRODUCTIONS AND BIOLOGICAL CONTROL

by

H. ZWÖLFER

Commonwealth Institute of Biological Control
European Station
Delémont, Switzerland

When, in the course of biological control operations, an animal species, usually an insect, is introduced into a foreign country, this is done specifically to exploit its possible influence on other organisms. Interest does not centre on the introduced species itself but on the synecological consequences of its introduction. In this respect, introductions made by biological control workers differ from introductions made with the object of enriching the fauna of a country. In both cases, however, the introduced organism, once established, will be freed in general from further manipulation; hence a great responsibility is involved in such introductions. It is necessary that the exact aim of the introduction be well-defined, that there be a carefully prepared strategy, and that an estimate be made of the possible side-effects of the introduction. These three aspects will be discussed here. Since the great majority of control agents used hitherto in biological control are insects, only this group will be considered.

I. The goal of the introductions

In biological control work, the two objectives in insect introductions are: *a*) to reduce, with the help of the introduced organisms, a pest insect or noxious weed to a level at which it does not cause economic damage; *b)* to stabilize the equilibrium position of the pest species at a low level. In this respect biological control by introduced insects is different from other control measures, which either tend to eradicate the pest (e.g. sterile male technique) or which have to be repeated at certain intervals (use of insecticides, herbicides, etc.). The steadily-increasing number of successful cases of biological control of pest insects and weeds by imported entomophagous insects demonstrates that in many instances the above-mentioned goals can certainly be reached. DeBach (1964) has published a careful estimate, which showed that in California alone net savings to agriculture as a result of successful biological control projects amounted to over $ 110,000,000 during the period 1923-1959. These savings were achieved by the introduction of beneficial insect species. The successes of biological control in California and in many other parts of the world prove that the introduction of beneficial insects is a realistic and promising approach to the control of pests and weeds.

Another consequence of biological control, which cannot be measured by net savings, but which is nevertheless important, is the fact that it may considerably reduce the number of applications of insecticides or herbicides needed to bring a pest under economic control (Simmonds, 1964). With regard to the general principles of nature conservation and the preservation of animal and plant life at a given site, biological pest control and biological weed control offer somewhat different prospects. The biological control of an insect pest by introduced parasites or predators may prevent damage (e.g. defoliation of forest trees, etc.) and restore the balance of the ecosystem concerned. A recent example of this is the successful control of the winter moth, *Operophtera brumata* L., in eastern Canada by introduced insect parasites (Embree, 1965).

Biological control of a single insect pest involves hardly any disadvantage from the view-point of nature conservation. On the other hand, biological control of a weed by introduced phytophagous insects may have a profound effect upon a number of plant species and therefore upon the whole ecosystem. In contrast to the case of an insect pest, a so-called noxious weed may offer ecological benefits under certain conditions and at certain localities. The noxious nature of a weed is therefore more ambiguous than that of an insect pest and more conflicting interests may become involved in weed control.

Goldenrods (*Solidago* spp.) introduced from North America into Europe illustrate this situation. A number of species have become naturalized in Europe, and in certain regions they have become serious pests in forest nurseries. Special studies undertaken in Canada (M. Capek and others, personal communication) revealed a number of beneficial insects which show promise for the biological control of *Solidago* spp. in Europe. However, beekeepers are highly interested in these naturalized goldenrod populations, and some botanists think that the advantage of goldenrod in covering and protecting the soil in relatively dry localities compensates for its disastrous effect in forest nurseries (Dr. H. Hügin, personal communication). Similar conflicting situations exist in California with regard to the star thistle, *Centaurea solstitialis* L., in Hawaii and Mexico with *Opuntia* spp., and in New Zealand with gorse, *Ulex europaeus* L. (Huffaker, 1959). In this last example, the conflicting interests resulted in a special policy of biological control: only a seed-destroying insect, the Curculionid, *Apion ulicis* F., was introduced, aimed at controlling only the seeding and spread of gorse. The introduction of this weevil resulted in the destruction of up to 98.67% of the seeds but the goal — to stop the spread of gorse — was not reached (Huffaker, 1959).

II. The strategy of the introductions

The policy of insect introductions in biological control experiments is not only dependent on the actual goal, which should be reached as nearly and as quickly as possible, but on two other principles as well: *a*) the introduction must not have harmful side-effects, and *b)* as far as possible, the introduction should be carried out in such a way that information can be obtained as to how the introduced insect species reacts to the new environment and the new host populations. Only a few aspects of these principles to be considered in the introduction of useful insects in biological control operations can be mentioned here.

1. *The avoidance of risks*

With the introduction of entomophagous insects into foreign countries risks are comparatively small, if it is certain that the species concerned are not hyperparasites, i.e. parasites which attack other parasites.

In a number of cases, primary parasites may also act as facultative hyperparasites. Thus, the Ichneumonid, *Itoplectis maculator* F., was observed to attack both the European fir budworm, *Choristoneura murinana* Hb., and some of its larval parasites. One of these, the potentially important *Cephaloglypta murinanae* Baur., is distinctly preferred to the budworm by the Ichneumonid (Zwölfer, 1962). This means that an introduction of *I. maculator* as a control agent against *Choristoneura* spp. cannot be recommended.

The introduction of entomophagous insects occasionally conflicts with biological weed control. A well-known case is that of *Cryptolaemus montrouzieri* Muls., a Coccinellid which has been introduced into South Africa against pest coccids, and which attacked *Dactylopius indicus* Green, a cochineal insect which had been introduced as a promising control agent of *Opuntia* (Huffaker, 1959).

Much greater risks are involved in the introduction of phytophagous insects against noxious weed species, since such insects, if not sufficiently host-specific, may become pests of crop plants or other useful vegetation in the area of introduction. This problem has been discussed by Huffaker (1959), Wilson (1964), and others. The best way to preclude the introduction of insect species which may show harmful side-effects with respect to cultivated plants, is to demonstrate that the phytophagous species being considered for introduction has a predictable host pattern which does not include plant species of economic importance (Harris, 1964).

2. *The problem of multiple introductions*

In connection with problems where several suitable biological control agents are available for introduction into a foreign country, the question arises whether several species should be introduced simultaneously, or whether additional species should be introduced only if the first introduction fails or proves unsatisfactory. As discussed by Smith (1929), Thompson (1929), Franz (1961), DeBach (1964) and others, a control complex composed of several species may cover a broader ecological range and may provide better compensation against disruption of control, particularly that arising from changed conditions. A number of examples from the practice of biological control show that a complex of several beneficial insects may give better control than a single species. On the other hand, a number of authors (e.g. Turnbull & Chant (1961), Watt (1965), Varley (1959)) emphasize the possibility that an efficient biotic control agent might be handicapped by competition with less efficient species. In such cases, multiple introductions might give results inferior to that achieved by the introduction of a carefully choosen single species. A number of observations possibly support this hypothesis (Zwölfer, 1963).

In Fiji, the coconut moth, *Promecotheca reichei* Bal., was well controlled by native entomophagous insects until the accidental introduction of an entomophagous mite, *Pyemotes* sp., modified the composition of the host population. Whilst this consisted formerly of overlapping developmental stages, the attack of the mite transformed the population into a " one-stage condition ". This allowed the host to escape its native enemies and to become a pest, which had to be controlled by the introduction of additional entomophagous insects (Taylor, 1937).

The controversy over the problem of multiple or single introductions demonstrates that much research is still needed to solve the question of the optimal structure of biotic control systems. Generalizations are probably only of little value. Each biological control project requires studies on the synecological interactions of the biotic control agents before any policy of introductions can be established.

3. *The sequence of introduction*

If a decision in favour of a multiple introduction has been taken, it is preferable to introduce one species after another rather than simultaneously and to start with those control agents which in the area of origin are inferior in the case of direct competition with other entomophagous insects (Franz, 1961). That is, the most highly specialized species should be introduced first.

Recent investigations by our staff have shown that, in many native parasite complexes, highly specialized parasites cannot successfully compete with other less specialized forms. When such a successfully competing but not very specialized parasite is introduced and established first, it may be very difficult or even impossible later to establish the specialized species (Turnbull & Chant, 1961 ; Pschorn-Walcher, unpublished). Such situations, which are the consequence of overhasty parasite introductions, preclude the chance to learn how the specialized parasite species would react to a new environment where it is not exposed to competitors and hyperparasites, and may also preclude the artificial synthesis of a control complex with an optimal efficiency (Pschorn-Walcher, unpublished).

4. *Origin and quality of the introduced insects*

It is commonplace that every species consists of populations which show differences in their genetic constitution. When transferred into a new environment, new selective forces will operate upon the gene pool of the introduced population. To facilitate the process of local adaptation by selection, it may be useful to introduce a variety of populations from different areas of origin and these should be liberated at different release-points. It is a principle generally accepted by biological control workers that chances of a successful establishment of beneficial insects in a new area are greater if the material originates from localities with both similar abiotic and biotic conditions (Pschorn-Walcher, 1956).

In a number of biological control projects the beneficial insects selected for introduction are subject to a phase of mass-breeding before they were liberated in the new area. From an economic point of view mass-breeding may be a very convenient procedure to obtain large number of individuals for release. There is, however, a certain risk that extended laboratory propagation could entail a detrimental selection pressure on the population (Turnbull & Chant, 1961). Some field observations suggest that under certain circumstances the introduction of field-collected material may give better results than the release of material propagated in the laboratory (Karny, personal communication). An important point in biological control is the selection of special strains or races of beneficial insects (Simmonds, 1963). Among entomophagous and phytophagous insects a number of cases are known where a species contains races or strains with different host-ranges or host-preferences (DeBach, 1964) and there are indications that such intraspecific ecological differences are much more common than is generally realized among entomologists.

Other racial differences concern the immunity of a given host to a given parasite species, or the capacity of the parasite to overcome this host immunity. This is well-known in the case of the larch sawfly, *Pristiphora erichsonii* Mtg., and its Ichneumonid parasite, *Mesoleius tenthredinis* Morley (Muldrew, 1953). It should not, however, be thought that the biological control of a pest cannot be achieved if unfavourable races or strains of a beneficial insect species have by chance been chosen for introduction.

5. *Numbers of release-points and release-numbers of insects*

If sufficient insect material is available, every attempt should be made to select sufficient release-points to cover any possible range of host variation as well as variation of environment (Turnbull & Chant, 1961). This postulate is supported by much experience in connection with the introduction of many beneficial insect species. A promising beneficial species may fail to become established in a number of apparently suitable areas, even though it is successful in others (Simmonds, 1955).

The number of individuals which should be liberated at a single release point should be sufficient to allow the start of an initial colony. They will depend upon the systematic position of the beneficial insect and its mode of propagation (amphimictic, parthenogenetic), but also upon the density of the host population. Successful establishment of beneficial insects has been achieved with as little as 10 individuals (Turnbull & Chant, 1961). In the modern concept of biological control there is a trend to reduce the numbers of insects released at one locality and to increase the number of release-points, as well as the period of years during which releases are made.

There is an interesting hypothesis of Mayr (1963) which should be mentioned in connection with the problem of the optimal release numbers. Mayr states that genetic homeostasis is much more developed in large, open populations, where the " process of local adaptation by selection " may be continually " disrupted by the immigration of alien genes and gene combinations from the interior of the species range ". Closed, isolated populations of founders of a new colony lack this buffering effect of a rich gene pool. " The smaller the starting populations, the greater the degree of indeterminacy ", and hence the chances of a genetic change, which may allow the population to enter new ecological niches and to be successful there. This " founder principle " is well illustrated by a large number of animal introductions where extremely small initial colonies gave rise to very successful populations.

III. Ecological reactions between the introduced insect and the new ecosystem

If an introduced insect species becomes successfully established in a new environment it may induce ecological " chain reactions ", but it may also be largely controlled by the new ecosystem. Only a few aspects of these manifold interrelationships can be discussed here.

1. *Reactions of the host population*

If the biological control by an introduced beneficial insect is successful, then the equilibrium position of the pest population will be reduced to a sub-economic level. As already mentioned, this may, especially in the case of biological weed control, affect the whole ecosystem. Examples of such ecological chain reactions and spectacular modifications of an ecosystem are the biological control of *Opuntia* in Australia, or of *Hypericum* in the western United States. In California the introduced Chrysomelid *Chrysolina quadrigemina* Suffr. reduced the populations of *Hypericum perforatum* L. to a level of less than 1 % of its former density. Following this drastic reduction a number of other factors (climate, soil, etc.) gained an increased influence which controlled the weed, whilst *C. quadrigemina* the " key governing agent " is now apparently of relatively little importance (Huffaker & Kennett, 1959).

The introduction of *C. quadrigemina* also resulted in an interesting apparent change in the ecological preference of *Hypericum.* Whilst during the precontrol period *H. hypericum* showed a distinct preference for sunny, open areas, the activity of *C. quadrigemina* favours the survival of *Hypericum* at shaded localities. Hence the erroneous impression may now be obtained that the Californian *Hypericum perforatum* is a shade-loving plant (Huffaker, 1959).

As yet it is not known whether such a differential control effect of an introduced beneficial organism will cause the selection of special strains of the host. There is, however, one case where a strong selective influence of an introduced parasite on a host population is claimed: it is assumed that in North America the introduced Ichneumonid, *Mesoleius tenthredinis,* was the selective agent which transformed the formerly susceptible population of *Pristiphora erichsonii* into a strain resistant to parasitic attack (Muldrew, 1953).

2. *Controlling influence of the new ecosystem*

An analysis of the failures of biological control projects has revealed a broad range of checks which may operate on the introduced beneficial insect. One of these adverse factors is often the climate, which either directly affects the introduced insects by winter mortality, summer drought, etc., or which influences the phenology of the host in a way that reduces the synchronization between the host and its control agent. Such a poor synchronization, due to climatic factors, made *C. quadrigemina,* the efficient control agent of *Hypericum perforatum* in California, rather unimportant in western Canada (Harris, 1962). According to recent findings by Harris (1965) there is evidence that, following a period of from 6 to 14 years selection in the new environment, *C. quadrigemina* is now much better adapted to the local conditions in western Canada.

The introduction of entomophagous insects into a new area sometimes fails because the new ecosystem does not offer alternate hosts which are a prerequisite for the survival of host-alternating (heteroxenous) parasites and predators. Tadic (1958) claims that the failure to establish neartic parasites of the fall webworm, *Hyphantria cunea* Dr., in Yugoslavia was caused by such an absence of physiologically suitable and accessible alternate hosts in the area of introduction.

Probably the most important check by the new ecosystem on the introduced insect is formed by biotic agents, i.e. predators, parasites, and diseases. Such an interference by native predators and parasites has presumably restricted the results of biological control against insect pests and noxious weeds in many cases. Only two examples will be cited: in Bermuda native lizards attacked introduced Coccinellids, thus interfering with the biological control of scale insects on the Bermuda " cedar" (Simmonds, 1958); in South Africa, a native and an introduced Coccinellid controlled an introduced Coccid species, which showed promising properties as a control agent of *Opuntia* (Huffaker, 1959).

3. *Competition between ecologically homologous species*

In a recent study DeBach and Sundby (1963) discussed thoroughly the competition between animal species occupying identical (or almost identical) ecological niches. The importance of this phenomenon becomes evident in cases where an animal species is introduced into an area in which an ecologically homologous species is already present. Insect introductions made by biological control workers have resulted in a number of striking examples of competitive displacement of species holding the same ecological niche. In California two hymenopterous parasites of the Aphelinid genus *Aphytis* were successively introduced against the Californian red scale, *Aonidiella aurantii* Mask. *Aphytis chrysomphali* Merc, which was established about 1900, was in nearly all of its former range displaced by *Aphytis lingnanensis* Comp., an ecologically homologous species introduced from China in 1948. *Aphytis lingnanensis,* on the other hand, has been largely displaced by competition with a recently introduced species, *Aphytis melinus* De Bach, which in 1956/57 was imported from India and Pakistan (DeBach & Sundby, 1963). Similar phenomena of competitive displacement have been observed in many cases where entomophagous insects have been introduced against a pest insect. As an example the successive displacement of species of *Opius* (O. *longicaudatus* Ashm., *O. vandenboschi* Full., and *O. oophilus* Full.) may be mentioned. These species had been successively introduced into Hawaii to control the oriental fruit fly, *Dacus dorsalis* Hend., w.here O. *vandenboschi* replaced *O. longicaudatus,* whilst it was itself replaced by *O. oophilus.*

A number of further examples are given by DeBach (1964), Franz (1961), Delanouc (1964), and other authors.

A competitive displacement has also been observed in phytophagous insects; see O'Loughlin (1964), Harris (1961).

IV. Conclusion

The above gives a broad general outline of some of the more important factors involved in, and results to be expected from, introductions of insects in connection with biological control work. The whole purpose of biological control is to upset an ecosystem either in favour of a given crop, or to increase environmental pressure against a given weed. Many " pest " species, insect or weed, tackled in this way have themselves been introduced into a new area, and have themselves upset an existing ecosystem. In such cases biological control is aimed at restoring as far as possible the status quo, and reducing the impact of the introduced pest on the ecosystem of that area.

Thus, the principles of biological control by introduction of beneficial insects are in harmony with the general postulates of nature conservation. However, before deliberate introductions of beneficial insects against pests or weeds are made, a number of precautions should be taken to obviate risks, to increase the chances of success, and to ensure the possibility of a scientific evaluation of the results:

1. It is necessary that the exact aim of the introduction is well-defined.

2. Only insect species which do not show harmful side-effects should be selected for the introduction. Before any introduction is made, it should be demonstrated that entomophagous species do not attack other beneficial insects, and that phytophagous species have a predictable host pattern which does not include plant species of economic importance.

3. Before an insect species is selected for introduction, detailed information should be available on its identity, life-history, ecology, host-range, distribution, etc.

4. If multiple introductions are planned, the most highly specialized species should be introduced first, because it is often inferior in the case of direct competition with less specialized forms. The selection of the sequence of introduction of the single beneficial species requires detailed information on the interrelationships between the single control agents.

5. The strategy of the introduction of a beneficial insect species should be carefully prepared. Detailed information on the origin, host or host-plant, and habitat of the insect material intended for releases in the new area should be available. Initial releases should be made only, if follow-up studies are possible.

Résumé

Le rapport définit dans les grandes lignes quelques-uns des facteurs les plus importants impliqués dans les introductions d'insectes en relation avec le travail de lutte biologique et les résultats qu'on peut en attendre. L'objectif d'ensemble

de la lutte biologique est de perturber un écosystème soit en faveur d'une culture donnée, ou d'augmenter la pression du milieu contre une mauvaise herbe donnée. Beaucoup de ces espèces « nuisibles », insecte ou mauvaise herbe, attaquées de cette manière ont elles-mêmes été introduites dans une nouvelle région et ont elles-mêmes perturbé un écosystème existant. Dans de pareils cas, la lutte biologique vise à rétablir autant que possible le statu quo et à réduire l'impact de l'espèce nuisible introduite sur l'écosystème de cette région.

Ainsi, les principes de la lutte biologique par l'introduction d'insectes bénéfiques sont en harmonie avec les principes généraux de la conservation de la nature. Néanmoins, avant que des introductions délibérées d'insectes bénéfiques contre de la vermine ou des mauvaises herbes soient effectuées, un certain nombre de précautions devraient être prises pour prévenir les risques, pour augmenter les chances de succès et pour assurer la possibilité d'une évaluation scientifique des résultats :

1. Il est nécessaire que le but précis de l'introduction soit bien défini.

2. Seules les espèces d'insectes ne produisant aucun effet secondaire néfaste devraient être sélectionnées pour l'introduction. Avant de procéder à une introduction, il devrait être démontré que les espèces entomophages n'attaquent pas d'autres insectes bénéfiques et que les espèces phytophages s'en tiennent à un type d'hôtes déterminé excluant toutes espèces de plantes de valeur économique.

3. Avant de sélectionner une espèce d'insectes pour l'introduction, des données détaillées devraient être disponibles sur son identité, sa biologie, son écologie, ses habitudes alimentaires, sa répartition, etc...

4. Si plusieurs introductions sont projetées, l'espèce la plus hautement spécialisée devrait être introduite en premier lieu, étant donné qu'elle est souvent inférieure dans le cas de compétition directe avec des formes moins spécialisées. Le choix de l'introduction d'une seule espèce bénéfique exige des données détaillées sur les relations mutuelles existant entre les agents de lutte individuels.

5. L'introduction d'une espèce d'insecte bénéfique devrait être soigneusement préparée. Des données détaillées sur l'origine, l'hôte ou la plante-hôte et l'habitat des insectes sélectionnés pour introduction dans une nouvelle région devraient être disponibles. Les premières introductions ne devraient être faites que si des études complémentaires sont possibles.

REFERENCES

DEBACH, P. (1964). *Biological control of insect pests and weeds.* London, 844 p.

DEBACH, P. & SUNDBY, A. (1963). Competitive displacement between ecological homologues. *Hilgardia* 34: 105-166.

EMBREE, D. G. (1965). The population dynamics of the winter moth in Nova Scotia 1954-1962. *Mem. Ent. Can.* 46: 57 pp.

FRANZ, J. M. (1961). Biologische Schadlingsbekampfung. In *Handbuch der Pflanzenkrankheiten* (H. Richter, editor), 2nd edition, Vol. *6*, No. 3 : 1-302. Berlin.

HARRIS, P. (1961). Control of toadflax by *Brachypterolus pulicarius* L. (Col. Nitidulidae) and *Gymnetron antirrhini* Payk. (Col., Curculionidae) in Canada. *Canad. Ent.* 93 : 977-981

— (1962). Effect of temperature on fecundity and survival of *Chrysolina quadrigemina* Suffr. and *C. hyperici* F. (Col., Chrysomelidae). *Canad. Ent.* 94: 774-779.

HARRIS, P. (1964). Host specificity of *Altica carduorum* Guer. (Col. Chrysomelidae). *Canad. J. Zool.* 42 : 857-862.

— (1965). *Biological control of weeds* (unpublished manuscript).

HUFFAKER, C. B. (1959). Biological control of weeds with insects. *Ann. Rev. Ent.* 4 : 251-276.

HUFFAKER, C. B. & KENNETT, C. E. (1959). A ten-year study of vegetational changes associated with biological control of Klamath weed. *J. Range Management* 12: 69-82.

MAYR, E. (1963). *Animal species and evolution.* London, 797 p.

MULDREW, J. A. (1953). The natural immunity of the larch sawfly, *Pristiphora erichsonii* Htg., to the introduced parasite *Mesoleius tenthredinis* Morl., in Manitoba and Saskatchewan. *Canad. J. Zool.* 31 : 313-332.

O'LOLGHLIN, G. T. (1964). *The Queensland fruit fly in Victoria.* Depart. Agric. Victoria, Australia, Biol. Branch Publ. 983.

PSCHORX-WALCHER, H. (1956). Climatic and biocoenotic aspects for the collection of predators of *Adelges piceae* Ratz. in Europe. *Proc. 10th Int. Congr. Ent.* 4: 801-805.

SIMMONDS, F. J. (1955). Establishment of parasites of *Diatraea saccharalis* F. in Dominica and Guadeloupe. *Trap. Agr. Trinidad* 32: 198-200.

— (1958). The effect of lizards on the biological control of scale insects in Bermuda. *Bull. Ent. Res.* 49: 601-612.

— (1963). Genetics and biological control. *Canad. Ent.* 95 : 561-567.

— (1964). Biological control of pests in the tropics. *Tropical Science* 5 : 200-207.

SMITH, H. S. (1929). Multiple parasitism : its relation to the biological control of insect pests. *Bull. Ent.* 20 : 141-149.

TADIC, M. D. (1956). Biological control of the fall webworm, *Hypantbria cunea* Dr., in Europe. *Proc. 10th Int. Congr. Ent.* 4 : 855-858.

TAYLOR, T. H. C. (1937). *The biological control of an insect in Fiji. An account of the coconut leaf-mining beetle and its parasite complex.* Imp. Inst. Ent., London, 239P.

THOMPSON, W. R. (1929). On the part played by parasites in the control of insects living in protected situations. *Bull. ent. Res. 20 :* 457-462.

TURNBULL, A. L. & CHANT, D. C. (1961). The practice and theory of biological control of insects in Canada. *Canad. J. Zool.* 39 : 697-753.

VARLEY, G. C. (1959). The biological control of insect pests. *J. Roy. Soc. Arts 107* : 475-490.

WATT, K. E. F. (1965). Community stability and strategy of biological control. *Canad. Ent. 97:* 887-895.

WILSON, F. (1964). The biological control of weeds. *Ann. Rev. Ent.* 2 :225-244.

ZWOLFF.R, H. (1962). A comparative analysis of the parasite complexes of the European fir budworm, *Choristoneura murinana* Hb., and the North American spruce budworm, *C. fumiferana* Clem. *Techn. Bull Convm. Inst. Biol. Control* 1 : 1-162.

— (1963). Untersuchungen iiber die Struktur von Parasitenkomplexen bei einigen Lepidopteren. *Z. ang. Ent.* 15 : 346-357.

COMMENT

G. A. Petrides (U.S.A.) rapporteur: the several criteria considered by the biological control specialist before introducing new insects or other organisms into an environment, might very well be incorporated into introduced-species policies by persons working with other groups of animals and plants. It is clear that the introduction of species as biological control agents must be considered as a most important aspect of the problems under discussion.

THE INFLUENCE OF INTRODUCED SPECIES ON THE ECOSYSTEMS OF TEMPERATE OCEANIC ISLANDS

by

M. W. HOLDGATE

Deputy Director (Research), The Nature Conservancy,
London, U.K.

BIOGEOGRAPHICAL INTRODUCTION

Most groups of animals and plants have patterns of geographical distribution which can be reconciled with their evolution and dispersal in a world whose continents and oceans were arranged much as they are today. This is particularly the case for the land vertebrates and for freshwater fishes, whose biogeography has been discussed in considerable detail by Darlington (1957). In group after group, present and fossil records suggest evolution in the old world tropics, outward spread southwards into Africa and northwards into the Palaearctic land mass, and subsequent dispersal via Bering Straits, North America and Panama into the Neotropical region and via the Indonesian archipelago into Australasia. Although a temperate region during much of the Tertiary, Antarctica appears to have played no part as a dispersal route for southern hemisphere vertebrates (Simpson, 1940; Darlington, 1965), although it may have formed part of a " stepping stone " series over which some flowering plants spread (Skottsberg, 1960; Holdgate, 1961 ; Fleming, 1963; Darlington, 1965).

As a broad generalisation, since the dominant groups in the world's land flora and fauna are respectively angiosperms and placental mammals, both of which attained their dominance around the commencement of the Tertiary, modern biogeography must expect to be Tertiary biogeography. It is gratifying to find, therefore, that the broad distribution pattern outlined above accords with recent geophysical findings on land and sea distribution during the Tertiary. Palaeomagnetic determinations suggest that major continental drift movements were characteristic of the Mesozoic and concluded by the Eocene, when the present great ocean basins were substantially established. The geological evidence accords with the biological in revealing that despite this broad constancy of land and sea arrangements for the past 70 million years, there have been important local changes. Thus the present isthmus of Panama is a recent structure replacing a sea barrier only about 1 million years ago: the consequent fluxes of species across the re-established land link, culminating in the disappearance of many highly peculiar neotropical mammals and in the invasion of the nearctic by a few highly successful southern groups (such as opossums) have been discussed by Simpson.

The long isolation of Australasia, resulting in the absence there of almost all primary freshwater fishes and placental mammals, is well known (Darlington, !957). Similarly, New Zealand, with an even greater level of isolation, supports only a few ancient relict land amphibia and reptiles (Leiopelmid frogs, *Sphenodon)* and some highly distinctive birds. The Bering sea channel has been an intermittent but less significant barrier (Gressitt, 1963).

The conspicuous correlation of biogeographical discontinuities with sea barriers, commented upon by many authors for over a century, is enough to confirm that the present terrestrial flora and fauna evolved and dispersed overland. Because, throughout the Tertiary, over 90 per cent of the earth's land surface has intercommunicated by land links, there has been little selection pressure favouring the development of efficient mechanisms for long trans-oceanic dispersal. The consequence is that most dominant continental animals and plant groups lack such mechanisms. It is therefore inevitable that only a small atypical selection of continental species will succeed in reaching remote and small oceanic islands.

The biogeography of islands was first elaborated by Wallace (1895), although insular species and their evolution were considered at some length by Darwin in the *Origin of Species* (1859). Wallace's rather rigid separation of " continental " and " oceanic " islands is, as Darlington (1957) has pointed out, an oversimplification. Some continental islands, like Britain, Newfoundland or the Falkland Islands, it is true, are separated only by shallow, recent, epicontinental seas from the adjacent mainland, and have typically continental biotas derived largely by overland immigration at times of lower relative sea level. Other islands of continental type, such as New Zealand, the Seychelles or Madagascar, have more distinctive biotas probably reflecting longer isolation, while yet others, such as South Georgia, Campbell Island or Spitzbergen—or to a large extent, the entire continent of Antarctica—owing to the elimination of any earlier flora and fauna by glaciation or volcanicity, have recently been restocked by trans-marine immigration despite their continental geology or situation on shelf areas. In this respect the latter groups approximate to the true "oceanic" islands of Wallace (1895) which arise by volcanicity in the great ocean basins, often from submarine ridges, and are never linked by continuous land to any continental mass.

For the biogeographer, as Darlington (1957) emphasizes, the continents and islands can all be arranged in a single series, irrespective of their mode of origin, according to decreasing size or increasing isolation, the latter being assessed in terms both of the width and the age of the surrounding water barriers. In general, there is a correlation between size and degree of isolation, which also relates to mode of origin since oceanic volcanicity rarely builds up very large land masses. There is also a correlation in general between geological youth and degree of isolation. While relatively few absolute age determinations are available for oceanic volcanoes, the figures so far obtained (such as those for the Tristan da Cunha islands set out in Table 1) correlate fairly well with deductions from erosional state (e. g. Kear, 1957) and suggest that the average " expectation of life " of such an island may be of the order of 20 million years. Wilson (1963) has suggested that such islands arise as a consequence of the convective upwelling which in his view gives rise to the midoceanic ridges, and that continuous addition of basaltic material to the sea floor along such ridges " rafts " island volcanoes laterally and removes them from the zone of greatest activity: if this is so the older islands would naturally lie nearer to the continents than the younger ones, and they would tend to be less active and more degraded by erosion. Whatever the case may be, the evidence available does suggest that the oceanic volcanic islands of the southern ocean are mostly youthful, and have arisen since the commencement of the Tertiary (or often much more recently). Hence they must be assumed to have acquired their floras and faunas by trans-marine immigration under conditions of land and sea configuration similar to those obtaining at present. Owing to the stabilising influence of the oceanic climate, there is reason to suppose that the island habitats have not been greatly affected by the oscillations of the quaternary glaciations and definite evidence to this effect has been cited recently by Wace & Dickson (1965) for Nightingale Island and Tristan da Cunha. Similarly despite their proximity to the Antarctic Convergence, Iles Crozet have escaped recent glaciation (Adie, 1964). Skottsberg (1960), however, suggests that the major cooling of the southern hemisphere at the end of the Tertiary, may have had a more definite influence on the climatic zones of the region as a whole, and the present temperate islands may have had more subtropical conditions, such as characterise northern islands in comparable latitudes, prior to this change.

Table I. THE AGES AND DIMENSIONS OF THE TRISTAN DA CUNHA ISLANDS (from Miller in Baker *et al.* 1964)

Island	*Area* (km^2)	*Height* (*m*)	*Age* (*million yrs*)
Tristan da Cunha .	86	2,066	1
Gough Island . . .	57	910	4
Inaccessible Island .	12	700	6
Nightingale Island .	4	300	15
Discovery Seamount	—	—	26

THE PECULIARITIES OF INSULAR BIOTAS

All volcanic oceanic islands, and those islands of continental origin to have been subsequently sterilised by volcanicity or glaciation, must by definition have derived their floras and faunas by trans-oceanic immigration. It follows that:

a) Natural selection primarily requires a facility for long-range dispersal across water, which has not been a prerequisite for species success on mainlands at least throughout the Tertiary. Consequently, only a minority of mainland species are likely to succeed in reaching remote islands and since the basis of selection is for what is in mainland terms almost a non-adaptive character, this minority need not necessarily be conspicuous for its success on the continents. The result is that islands may be expected to acquire an *impoverished* and specialised biota.

b) Establishment after dispersal involves selection for another range of characters. Impoverishment is accentuated by the relatively small ecological diversity an island presents compared with a continent. Williams (1964) has pointed out that in general the species richness of a region may be expected to bear some relation to its area, since the larger areas generally possess greater ecological diversity. Small islands, rendered still more uniform by the equable oceanic climate, offer strikingly few niches and a relatively high proportion of successful immigrants may fail in establishment. Holdgate (1965) has pointed out in this context that 10 per cent of the known terrestrial fauna of the Tristan da Cunha group consists of vagrant birds and lepidoptera, some of which appear with considerable regularity yet fail to establish breeding populations. Judging from the frequency in aerial plankton of many small and inconspicuous forms (Gressitt et al. 1963 : Holdgate, 1965), the percentage may be even higher.

c) Primary selection for dispersal capacity means not only that the immigrant biota will be species-poor, but that it will be *disharmonic.* Major continental groups, including most forest trees, all land vertebrates except birds and bats, several insect groups such as Plecoptera, Trichoptera, Ephemeroptera, Megaloptera, and Odonata, and all primary freshwater fishes, are almost universally absent from remote islands. Even within the groups which have representatives, it often happens that only one or two families or genera out of many hundreds succeed in trans-oceanic colonisation. Some such genera appear " specialists " in the process, as does *Lancetes* among southern Dytiscidae or *Pentarthrum* among Curculionidae (Kuschel, 1962).

d) The isolation of insular populations, which are likely to be only rarely reinforced by further immigrants, means that genetic drift readily occurs especially since the populations are small. It is likely that insular conditions will differ from those in the continent of origin and hence selection favours evolutionary divergence. The result is the production of insular *endemics.* Many of these, in the insects and land birds, are celebrated for their flightlessness (Wallace, 1895 ; Darlington, 1943 ; Holdgate, 1965). In the broad context of evolution, these highly localised species are of no significance and no established case is known of any insular species invading a mainland, but they are of great scientific interest and make remote islands " laboratories " for evolutionary study (Darwin, 1859; Lack, 1947). Very frequently, considerable radiation of initial immigrant stocks into daughter species adapted to exploit different ecological niches occurs, and the degree to which this has advanced may be correlated in part with the age of the fauna, as well as with the area and diversity of the islands and perhaps with the climate. Thus Hawaii, an ancient and diverse group, has 3722 endemic insect species derived from about 250 initial immigrants : Tristan da Cunha must have had at least 20 immigrants ancestral to 47 endemic species (Zimmermann, 1948; Holdgate, 1960).

e) The impoverishment, at least initially, of insular biotas presumably results in relaxed interspecific competition. From this it follows that species may, in the absence of competitors, be able to invade unfamiliar habitats. The freshwater faunas of oceanic islands display this well. Holdgate (1961) pointed out that of the 8 freshwater invertebrates collected by him on Gough Island, two were marine species which had invaded the stream systems in the absence of any freshwater representatives of their groups. On some other islands as much as 40-50 % of the freshwater animals are of direct marine ancestry, and all fishes found in island streams have this origin. Relaxed competition also leads to increased ecological amplitude among land plants and invertebrates, and this has been discussed for the Tristan da Cunha group by Wace & Holdgate (1958) and Wace and Dickson (1965).

f) While terrestrial species are at a disadvantage in the colonisation of remote islands, there are corresponding factors facilitating their exploitation by seabirds and seals. There are no land predators (apart from predatory marine birds such as skuas). Consequently, seabirds are not restricted for breeding sites to inaccessible offshore stacks and high cliffs. In the southern ocean, whose waters are especially rich in food and deficient in breeding grounds (Murphy 1964), most undisturbed oceanic islands are occupied by burrowing or ground nesting birds whose populations may amount to of the order of millions. On Gough Island, Swales (1965) estimated and described a complex zonation and phasing of nesting. On Beauchêne Island, off the Falklands, Strange (1965) described mixed rookeries of blackbrowed albatross and rockhopper penguins covering 1.3 sq. km and totalling of the order of 6 million birds. The great penguins rookeries of the Antarctic are legendary. Similarly, the coastal zones of many islands are or were the resort of great colonies of seals : on South Georgia, for example, there were 310,000 elephant seal in 1960, while 1,200,000 fur seal were taken by sealers between 1790 and 1822.

g) The oceanic climate also has certain positive influences on the biota. High humidity and rainfall undoubtedly favours the development of cryptogamic vegetation, and partly explains the high representation of ferns and bryophytes (Wace, 1961 ; Wace and Dickson, 1965). These plants also have light and readily dispersed spores and are so at an advantage in this respect. The wet climate of temperate oceanic islands favours peat accumulation and the wide development of mire communities. High winds result in the generally low-growing and often prostrate habit of scrub woodland irrespective of the species involved (Wace and Holdgate, 1958). Heavy salt spray deposition characterises most islands and may account for the microphyll character of most of the arboreal dominants, while in the southern temperate zone the maritime fringe of perennial tussock grassland is almost certainly related to the combination of heavy salt deposition and nitrogen and phosphate production by nesting birds. This perennial tussock grassland, formed for the most part of *Poa* species (Wace, 1960), has evolved only in the absence of grazing land animals, to which it is not adapted.

VULNERABILITY OF INSULAR BIOTAS

Ecosystems as unusual and as isolated as those of remote islands might be expected to be vulnerable to outside pressures which modify either the habitat or species composition of the biota. This is so for the following reasons:

a) The isolation of the islands by water barriers is essentially a protection. Those few species capable of colonising the islands are protected by the barrier from those numerous species less adapted to trans-oceanic dispersal. We have seen that this large excluded category comprises the majority of continental dominants : it follows that were the isolation terminated and such dominants able to invade and compete on equal terms with the insular biota drastic ecological changes would be likely.

b) In particular, many insular species and communities have evolved in isolation and exploited niches in a way that might not have been possible under the stress of heavier competition, predation, or grazing. The peripheral freshwater fishes and other marine organisms that have invaded fresh waters have done so only in the absence of specialised freshwater forms (they do not do so where their ranges overlap with freshwater species about the continents). The vegetation, such as tussock grassland on temperate southern islands, has developed its characteristics in the absence of grazing mammals and is not adapted to them: the perennial stools of the grasses, and their fleshy roots, are palatable and readily grazed out by sheep, goats or cattle. The great abundance of seabirds breeding on most remote islands could not remain were ground predators to become common since their sites offer no defence against such animals. Most islands lack annual herbs capable of rapid colonisation of fresh scars made by burning or trampling, and hence their vegetation is especially liable to destruction by erosion if agents liable to create such scars become common.

THE IMPORTATION OF ALIEN SPECIES BY MAN

1. *The development of human occupation*

Man, like other land vertebrates, is a continental animal and only within the last few millennia has developed trans-oceanic vessels capable of reaching remote islands. The southern temperate islands, in contrast to the tropical and subtropical groups of the Pacific or the North Atlantic archipelagos, were among the last areas to be visited, many of them being discovered during the Portuguese explorations of the late 15th and early 16th centuries, or in even more recent periods. The early discoverers did little to exploit these remote land areas, unless, like St. Helena or Juan Fernandez, they lay conveniently to shipping routes and were therefore suitable as watering or victualling points. Many of the southernmost groups were not landed on or affected by man until the sealing industry invaded the southern hemisphere in the late eighteenth and early nineteenth centuries. Sealers, living ashore in small parties for periods of up to two years, probably had a relatively small direct impact on the flora, since they imported few plant species. It seems likely that they did bring in potatoes to a few places such as Gough Island, and they may incidentally have introduced other species as stray seeds in provisions and clothing. The importation of mice to Gough Island and perhaps some other areas may also be attributed to sealers. These initial explorations were only locally followed, as at the Falkland Islands, Tristan da Cunha, Amsterdam, Campbell Island, Auckland Island and Iles de Kerguelen by attempts at agriculture. Whaling stimulated further shore based settlement at Kerguelen and South Georgia and also at the South Orkney Islands and South Shetland Islands in the Antarctic zone.

As a result of these pressures virtually no island escaped some human contact between 1599 and 1900, even though the intensity of it varied widely. However, there was some withdrawal from the areas in which settlements at subsistence level were made, in the early twentieth century and only the most recent era of establishment of weather stations from 1945 onwards has seen a widespread re-occupation.

2. *Importation of alien plants*

It might be expected that the degree to which alien plant species have become established on southern oceanic islands would bear some relationship to the duration and intensity of human occupation, and this is the case. St. Helena, discovered in 1501 and colonised almost at once has a long list of alien plants, now far outnumbering the remnants of the native flora. Within the Tristan da Cunha group, the main island which is the only one to have been permanently settled and farmed has far more alien plants than either of the smaller neighbouring islands, even though they have been periodically visited by Tristan islanders since 1810 and have been the scene of intermittent agricultural attempts. In the New Zealand area, Auckland and Campbell Islands similarly support many more alien species than the undisturbed smaller outliers.

Mere lists of alien species alone do not reveal the true ecological significance of their impact. Many of them have remained infrequent or restricted to the immediate neighbourhood of human settlement. For the conservationist the vital consideration is not whether alien plants have been or are being imported by man, but whether they are capable of invading and modifying the native vegetation. If the answer to this latter question is negative, rigorous prohibition of all imports may be unnecessary; if it is yes, then most careful protection will be required. There has been considerable discussion of this topic, especially in relation to the flora of New Zealand, and it is examined further by Wace elsewhere in the present volume. As a generalisation from first principles one might expect that imported aliens would spread into native vegetation most readily on islands with an initially poor flora. It is therefore instructive to compare the situation on the genuinely oceanic Tristan da Cunha group (Wace and Dickson, 1965), with the continental Falkland Islands (Moore and Sladen, 1965). On Tristan, and also in the Falklands, sheep grazing and human clearance have eliminated coastal tussock grassland from many areas and greatly modified the overall vegetation nearest to settlements. Undisturbed vegetation remains over the greater part of Tristan, but sheep have affected a great deal of the Falklands. On Tristan 12 aliens, 15 % of the total, are established in native vegetation types and two species, *Rumex acetosella* and *Holcus lanatus,* dominate extensive tracts of wet heath on the Peak. In the Falkland Islands 20 aliens, 33 % of the total, are established in the " camp ", away from settlement areas and the most prominent as a dominant is *Poa annua* about bird colonies, probably in areas formerly occupied by tussock grassland. In both islands, aliens are most prominent where considerable disturbance, particularly through the intermediary of grazing stock, has occurred. Early accounts of the lowland plain at Tristan, now covered by a close, grazed sward of imported grasses, make it clear that it formerly supported dense bush and tussock grassland (Holdgate and Wace, 1961): its clearance by cutting and burning was begun about 1810. On the Peak, grazing by feral goats or sheep may have played some part in inducing change. On the less disturbed islands of the Tristan group, such as Gough Island, aliens are certainly less frequent in native vegetation away from the coasts.

3. *Importation of alien invertebrates*

Numerous alien invertebrates have been transported to southern oceanic islands by man. Synanthropic diptera, carried probably as larvae or pupae in human foodstuffs and packing materials, or aboard ships, have become very widespread. Phytophagous beetles, aphids, earthworms, millipedes and centipedes, and many other groups, have also been spread widely. On the four islands of the Tristan da Cunha group, Holdgate (1965) listed 58 definite aliens on Tristan (making up 41 % of the fauna of that island), 19 (18 %) on Gough Island, 10 (12 %) on Inaccessible Island and 6 (10 %) on Nightingale Island. These percentages would all be increased by the addition of species of doubtful status. As with the alien plants, these animals have shown a considerable spread into more or less native vegetation, but with substantial interspecific variation. The three alien diplopods of Tristan, for example, all European in origin, are concentrated about the Settlement area and two species are restricted to this vicinity, but one, *Cylindroiulus latestriatus,* is also widespread in scrub throughout the island. This species is alone naturalised on Gough Island where it occurs everywhere in the forest below 350 m and is one of the most important litter decomposers.

Such widespread alien invertebrates probably have significant ecological effects. In the Tristan islands, for example, litter decomposing invertebrates are relatively few, and imported millipedes and earthworms may therefore be having a substantial impact on the soil types. Ground predators are also infrequent, and the rapid spread on the main island of a centipede, *Lithobius melanops* may consequently modify the faunal spectrum. On Gough Island, only two parasitic hymenoptera are recorded, both attacking aphids of doubtful status, and were such species to become more common they might have a substantial impact on the native ecosystem. The steady influx of species is certainly continuing. In 1956, for example, the large aphid *Tuberalachnus salignus* was imported to Tristan with tree saplings. The weevil *Pantomorus cervinus,* the coccinellid *Adalia flavomaculata,* and the carabid *Harpalus agilis* were all imported between 1956 and 1962, and are spreading. Since no coccinellids or carabids are native to the group, ecological niches are widely available for these species which may be expected to invade native habitats. It would appear, indeed, that alien invertebrates are likely to spread rather more readily on oceanic islands of this type than are alien plants and far too little is known about their ecological impact. In terms of conservation the control of such introductions is extremely difficult.

Serious concern has been expressed on various occasions about the danger of importing diseases and their vectors, and so decimating the populations of endemic land birds or breeding seabirds on oceanic islands. No actual case of such importation is recorded, but the prospect remains a real one. The danger of importing species which would either defoliate plants (in the absence of control species), or spread fungal diseases is perhaps even more acute since the species-poor island vegetation in many respects parallels crop monocultures in providing abundance of a few species and at the same time has a small range only of predatory, parasitic and competitive invertebrates or insect eating birds to control an outbreak (Elton, 1958). All these aspects of equilibrium in invertebrate communities of oceanic islands yet await detailed study.

4. *The importation of vertebrates by man*

By far the best documented and spectacular of the disturbances which the ecosystems of southern islands have suffered through human agency have resulted from the importation of mammals. On several islands, these animals have so devastated the native vegetation and avifauna as to totally change the whole character of the environment. The impact of the different species will be considered here, while the island by island summary in Appendix A provides a cross-index of their effects.

HERBIVOROUS MAMMALS

a) *The effect of goats*

The most spectacular effects of the liberation of goats (a common act of early Portuguese and British navigators who hoped thereby to increase the victualling capacity of these islands) are to be seen on subtropical rather than temperate islands. The record on St. Helena has been admirably documented by Wallace (1895) in the following words:

" When first discovered, in the year 1501, St. Helena was densely covered with a luxuriant forest vegetation, the trees overhanging the seaward precipices and covering every part of the surface with an evergreen mantle. This indigenous vegetation has been almost wholly destroyed, and although an immense number of foreign plants have been introduced and have more or less completely established themselves, yet the general aspect of the island is now so barren and forbidding that some persons find it difficult to believe that it was all once green and fertile. The cause of the change is however easy to explain. The rich soil formed by the decomposed volcanic rock and vegetable deposits could only be retained on the steep slopes so long as it was protected by the vegetation to which it in great part owed its origin. When this was destroyed the heavy tropical rains soon washed away the soil and left a vast expanse of bare rock and sterile clay. This irreparable destruction was caused in the first place by goats, which were introduced by the Portuguese in 1513 and increased so rapidly that in 1588 they existed in thousands. These animals are the greatest foes to trees, because they eat off the young seedlings and thus prevent the natural restoration of the forest. They were however aided by the reckless waste of man. "

Holdgate and Wace (1961) continued the story in summary as follows:

" In 1709 the Governor of the island complained that the timber was rapidly disappearing, and asked that the goats be destroyed, to preserve the woods and because the island was suffering from droughts. The reply was " The goats are not to be destroyed, being more valuable than ebony. " In 1809 the Governor reported the total destruction of the forests, and that in consequence the cost of importing fuel for Government use in the one year had been £ 2729. 7 s. 8 d. About this time large numbers of European, American, Australian and South African plants were imported and many of these ran wild and increased so fast as to drive out and exterminate much of the relics of the native flora. "

On St. Helena today, small relict patches of the native vegetation are to be found only on some of the highest summit ridges and in inaccessible ravines. The rich endemic insect fauna has survived rather better, but undoubtedly many unique species have been lost and over the island as a whole a distinctive ecosystem has been replaced by a commonplace assemblage of continental imports. Soil erosion is a continuing problem (Wace, 1966). A rather similar but fortunately less extreme fate has overtaken the three islands of Juan Fernandez, to which goats (with pigs and donkeys) were imported soon after discovery in 1574. Here, despite bizarre control measures (the introduction of mastiffs, which ran wild and became so fierce and dangerous that they had to be exterminated), severe soil erosion has occurred and many alien plants have spread at the expense of the vulnerable native vegetation. The native vegetation now persists chiefly in ravines and on high ridges, where the goat cannot penetrate.

On Tristan da Cunha, where goats were liberated before 1790, damage was less significant and the population never seems to have reached the high levels reported from St. Helena or Juan Fernandez. The same pattern is repeated at Nouvelle Amsterdam in the Indian Ocean, an island similar to Tristan in climate and native vegetation, and at Campbell and Auckland Islands south of New Zealand. Goats still persist locally on the latter but do not seem to be causing significant damage. It would appear therefore that the goat, as a serious agent of devastation, is a subtropical animal and that its rate of increase is slower, or mortality higher, on the cooler southern islands where, too, it has proved far easier to exterminate.

b) *Cattle*

Cattle have been liberated, at various dates, on Tristan da Cunha, Nouvelle Amsterdam, Auckland Islands south of New Zealand, and the continental Falkland Islands. In this cool temperate zone they have been more successful in establishing feral populations than goats and have caused more damage to the habitat. In the Falkland Islands the vast herds of wild cattle provided sport for visitors in the 1830's (Darwin, 1839), and gravely interfered with subsequent farming developments.

On Tristan da Cunha cattle were landed around 1820 and fairly soon afterwards a herd was established at free range on lowlands at the south of the island. This herd is now semi-wild and has adopted truly wild behaviour patterns. Its numbers have been controlled in part by human predation but substantially by food availability. Owing to the terrain the animals cannot range freely over the island as a whole and in the limited area which they graze they have converted the vegetation into a low sward incorporating many alien species, and with substantial erosion. On Nouvelle Amsterdam the situation is more serious. Cattle were imported here in 1871 and have now become truly feral, population numbers having reached a peak at about 1,000-2,000 but now somewhat declined. They have largely been responsible for the elimination of bush over this fairly small island, and much of the rough volcanic terrain now supports a close sward of alien grasses, broken intermittently by erosion scars. By analogy with Gough Island, where lowland *Phylica* bush overlies deep unconsolidated peaty soils, one may conclude that this grazing and erosion have also been associated with major changes in the substratum and undoubtedly also in the invertebrate fauna.

The cattle imported to Auckland Islands in 1849 were later killed out by sealers. In 1895 others were landed on small off-lying islands at the north of the archipelago and these gave rise to populations which persist today. By 1916 they had so increased as to have damaged the vegetation by overgrazing and in consequence were suffering from starvation. In all three oceanic island groups therefore there is parallel evidence that cattle increase to population levels where food resources become limiting, and that in so doing they greatly modify the vegetation, replacing bush and tussock grassland by low-growing swards of aliens and causing elimination of deep organic soils and substantial erosion. An alleged concomitant of these trends is a change in the sex ratio of the cattle, in which bulls come to outnumber cows by up to 3 : 1. This occurred on Nouvelle Amsterdam, but its incidence in the other populations is not clear.

c) *Sheep*

The cool, temperate climate of many islands in the southern ocean is appropriate for sheep and commercial farming has been attempted on Campbell, Auckland, Kerguelen and Tristan, as well as in the Falkland Islands. Sheep have also been imported at different dates to Nouvelle Amsterdam, Saint Paul, Marion Island, Macquarie Island, Gough Island and South Georgia. Except in the Falkland Islands and Tristan da Cunha (and to a lesser extent at Iles Kerguelen), organized sheep farming no longer exists but small numbers are kept to provide meat for scientific stations at Gough Island (possibly no longer), Marion Island and Macquarie Island. Feral populations remain on Campbell Island, where considerable damage to vegetation was reported in 1950. Sheep preferentially graze the large, palatable, tussock-forming *Poa* species and these perennial grasses are quickly eliminated. On the Falkland Islands tussock of P. *flabellata* was so extensive in the 17th century that the waving crowns of the grass were mistaken for the canopy of a forest by an early visitor. Now this vegetation type persists only on offshore islands and remote headlands inaccessible to sheep. On mainland coasts eroding sand dune or depauperate swards of alien grasses have replaced the tussock, and about penguin colonies in such areas the vigorous alien P. *annua* is especially prominent (Moore and Sladen, 1965).

On Campbell Island *Poa foliosa* was the dominant tussock, and in 1950 when 1,500 feral sheep were present, it and *Danthonia flavescens* were noted as greatly reduced while *Poa litorosa* tussock was under pressure. Bare eroding peat covered many slopes and erosion was extending as the tussock was killed back. The alien *Poa annua* was increasing as was the unpalatable native *Chrysobactron rossi.* Thus grazing pressure on tussock grasses by sheep was causing the loss of this distinctive southern temperate island vegetation type, and the consequent reduction in many associated species of plant and invertebrate. *Pleurophyllum hookeri,* one of the most distinctive plants, was becoming confined to inaccessible cliffs. A similar situation exists at Iles de Kerguelen, where sheep, established on some of the smaller islands, have caused damage to tussock grassland and to the unique « Kerguelen cabbage », *Pringlea antiscorbutica.*

Wherever they have become established, therefore, sheep have been associated with major vegetation changes especially through the destruction of the perennial tussock grasses, and this damage has often caused erosion and the spread of alien plants.

d) *Rabbits*

Rabbits were imported by sealers to Macquarie Island in 1880 and to Ile Saint Paul at a similar period. They are said to have occurred on Ile de la Possession (Archiped Crozet) in 1875. They were liberated on the main island of Iles de Kerguelen by a British scientific expedition in 1874. They were also liberated on Rose and Enderby Islands in the Auckland group. On all these islands they increased rapidly and devastated the vegetation. On Ile Saint Paul, for no known reason, the population declined subsequently and by 1957 recolonization of the bared ground was. nearly complete. No rabbits are said now to remain on Iles Crozet. At Kerguelen however, the converse is the case. Grazing of inland heath of *Azorella* and of coastal tussock grassland and *Pringlea* has led to the restriction of the latter to off-lying islands and cliffs and to the invasion of *Azorella* heath by *Acaena,* with much erosion of peat and soil. A unique endemic invertebrate fauna was formally associated with the original vegetation, and this, too, has been reduced in range and abundance.

At Macquarie Island the devastation has been worse and made more dramatic by the small size of the island and its steep terrain. On the coastal slopes, the dominent tussock grass, *Poa foliosa* was rapidly grazed out and the native flora of only 35 species contained no unpalatable plant with comparable soil-binding capacity. Erosion has consequently been general, stripping the peaty covering of the slopes down to bedrock, and gullying is extending back into the oceanic heath above and causing further severe changes (Costin and Moore, 1960).

Like sheep, therefore, rabbits have caused severe damage to vegetation and soil on those temperate southern islands to which they have been imported. On Saint Paul, Ile de la Possession and Rose Island (Auckland Islands) unexplained population declines have also occurred, but the damage done is only partly reversible. Only at South Georgia has a primary introduction (in 1872) certainly failed, probably because of the colder climate.

e) *Pigs*

Pigs are omnivorous animals and the feral population established at different times on Inaccessible Island (Tristan da Cunha), Nouvelle Amsterdam, Ile aux Cochons (Archipel Crozet), Auckland Island and Campbell Island have not only damaged vegetation but also devastated bird populations. On Ile aux Cochons, in 1820, the wild pigs were described as both numerous and fierce, feeding on tussock grass roots and seabirds and causing great damage in the penguin colonies. For these reasons the population was eliminated in the late 19th century. The pigs of Amsterdam, Campbell Island and Inaccessible Island have also been killed out, but a feral population remained on Auckland Island in 1955.

f) *Other herbivores*

Horses were kept on South Georgia for some years after 1905 and at Kerguelen since 1950, and donkeys are present on Tristan da Cunha. Various birds (poultry, geese, game birds) have been imported to some islands. None of these species seems to have had any significant ecological impact. Reindeer, taken to South Georgia in 1911 and to Kerguelen in 1955, have, however, built up substantial feral populations on the former island (Bonner, 1958) and caused significant damage to vegetation and consequent local erosion.

Predatory Mammals

a) *Dogs and cats*

Man has deliberately imported dogs and cats to many southern islands, but feral populations of dogs have never been common and do not now constitute a problem anywhere. Wild cats derived from domestic stock are, however, numerous on Tristan, Nouvelle Amsterdam, Marion Island, Macquarie Island and Auckland Island, while feral populations were once present on Iles de Kerguelen and Ile Saint-Paul but have now died out. Lack of critical scientific study makes it impossible to assess the true impact of these predators, more especially since they normally co-exist with rats, which are probably even more destructive. However, it is unquestionably significant that groundnesting sea bird populations have declined, dramatically, on all those islands to which these mammals have been imported. Ecologically, this is to be expected since, as was demonstrated in an earlier section, the vast bird colonies of southern islands developed in the absence of ground predators and their nesting sites offer little defence against such mammals.

b) *Rats*

Rats (often *R. rattus* subspecies rather than *R. norvegicus)* inadvertantly distributed by man have colonised most southern temperate islands including South Georgia, Tristan da Cunha, Ile Saint-Paul, Nouvelle Amsterdam, Iles de Kerguelen, Macquarie Island and Campbell Island. Where they occur, commonly together with cats, there has been a general decline in the smaller seabirds. On Nouvelle Amsterdam, where the habitat has also been generally devastated by overgrazing and consequent erosion, Paulian (1959) has demonstrated the former occurrence of several species from skeletal remains.

c) *Other species*

Mice (*Mus musculus*) are widespread on southern islands but their ecological role has never been investigated. They occur up to high altitudes in montane feldmark and heath in the Tristan da Cunha group, where they probably subsist on invertebrates and plant food, but readily revert to a domestic scavenger role when man establishes camps.

A predatory ground-dwelling bird *Gallirallus australiis* has been introduced to Macquarie Island and is said to be destructive of ground nesting seabirds and (with rats and cats) to be incriminated in the decline of nine species of ground nesting petrels.

Discussion

The current state of human disturbance on a series of southern oceanic and continental islands is summarized in Appendix A. From this table and the foregoing analysis of the ecological factors involved in these situations, certain principles are apparent.

In the first place, the species-poor and unusual ecosystems of oceanic islands are manifestly liable to drastic change as the result of human agricultural activities and the importation of grazing and predatory mammals. Secondly, because of the low level of species diversity in such ecosystems, instability produced by the elimination of a single vulnerable key species (such as the tussock grass on the steep coastal slopes of Macquarie Island) may be acute. There may be no other species in the biota capable of replacing the vulnerable one and restoring closed vegetation. Consequently, the disturbed biotic balance (as Fosberg (1963) has pointed out) is not restored by a swift transition to a new point of equilibrium, as would probably happen in a continental area where grazing pressures shifted, but by degenerative processes. These lead to physical alteration of the habitat for example by soil erosion (as on St. Helena, Juan Fernandez, Macquarie Island or Campbell Island), by substitution of one soil type for another (as on much of the lowland plain of Tristan da Cunha), by changes in ground water table following upon gullying, or by microclimatic changes reflecting alterations in vegetation cover. The disturbance of the habitat presents opportunities for alien colonists, especially annual plants adapted to quick invasion of open ground, and thence to the ultimate development of new vegetation and soil types.

In a review of this situation as applied to Pacific Islands, Fosberg (1963) raises several major questions which may with equal validity be asked concerning southern temperate examples. First, is any state approaching true biotic balance to be found on youthful and small oceanic islands such as we have been considering here? Secondly, even if such balance formerly existed, does it now remain in any island in the world ? Thirdly, where insular biotas are exposed to severe modification, to what extent are these changes reversible? This third question is perhaps the vital one for the conservationist. It is therefore the one we must consider in greatest detail here.

First to dispose of Fosberg's initial question. As Elton (1958) has recently reminded us, few biotas are static. Biogeography is concerned with continuing changes in distribution, in relation to great fluxes in climate and rearrangements in land forms. Invasions are a fact of life both in a continental and an oceanic setting. But whereas the great species diversity of a continental ecosystem buffers it against the process—the replacement of one species by another often involving no more than a substitution in the network of interactions—the invasion of an island by a new species can also mean the addition of a whole new component to the ecological system. One might expect the oceanic system to exhibit a far less balanced state than the continental in consequence.

The oceanic system is however buffered by certain factors. The surrounding barrier of water slows down the invasion process and filters out many potential colonists. The stability of climate militates against biotic change. The relatively low diversity of rock and soil on oceanic volcanoes, and the universal exposure to salt laden rains and sea bird pressures, makes for a certain degree of uniformity. These resemblances probably account for physiognomic similarity in, for example, oceanic scrub formed by *Phylica arborea*, *Metrosideros* spp., *Erica azorica* and *Nothofagus betuloides* in different maritime settings, and for the parallel development of the tussock grass growth form around the southern temperate zone. As a result, the state of imbalance may be less acute than might be predicted on theoretical grounds.

In the southern temperate zone the biologist is more fortunate than in the Pacific. Fosberg, speaking of the latter after 30 years of experience, could recall virtually no ecosystems which he could be confident were undisturbed. In the southern temperate zone, vegetational disturbance is assuredly less, because of the lack of human colonization of many islands and the lack of human contact in any form until the last two to four centuries. Although alien species are present, islands such as Gough or Nightingale in the Atlantic, Prince Edward or Ile de l'Est in the Indian Ocean, or the remote outliers of the Falkland, New Zealand, Fuegian or Kerguelen archipelagos probably do genuinely display whole series of plant and animal communities in substantially unmodified form.

These islands give standards for comparison with the adjacent devastated examples. It is possible to deduce from the series that the tussock grassland vegetation type, where dominated by a single species as on Macquarie Island, or the Falkland Islands, is acutely vulnerable to the sheep or the rabbit. Where there is a slightly more complex vegetation, as on Campbell Island, the impact of grazing is less drastic since there are species which can increase in compensation. Thus on Macquarie Island, elimination of *Poa foliosa* leads directly to eroding scars and soil wastage. On Campbell, grazing eliminated *P. foliosa* and *Danthonia flavescens* likewise, but *Poa litorosa* showed more resistance and the biota included a species, *Chrysobactron rossi* which was unpalatable and could take over locally as a soil binder. It is similarly possible to deduce that the goat is a severe threat to ecological stability in the warmer islands but of no great danger farther south where feral populations have generally died out: conversely cattle, sheep, and rabbits are a serious problem in approximately that order of penetration. Detailed use of the island series has yet to be made, but there is a sufficiency of examples for research valuable alike to conservation and ecology.

To what extent are the changes brought about by man and domestic stock reversible? Turbott (1963) has demonstrated for a warmer island, Great Island in the Three Kings Group (New Zealand), that agriculture and the goat produced a change from species-rich scrub forest to monospecific forest, dominated by an unpalatable species, and a reduction in associated species. Many of the latter survived only in a few inaccessible places, and while no endemic plant is known actually to have become extinct, several became threatened. The changes in the invertebrate fauna are not recorded but impoverishment and restriction seem probable. Goats were eliminated from the island in 1946, and the process of vegetational recovery has been dramatic, with an evident regeneration of the less common as well as the dominant species. From this example Fosberg (1963) concludes that changes induced by man and stock are indeed reversible where the gross character of the ecosystem has not been altered: where scrub has only become impoverished and where soil has not been eroded away. By analogy, one might similarly expect recolonization by native vegetation were cattle eliminated from Ile Nouvelle Amsterdam where the native bush, *Phylica arborea,* survives on the steep western cliffs and where there are no other tree or bush species to compete.

Forest might equally reappear were goats cleared from Mas Afuera where native trees survive well in gullies. One might expect the vegetation changes induced by rabbits on Archipel de Kerguelen, or cattle and sheep on Tristan da Cunha, to be reversible since seed parents exist nearby and since there has been no catastrophic soil loss or introduction of vigorous aliens more liable to dominate the vegetation. But it would be naive to expect the species-rich St. Helena forest to re-establish itself on the eroded slopes now covered by imported aliens, or the eroding flanks of Macquarie Island quickly to revert to tussock grassland.

The conservationist, considering these examples, may conclude that there is therefore practical merit in eliminating grazing mammals from oceanic islands wherever possible, even if they have induced considerable change. Such a policy has been considered at Campbell Island and Auckland Island. Where the herbivore is large—cattle, sheep, goats, or pigs for example—an elimination policy is feasible. Smaller species, notably rabbits, are probably ineradicable from their present haunts. The elimination of predators would undoubtedly bring about similar reversals of trends on islands such as Tristan da Cunha, where sea bird populations persist albeit at low levels. There is practical experience on that island that reduction in human predation on the mollymawk *Diomedea chlorhynchos,* was followed by an immediate response, and the spectacular recovery of southern fur seals in the last half century despite their virtuaf extinction between 1800 and 1880 is another testimony to the capacity of species to restock their former range in the absence of pressures. But recovery is impossible where endemic species have been once eliminated, and will be slow where non-endemic sea bird stocks have been destroyed. In the doubtful event of rats and cats being removed from Nouvelle Amsterdam, it is most unlikely that the smaller petrels, so far definitely recorded there only as skeletons (Dorst & Milon, 1964) would recolonise the island for a very long period.

Elimination of herbivores and predators would probably reverse many of the changes they have induced on many southern islands. But the reversal would not be total. Some alien species established away from disturbance zones would persist: such species include *Rumex acetosella* or *Holcus lanatus* on Tristan da Cunha, and the invertebrates *Cylindroiulus latestriatus, Oxychilus alliarius,* or *Lucilia sericata* on the same island. Granted continued human contact, the situation would come to resemble that on the relatively undisturbed southern islands such as Gough or Nightingale where mammalian herbivores and predators are absent. There would be a slow, steady, influx of aliens, much faster than occurred before man provided a mobile dispersal route, but still far from catastrophic. Gradually, the situation would trend—as it always has—towards the more species-rich, more harmonic, more stable, continental pattern. But the predominant features of oceanicity would remain.

CONCLUSION

The southern oceanic islands—like all oceanic islands—are of high scientific interest because of their biological uniqueness, developed as a consequence of their volcanic origin and great isolation. At the present time, many of them are substantially undisturbed apart from a minor component of alien species in their total biota. These islands merit deliberate conservation directed towards the prevention of any introduction of herbivorous or predatory land mammals. A prohibition of such imports would alone lead to fairly effective conservation, and minimal hardship is involved to human groups since there are few or no residents on the islands concerned and negligible agricultural potential. It is desirable further to restrict all imports of alien plants, but this is a refinement compared with the major need. Gross human interference with the habitat, which largely creates conditions for the spread of alien plants and invertebrates should also be avoided. Islands in this category, where relatively simple conservation measures would be effective include Gough Island, Inaccessible Island, Nightingale Island, outliers of the Falkland Islands, outliers of South Georgia, Prince Edward Island, several of the Archipel Crozet, Heard Island, and some of the New Zealand shelf islands. In most of these, conservation measures are actually in operation.

Other islands need positive measures to control herbivorous and predatory mammals. On certain islands where farming and other human activities have been discontinued, as at Campbell Island, Auckland Islands and Nouvelle Amsterdam, there is merit in deliberately reducing the populations of herbivores. Even where predators such as cats and rats cannot be controlled, the elimination of grazing would cause vegetational recovery with consequent gains to science. In other cases, where human societies have a valid claim on the island land, as at Tristan da Cunha, there is need for rational control of grazing and of the taking of wild life, so that imported mammals do not become feral and bird stocks are not eliminated. Finally, in the most grossly disturbed of islands it may be impossible materially to restore the situation, but there may be a substantial research opportunity in the study of the new communities formed from alien species often of diverse biogeographical origins.

The justification for the conservation of oceanic islands is in part aesthetic, because of their uniqueness, their dramatic biotic features and their great scenic beauty, and in part scientific. The island ecosystems are the converse in origin and composition of many continental situations. Their species poverty offers opportunities—perhaps illusory but none the less meriting appraisal—for " complete " analysis of the contribution made by each component. In some ways they are the natural counterpart of the crop monoculture, exhibiting similar vulnerability to ecological change. The evolutionary changes to be seen on so many island groups, while probably of no great significance in contributing to the broad stream of faunal and floral development, provides laboratory conditions for the study of fundamental processes. So far there are good research facilities only in two major oceanic island groups in the world—Hawaii and the Galapagos. There are laboratories at a few more—Snares Islands, Archipel Kerguelen—and proposals for research facilities in the Tristan group. Conservation is essential if the potential of these situations is to be realised for science while something approaching a natural ecological situation exists.

Summary

The dominant groups in the world's fauna and flora—placental mammals and angiosperms—evolved at a time when the continental arrangement was broadly similar to the present. Consequently transoceanic dispersal was not a requirement for evolutionary success. Oceanic islands surrounded by large water barriers have been colonised only by a few species with exceptional dispersal capacity. Many major plant and animal groups are completely excluded from such oceanic biotas which are spoken of as disharmonic. Because of their isolation, island populations show evolutionary divergence and because of a low level of competition species may invade new habitats. Remote islands are further characterised by a great abundance of breeding marine birds and mammals which are immune from ground predators.

These unusual and isolated ecosystems are peculiarly vulnerable to interference. Human transport methods have broken down the barriers isolating them from vigorous continental species and the importation of herbivorous and predatory vertebrates has had a catastrophic impact on vegetation and fauna not hitherto exposed to them. A detailed assessment of these impacts leads to the conclusion that for the conservation of scientific interest the first essential is to prevent such importations wherever possible. Where populations of imported mammals are now established they should be eliminated as far as possible. Gross human interference with the habitat accelerates the spread of alien plants and invertebrates and should also be avoided. Among the remote temperate islands of the southern hemisphere there remain a significant number which have suffered only minimal disturbance and a list of these has been drawn up as a basis for conservation proposals.

Résumé

Les groupes dominants de la faune et de la flore mondiales — mammifères à placenta et angiospermes — ont évolué à une époque où la configuration des continents était grosso modo la même que maintenant. Par conséquent la dispersion transocéanienne n'était pas indispensable au succès de l'évolution. Des îles océaniques entourées de vastes barrières d'eau ont été colonisées seulement par quelques espèces dotées d'une capacité de dispersion exceptionnelle. Beaucoup de groupes importants de plantes et d'animaux sont totalement exclus de ce genre de biotopes, que l'on qualifie de non harmoniques. Du fait de leur isolation, les populations insulaires présentent des variations évolutionnaires et, en raison du degré insignifiant de compétition qu'elles rencontrent, d'autres espèces peuvent envahir de nouveaux habitats. Les îles éloignées sont de plus caractérisées par une grande abondance d'oiseaux et de mammifères marins qui sont inaccessibles aux prédateurs terrestres.

Ces écosystèmes inhabituels et isolés sont particulièrement vulnérables aux ingérences. Les méthodes de transport humain ont aboli les barrières les isolant d'espèces continentales vigoureuses et l'importation de vertébrés herbivores et prédateurs a eu une incidence catastrophique sur la végétation et la faune qui jusqu'ici n'y étaient pas exposées. L'évaluation détaillée de ces répercussions

mène à la conclusion que pour maintenir l'intérêt scientifique de ces écosystèmes l'essentiel est d'empêcher de telles importations partout où c'est possible. Là où les populations de mammifères importés sont maintenant naturalisées il faudrait les éliminer autant que possible. L'ingérence brutale de l'homme dans l'habitat accélère la propagation de plantes et d'invertébrés exotiques et devrait aussi être évitée. Parmi les îles éloignées à climat tempéré de l'hémisphère sud, il en reste un nombre important qui n'ont subi que des perturbations minimes, et une liste en a été établie pour servir de base à des propositions de conservation.

REFERENCES

ADIE, R. J. Editor (1964). *Antarctic Geology.* Amsterdam, North Holland.

BAKER, P. E., GASS, I. G., HARRIS, P. G. and LE MAITRE, R. W. (1964). The volcanological report of the Royal Society Expedition to Tristan da Cunha, 1962. *Phil. Trans. Roy. Soc. Lond.,* Vol. 256, No. 1075, pp. 439-578.

BONNER, W. N. (1958). The introduced reindeer of South Georgia. *Falkland Islands Dependencies Surveys Scientific Reports,* No. 22, pp. 1-8.

COSTIN, A. B. and MOORE, D. M. (1960). The effects of rabbit grazing on the grasslands of Macquarie Island. *J. Ecol.,* Vol. 48, No. 3, pp. 729-732.

DARLINGTON, P. J. (1943). Carabidae of mountains and islands; data on the evolution of isolated faunas and on the atrophy of wings. *Ecol. Monogr.,* Vol. 13, pp. 37-61.

DARLINGTON, P. J. (1957). *Zoogeography; the geographical distribution of animals.* New York, Wiley.

DARLINGTON, P. J. (1965). *Biogeography of the southern end of the world.* New York.

DARWIN, C. R. (1839). *The voyage of the Beagle.* (Everyman Edition, 1906, reprinted 1955, London, Dent.)

DARWIN, C. R. (1859). *Origin of Species.* London.

DORST, J. and MILON, P. (1964). Acclimatation et conservation de la nature dans les îles subantarctiques françaises. In *Biologie Antarctique,* Ed. R. Carrick, M. Holdgate and J. Prevost. Paris, Hermann.

ELTON, C. S. (1958). *The ecology of invasions by animals and plants.* London, Methuen.

FLEMING, C. A. (1963). Palaeontology and Southern Biogeography. In *Biogeography of the Pacific Basin, Proc. 10th Pacific Science Congress* (Ed. Gressitt, J. L.). Hawaii, Bishop Museum.

FOSBERG, F. R. (1963). Disturbance in Island Ecosystems. In *Biogeography of the Pacific Basin,* Ed. J. L. Gressitt. Hawaii, Bishop Museum.

GRESSITT, J. L. (1963) (Editor). *Biogeography of the Pacific Basin. Proceedings of the 10th Pacific Science Congress.* Hawaii, Bishop Museum.

GRESSITT, J. L., and YOSHIMOTO, C. M. (1963). Dispersal of animals in the Pacific. In *Biogeography of the Pacific Basin,* Ed. J. L. Gressitt, Hawaii, Bishop Museum.

HOLDGATE, M. W. (1960). The fauna of the mid-Atlantic Islands. *Proc. Roy. Soc. B.,* Vol. 152, No. 949, pp. 550-567.

HOLDGATE, M. W. (1961). The freshwater fauna of Gough Island (South Atlantic). *Proc. Linn. Soc. Lond.,* 172, Part 1, pp. 8-24.

HOLDGATE, M. W. (1965). The fauna of the Tristan da Cunha Islands. *Phil. Trans. Roy. Soc. Lond.,* B., Vol. 249, No. 759, pp. 361-402.

HOLDGATE, M. W. (1961). Biological Routes between the Southern Continents. *New Scientist,* No. 239, pp. 636-638.

HOLDGATE, M. W. and WACE, N. M. (1961). The influence of man on the floras and faunas of southern islands. *Polar Rec.* Vol. 10, No. 68, pp. 475-493.

KEAR, D. (1957). Erosional stages of volcanic cones as indicators of age. *N.Z.J.Sci. Technol.,* B., Vol. 38, pp. 672-682.

KUSCHEL, G. (1962). The Curculionidae of Gough Island and the relationships of the weevil fauna of the Tristan da Cunha group. *Proc. Linn. Soc. Land.* Vol. 173, Pt. 2, pp. 69-78.

LACK, D. (1947). *Darwin's finches.* Cambridge.

MOORE, D. M. and SLADEN, W. J. L. (1965). Some recent records of native and alien flowering plants from the Falkland Islands. *British Antarctic Survey Bulletin,* No. 7, pp. 29-35.

MURPHY, R. C. (1964). Conservation of the Antarctic fauna. In *Biologie Antarctique,* Ed. R. Carrick, M. Holdgate and J. Prevost. Paris, Hermann.

SIMPSON, G. G. (1940). Antarctica as a faunal migration route. In *Proceedings of the Sixth Pacific Science Congress.* Berkeley, California.

SKOTTSBERG, C. J. F. (1960). *Proc. Roy. Soc,* B, 152.

STRANGE, I. J. (1965). Beauchene Island. *Polar Rec,* Vol. 12.

SWALES, M. K. (1965). The sea-birds of Gough Island. *Ibis,* Vol. 107, No. 1, pp. 17-42, No. 2, pp. 215-229.

TURBOTT, E. G. (1963). *Proc. 10th Pacific Sci. Congress.* Hawaii, Bishop Museum.

WACE, N. M. (1960). *Proc. Roy. Soc,* B, 152.

WACE, N. M. (1961). The vegetation of Gough Island. *Ecol. Monogr.,* 31, 337-67.

WACE, N. M. (1966). The last of the virgin islands. *Discovery,* 27 (2).

WACE, N. M. and DICKSON, J. H. (1965). The Terrestrial Botany of the Tristan da Cunha Islands. *Phil. Trans. Roy. Soc. Land.,* 247, 273-361.

WACE, N. M. and HOLDGATE, M. W. (1958). The vegetation of Tristan da Cunha. *J. Ecol,* 46, 593-620.

WALLACE, A. R. (1895). *Island Life* (2nd Ed.). London, Macmillan.

WILLIAMS, C. B. (1964). Patterns in the balance of nature and related problems in quantitative ecology. London, Academic Press.

WILSON, J. T. (1963). Hypothesis of earth's behaviour. *Nature,* Lond., 198, 925-929.

ZIMMERMAN, E. C. (1948). *Insects of Hawaii.* Vol. I. Introduction.

COMMENTS

J. C. de M. Carvalho (Brazil) asked why no observations had been made on Trindade Island, a Brazilian possession, where goats, pigs and rats have been introduced and where some studies have been carried out by the Museu Nacional, Rio de Janeiro. *M. Holdgate* replied that South Trindade and Martin Vas are most interesting islands, and had only not been specifically mentioned because outside the climatic zone with which his paper was largely concerned.

R. A. Falla (New Zealand): research opportunities should also be used to study introduced populations of well-established exotics before their destruction occurs or is deliberately carried out. On Campbell Island, sheep numbers had declined after pastoral care ceased and rabbit populations had also become depleted on Auckland Island. *Dr. Holdgate:* unexplained population declines have occurred on several other southern oceanic islands, for example with rabbits on Ile Saint Paul, which merit critical study. Some situations might be allowed to take their course for the purposes of research, but emergency control measures should, however, perhaps always be prepared and kept in reserve, in case the unrestricted increase of particular plant or animal populations was clearly likely to result in damage to a habitat which was irreversible and which, for equally good scientific reasons, it was desirable to avoid.

APPENDIX A

THE PRESENT STATE OF THE PRINCIPAL SOUTHERN OCEANIC AND CONTINENTAL ISLANDS IN THE ATLANTIC, INDIAN, AND SOUTH WEST PACIFIC REGIONS

Island	*Climatic zone*	*Native biota*	*Human impact*	*Alien fauna impact*	*Conservation state*
a) *Atlantic Zone*					
St. Helena (United Kingdom)	Warm temperate - Oceanic subtropical	Rich forest and scrub. Endemic birds and diverse native insect fauna.	Discovered 1501. Many alien plants and animals imported. Land burned and cleared. Now colonised and with substantial population.	Goats feral since 1501 ? Many other species.	Native biota devastated. Original vegetation relict on some peaks (protected). Status of native invertebrates and avifauna uncertain.
Tristan da Cunha (United Kingdom)	Cool temperate	Scrub, tussock grass, heath and montane vegetation. Three endemic land birds. Large sea bird colonies. Numerous endemic invertebrates. Large fur seal and elephant seal populations.	Discovered 1506. Early sealing destroyed stocks. Settled 1810. Cattle, donkeys, sheep, goats, poultry, rabbits, pigs, mice, rats, cats and dogs all imported. Much burning of coastal vegetation and agricultural modification. Many alien plants and invertebrates imported.	Substantial changes in lowland vegetation near settlement and where grazed. Predators eliminated endemic gallinule and bunting. Sea bird colonies greatly reduced by cats, rats and men.	Native vegetation, invertebrates and one endemic land bird remain, with some remnant sea bird and seal groups. South east quadrant of island little disturbed. Conservation by local ordinance (under Government of St. Helena). Reasonable prospect for conservation at present level.
Nightingale Inaccessible Gough Islands (United Kingdom)	Cool temperate	As for Tristan da Cunha. Endemism varies from island to island but all have some peculiar land birds and many invertebrates. Fur seals abundant on Gough Island and sea birds on all islands.	Discovered 1505-6. Early sealing destroyed stocks by 1890. No settlement but parties of sealers and shipwrecked lived ashore. Nightingale and Inaccessible visited regularly by Tristanislanderssince 1810. Some sea birds taken for food and abortive farming venture on Inaccessible. Gough Is. weather station established 1955, now operated by South Africa.	On Inaccessible, cattle, goats, sheep, pigs and dogs have occurred but caused no evident major change. On Gough Island, sheep, poultry, goats imported, but mostly destroyed before harmful impact. Feral mice on Gough have minimal effect. In general impact is slight or negligible.	Excellent at present. These three islands almost unique as undamaged temperate examples. Conservation by local ordinance (Tristan da Cunha, as agent of St. Helena Government) and by agreement with South African Weather Bureau.

Island	Climatic zone	Native biota	Human impact	Alien fauna impact	Conservation state
Falkland Islands (United Kingdom)	Cool temperate	Tussock grassland with inland heaths. Many land and sea birds, seals, native invertebrates.	Settled since 18th century. Cattle, horses, sheep, pigs, hares, rats, cats, dogs all present. Now used for sheep ranching.	Coastal tussock grassland now almost eliminated from mainland. Small offlying islands alone retain large sea bird colonies. Land bird fauna and montane vegetation undamaged but vegetation generally modified by sheep.	Recent good Conservation legislation (British Crown Colony) provides for protection of most birds and for establishment of small offshore islands as sanctuaries.
South Georgia (United Kingdom)	Subantarctic	Tussock grassland and wet heath low down. Montane inland vegetation. Heavy ice cover. Two endemic land birds and large sea bird and seal colonies. Many endemic invertebrates.	Occupied by sealers since 1796 and whalers subsequently. Feral reindeer established since 1910. Horses, sheep, rats, rabbits, upland geese, imported but only rats now persist. Some alien plants and invertebrates. Small civilian settlement whose future is related to that of whaling.	Reindeer grazing has modified some areas of vegetation. Also disturbance around whaling stations. Rats probably reduced some bird populations especially of endemic pipit. Human predation has affected endemic teal. Disturbance generally slight. Elephant seal population harvested in scientifically controlled manner.	Conservation prospects very good. Control of sealing industry has been sound. No conservation legislation but Falkland Island laws may be applied.
Antarctic Islands in Atlantic (South Sandwich, South Orkney, South Shetland groups). (United Kingdom : Antarctic Treaty Zone).	Maritime-Antarctic	Cryptogamic vegetation with permanent ice over large tracts of land. Species-poor invertebrate fauna. No land birds. Large sea bird and seal colonies.	Sealers devastated fur seal population from 1800-1870. Whaling industry had some shore bases and local impact. Antarctic bases established since 1944 at some points, with Husky dogs.	Negligible.	Except for South Sandwich group of very inaccessible volcanoes, areas covered by Agreed Measures for Conservation of Fauna and Flora in the Antarctic, which provide satisfactory basis.
Bouvet0ya (Norway)	Maritime-Antarctic	Highly impoverished and restricted cryptogamic vegetation and soil fauna. Sea birds and seals present in some numbers.	Very slight. Island rarely visited and difficult to land on. Some fur seal killed in 1929-33 period. Proposal for weather station at present time.	None	Island a Norwegian Colony. Seals protected by Norwegian ordinance, and conservation prospects good.

b) *Indian Ocean Sector*

Nouvelle Amsterdam (France)	Cool temperate	Lowland dense scrub, coastal tussock grassland and upland wet heath. Large sea bird and seal colonies.	Visited by sealers. Fishery in 1843-53. Farmed in 1871. Cattle, sheep, goats, pigs, cats, rats, mice imported, and cattle, cats, rats, mice still feral. French weather station since 1950.	Cattle have destroyed scrub woodland and tussock grassland and there has been soil erosion. Alien vegetation now covers most of island. Cats and rats have largely eliminated sea birds.	French weather station staff protect fur seal population which is increasing. No direct human activity threatens remaining fauna but alien mammals are not controlled and ecological balance probably irreparably disturbed. Conservation prospect bad.
Ile Saint Paul (France)	Cool temperate	Almost wholly covered in dense tussock grassland, large sea bird populations.	Centre of a fishing industry from 1843-1914, and intermittently since 1927. Wild pigs numerous in 1823 and goats ca. 1850, both eliminated by 1874. Rabbits introduced and abundant until 1957. Cats present in 1874. Rats and mice abundant then and subsequent-	Rabbit grazing caused severe erosion, but owing to population decline recolonization now said to be complete. Cats and rats probably severely damaged bird populations. Alien plants said to be widespread in disturbed areas.	Ecosystem clearly seriously disturbed and although no human pressures now threaten flora and fauna recovery is unlikely. Conservation prospects poor.
Archipel de Kerguelen (large group of many islands varying widely in size) (France)	Subantarctic	Lowlands support tussock grassland and wet heath, with remarkable endemic *Pringlea antiscorbutica*. Considerable seal and sea bird colonies. One endemic land bird (a teal, *Anas eatoni)* and numerous remarkable endemic insects.	Sealers active 1800-1830 and subsequently. Scientific expedition released rabbits 1874. Sheep imported 1908-11. Weather station established 1949. Ponies, reindeer, cattle, pigs, cats, dogs, rats all reported locally affecting vegetation or fauna, but many small islands lack these species and also rabbits. Some commercial sealing in part. Efficient local farming for weather station.	Rabbits have devastated vegetation and caused soil erosion in many places. Sheep have caused some damage to vegetation. Cats and rats have locally damaged avifauna. Some alien plants and invertebrates have invaded disturbed areas.	French administration concerned to protect fauna and local National Parks decree covers some areas. Effective conservation of endemic biota possible on smaller islands where rabbits absent. Over much of mainland, ecosystem probably irreparably damaged, although birds including endemic duck remain common.

Island	*Climatic zone*	*Native biota*	*Human impact*	*Alien fauna impact*	*Conservation state*
Archipel Crozet (France)	Subantarctic	Tussock grassland, wet heath and montane vegetation covers these islands. There is no ice cap. Large seal and sea bird colonies occur, and many endemic insects. Area poorly explored scientifically.	Sealers and shipwrecked parties were numerous in early 19th century. Wild pigs established on one island in 1820-60. Rabbits reported on one island in 1873 and goats in 1875. None of these species now remains. French weather station established 1963.	Uncertain, owing to lack of scientific data. Probably slight only on most islands.	Islands of very high scientific value, retaining native ecosystem in many areas. Conservation outlook uncertain.
Prince Edward and Marion Islands (South Africa)	Subantarctic	Tussock grassland and extensive wet heath and bog, with montane vegetation above. Large seal and sea bird colonies and many invertebrates.	Sealers visited these islands during 19th century. Permanent occupation of Marion Island commenced in 1947 (South African Weather Station). Sheep imported failed to become feral. Fowls kept. Cats introduced and now wild over Marion. Many alien plants deliberately introduced. Prince Edward Island not known to be disturbed.	Vegetation probably in native state except near station. Cats undoubtedly damaging avifauna of Marion Island, and control measures being attempted.	Conservation measures now in force are identical with those for Antarctic Treaty Zone. Serious scientific and conservation effort being made. Prospects, especially for Prince Edward Island, good.
Heard Island (Australia)	Subantarctic	Sparse vascular plant vegetation by coast, with very few invertebrates. Climate almost Antarctic and island heavily ice capped.	Sealers visited the island during the 19th century. An Australian scientific station operated in 1947-54- No alien species are known to have been introduced.	None	No present threat to native biota. Conservation prospects good.

c) *New Zealand Shelf Islands*

Snares Islands (New Zealand)	Cool temperate	Scrub and tussock grassland over most of surface. Abundant sea birds and some endemic land birds and invertebrates. Sea Hon occur.	Slightly disturbed but no known alien mammals or severe human impact.	None	A reserve, with bological station operated by Canterbury University. Conservation prospects good.
Bounty Islands (New Zealand)	Cool temperate	Tussock grassland over most of area. Many sea birds.	No known serious human impact?	None?	Reserve for flora and fauna. Conservation prospects good.
Antipodes Islands (New Zealand)	Cool temperate	Tussock grassland and scrub. Many sea birds.	No known serious human impact.	None?	Reserve forflora and fauna. Conservation prospects good.
Auckland Islands (Six islands of varying size) (New Zealand)	Cool temperate	Lowland scrub forest and tussock grassland with wet heath and montane vegetation above. Many sea birds and endemic invertebrates and numerous land birds including endemic rail on Adams I.	Settled by Maoris in 1841 and by Enderby Brothers, as shore based whaling station in 1849-52. Evacuated 1856. Subsequent spasmodic farming attempts. Pigs, goats and cats remain on main island, where sheep formerly occurred. Rabbits and cattle are feral on some smaller islands. A weather station operated from 1941-45.	Rabbits and cattle have caused severe damage on Rose and Enderby Islands, and pigs and goats have caused local damage on the main island. Cats are stated to damage sea and land birds. On the whole, ecosystem not severely disturbed and second island of group, Adams Island, is reported little damaged.	Group is a reserve for flora and fauna, and conservation and scientific interest is high. Prospects for conservation and study are good.

Island	*Climatic zone*	*Native biota*	*Human impact*	*Alien fauna impact*	*Conservation state*
Campbell Island (New Zealand)	Cool temperate	Coastal tussock grassland with a little lowland scrub and inland wet heath. Sea birds abundant, and numerous endemic invertebrates.	Sheep farming carried out from 1890-1927, with up to 8000 animals. Shore based whaling station worked from 1908-1914. In 1960 about 950 feral sheep remained. Cattle, rats and cats also occur while goats, pigs, game birds and guinea fowl formerly occurred. A meteorological station has been established on the island since 1941.	Sheep grazing formerly caused major changes in vegetation and initiated erosion, and in affected areas alien plants are spreading. Predatory ground mammals reportedly damage smaller sea bird populations. Despite these adverse influences the island retains considerable scientific interest.	Island is a reserve for faunaand flora andcontrol measures are being applied to sheep and other feral mammals. Conservation prospects are reasonably good.

d) *Islands south of New Zealand and Australia*

Island	*Climatic zone*	*Native biota*	*Human impact*	*Alien fauna impact*	*Conservation state*
Macquarie Island (Australia)	Subantarctic	Coastal tussock grassland with wet heath and bog higher up. Large sea bird colonies and seal populations.	Sealers active from 1820-80. Rabbits imported 1880. Sheep and goats imported by Weather station authorities, 1947, but latter destroyed soon after. Horses, dogs also once present. Cats feral since 1821 and rats probably also imported by sealers. *Gallirallus australis* (a ground-living predatory bird) introduced in 1879. Scientific and weather station established since 1945.	Rabbits now abundant over most of island, causing severe erosion on steep coastal slopes. Cats, rats and *Gallirallus* have severely reduced population of smaller sea birds. Penguin and seal colonies unaffected by these agencies, but terrestrial ecosystem probably irreparably damaged.	Scientific research is being combined with protection of birds and seals but feral mammals are probably too well established for control. Hence conservation likely to be effective only for seals and larger sea birds.

ANIMAL INTRODUCTIONS AND THEIR ECOLOGICAL EFFECTS IN EUROPE

by

R. S. R. -FITTER

Hon. Secretary, Fauna Preservation Society, London

I propose to restrict this paper to vertebrate animals, and more especially to mammals. Even this limitation leaves too vast a field to be covered adequately. Niethammer (1963) lists 47 mammal and 48 bird species more or less successfully introduced into Europe, and Fitter (1959) lists 13 mammal, 10 bird, 2 reptile, 2 amphibian and 10 freshwater fish species successfully introduced into the British Isles. These statistics probably cover the great majority of the successful introductions into Europe — it is unlikely that many successful introductions are unknown, though there may well be a few — but we can never know of all the far more numerous unsuccessful ones.

The really successful introductions, animals which have spread and maintain themselves over a wide area, include the house mouse *Mus musculus* and the brown rat *Rattus norvegicus* throughout Europe, and the rabbit *Oryctolagus cuniculus,* the muskrat *Ondatra zibethica* and the fallow deer *Dama dama* over a large part of it. Other mammals which have established substantial territories for themselves include the black rat *Rattus rattus,* the coypu *Myocastor coypus,* the sika deer *Cervus nippon* (British Isles, France), the muntjac or barking deer *Muntiacus muntjak* (British Isles), the beaver *Castor fiber* (Scandinavia, Eastern Europe), the raccoon *Procyon lotor* (Germany, Eastern Europe), the American mink *Mustela vison* (Great Britain, Iceland), and the various fur-bearers deliberately released to increase the natural resources of the USSR, such as the raccoon-dog *Nyctereutes procyonoides,* which is spreading widely in eastern Europe.

Among birds, the most widely successful introduction has been the pheasant *Phasianus colchicus*; in the British Isles the red-legged partridge *Alectoris rufa,* the Canada goose *Branta canadensis* and the little owl *Athene noctua* have also successfully established themselves over significant areas.

Speaking mainly from British experience, it is clear that certain conditions are necessary for an introduction of any species into alien territory to succeed. The most important is the existence of a vacant ecological niche. The British Isles contain a comparatively large number of such niches, for its fauna and flora are poorer than those of Continental Europe because of the comparatively short time that elapsed between the final retreat of the ice, around 11 000 years ago, and the breaking of the land bridge where the North Sea now lies about 7,500 years ago. This is why such species as the little owl, filling a niche for a small diurnal bird of prey, and the Canada goose, filling a niche for a large aquatic bird breeding on waters in open woodland or parkland, have been able to establish themselves. Other animals have succeeded because the niche they now occupy was temporarily unoccupied, e.g. the North American grey squirrel *Sciurus carolinensis* dropped into the niche temporarily vacated by the red squirrel *Sciurus vulgaris,* which was undergoing a downward population fluctuation; and the rainbow trout *Salmo gairdnerii* was able to obtain a foothold in the Derbyshire Wye because the brown trout *Salmo trutta* has been driven out by pollution from sewage from the town of Buxton, which the rainbow was better able to withstand.

Some introductions are actually reintroductions, for instance the capercaillie *Tetrao urogallus* and the red squirrel into Scotland, the roe deer *Capreolus capreolus* into southern England and the beaver into Scandinavia. Others represent a reinforcement of stocks reduced by excessive hunting, as with the partridge *Perdix perdix* and the red deer *Cervus elaphus,* both of which have been widely restocked all over Europe from Hungary, and the brown trout, which is extensively reared in trout farms to restock rivers. In the case of the pheasant *Phasianus colchicus* the original European stock of the typical race *colchicus* from the Caucasus had to be reinforced in the 18th century by *torquatus* stock from China, and in the 19th and early 20th also by several other eastern Asiatic races, such as *mongolicus* and *principalis.* As a result, in England at least, the present-day pheasant stocks are an extraordinary mixture of the pheasant races of the world, with *torquatus* and *colchicus* predominating.

The ecological consequences of successful vertebrate introductions in Europe may be discussed under the following headings (1) changes in habitat; (11) changes in the balance of predators; (III) impact on species occupying similar ecological niches; (IV) augmenting of natural resources; and (V) damage to natural and artificial resources.

I. Changes in Habitat

Very few of the introduced species have had a major impact on the plant communities of Europe, but the two main exceptions are important indeed. These are the rabbit and the muskrat. Rabbits produce substantial changes in the vegetation of grassland, to the point of destroying it if they become very numerous. The after effects of the myxomatosis epidemic of 1954/56 in Great Britain, which produced a catastrophic fall in the rabbit population included the rapid bushing up of open grassland, especially on chalk and limestone, showing that the rabbits had hitherto been responsible for keeping the scrub, mainly of hawthorn *Crataegus monogyna,* in check. Ragwort *Senecio jacobaea* is resistant to rabbits; they do not eat it, and a rabbit-infested pasture is often covered with ragwort, which in turn will be infested with the black-and-yellow larvae of the red-and-black cinnabar moth *Hipocrita jacobaea.* Here therefore is a food-chain stimulated by the presence of an introduced mammal.

The muskrat from North America produces substantial changes in the ecology of the rivers it colonises, by undermining their banks with its burrows; it is therefore a swamp producer like the beaver and to a much lesser extent the coypu, whose burrowing only has serious effects when the population becomes quite dense. So serious is the damage caused by the burrowing of the muskrat that in order to avert the danger in the 1930's the Ministries of Agriculture in both Great Britain and Ireland mounted expensive campaigns to exterminate (successfully) the small colonies of muskrats escaped from fur farms which had established themselves in both countries. In Europe the consequences for the rivers of Central Europe of the progeny of five individuals released by a Czech landowner in 1905 have been far reaching. However, in other parts of Europe, such as Finland, muskrats have actually been released to provide a stock of wild fur-bearers.

II. Changes in the Balance of Predators

Introduced rodents have provided an enormously increased biomass for predators to feed on in various parts of Europe. Before the myxomatosis epidemic, for instance, rabbits were an important food for the buzzard *Buteo buteo* in western Britain, while both house mice and brown rats form a substantial element in the diet of many mammal and bird predators. On the other hand introduced predators may seriously upset the balance of the available prey, as has certainly happened with the waterfowl population of Iceland following the introduction of the American mink, and will probably happen in Great Britain also when mink become fully established, as they doubtless will. Nothing seems to have been on record of the effect on other predators or prey species of the massive introductions of fur-bearing mammal predators in eastern Europe, especially the USSR, until the paper, which follows, by Professor Lavrov and Dr. Pokrovsky, was circulated for this conference.

III. Impact on Similar Species

Little work has been done on the impact of introduced species on native species occupying similar ecological niches, though we know that in Great Britain the grey squirrel has prevented the native red squirrel from reoccupying the ground it had temporarily vacated at the time of the grey's introduction; in some fringe areas the grey seems definitely to have driven the red out. In parts of eastern England, the red-legged partridge is now commoner than the native partridge *Perdix*, but as we lack any population figures for the latter in the 18th century we cannot say to what extent, if any, the incomer has displaced the native bird. Nor is enough known about the ecology of the various species of deer now inhabiting Europe to say to what extent if any the fallow, sika and muntjac deer are occupying habitat that would otherwise be available to the native red and roe deer. It is likely that the niches of all five species are sufficiently different to enable them to make use of the same habitats, although there may be some overlap between the fallow and the red deer on the one hand and the sika on the other.

IV. Augmenting Natural Resources

Introduced species have brought to Europe substantial fresh resources of meat (deer, rabbits) and skins (rabbit, muskrat, coypu, beaver, etc.), and this is recognised by the substantial introductions of fur-bearers in the USSR — in western Europe introductions of fur-bearers have usually been by accident. According to Shaposhnikov (1960) some 200,000 individuals of 35 fur-bearing species have been released in the Soviet Union since 1924. The acclimatisation of the sable *Martes zibellina,* coypu, beaver, American mink, raccoon and ground squirrel *Citellus fulvus* is considered successful, but that of the red squirrel and raccoon-dog doubtfully successful.

V. Damage to Resources

Undoubtedly the most harmful introductions have been those of the house mouse (in Neolithic times) and the black and brown rats, whose depredations on human natural and artificial resources need no underlining. In Great Britain the rabbit is classed as a pest, for its damage to crops and grassland, despite its meat and fur. The muskrat is another equivocal addition to the fauna of Central Europe, on account of the damage it does to river banks. Deer can do serious damage to crops, and this is a risk taken in introducing almost any ungulate, rodent or lagomorph. The dangers of introducing predators are that they may attack domestic stock (though usually only if it is carelessly guarded), or game species, including fish.

REFERENCES

ELTON, C. S. (1958). *The Ecology of Invasions by Animals and Plants.* London.

FITTER, R. S. R. (1959). *The Ark in Our Midst: the story of the introduced animals of Britain : birds, beasts, reptiles, amphibians, fishes.*

NIETHAMMER, G. (1963). *Die Einbürgerung von Säugetieren und Vogeln in Europa.* Hamburg.

SHAFOSHNIKOV, L. V. (1960). *Okhrana Prirody i Zapovednikovoe Delo v SSSR,* 4:37-51.

ECOLOGICAL RELATIONSHIPS BETWEEN LOCAL FAUNA AND SPECIES COMMERCIALLY INTRODUCED IN THE USSR

by

PROF. N. P. LAVROV AND DR. V. S. POKROVSKY

The USSR Ministry of Agriculture, Central Laboratory on Nature Conservation, Moscow V-331

During the years of the Soviet power, work on animal acclimatization has assumed an ever-increasing importance in the USSR. 32 species of mammals, 10 species of birds, nearly 50 species of fishes, as well as 15 species of insects and a number of other species of invertebrates, have been established on commercial and experimental scales. A number of our native species have enlarged their range after artificial settlement in new places. Many have again become important from the point of view of fur supplies.

As a result of the work on acclimatization, the fauna of our country has been enriched by new economically valuable species and the basis for commercial hunting and fishing has been widened.

It is the aim of this article to give in a concise form the results achieved in the USSR on acclimatization of a number of exotic fur-bearing animals as well as well as some examples to show the complicated diversity of ecological bonds emerging in the course of acclimatization of new species of animals.

THE MUSKRAT (*Ondatra zibethica* L.)

The muskrats to be used for breeding in natural conditions of the USSR were brought from Canada, Finland and England.

For the most part the animals brought from the above countries belonged to the typical subspecies — *Ondatra zibethica zibethica* L.—and only few of them to the subspecies *O. zibethica macrodon* Merriam.

About 1650 imported beasts were released in 1928-1932 in a number of regions of the European North (including the island of B. Solovetskii in the White Sea), in West and East Siberia and in the island of Karaginskii near the shores of Kamchatka.

The work of establishing the muskrat taken from different regions of the Soviet Union was carried out in the years that followed. Up to 1965 about 250,000 of the animals had been released at waters situated in different natural and geographical zones. After the muskrat was settled and spread to many places independently, its actual zoological range in the USSR had become greater than its original natural range in North America. It is roughly limited by 20° 10' - 164° 20' E. and 39° 15' - 71° 30' N. In some of the waters of the Leningrad region as well as in the Stavropol territory areas isolated from those inhabited by the brown muskrat are occupied by the black muskrat.

As in its country of origin, the muskrat lives in waters of different types, ranging from small lakes and ponds up to extensive regions of the sea coasts. The growth rates of this species in different regions, the total number and density of population in individual parts of the area are all extremely heterogeneous. This is mainly determined by hydrological differences in the habitat and food conditions, and in certain regions by the epizootological situation as well. The areas of the southern regions and the basins of the deltas in particular have proved to be most suitable and highly productive compared with any other parts of the country. Successful acclimatization of the muskrat in the Yakut Republic, above the north polar circle, is of definite practical interest.

Muskrat hunting started in 1935 in the USSR. Trade returns went on increasing up to 1965 when the State obtained about 5 million skins of the beasts. In some of the regions the State purchases of muskrat skins in cash payments amounted to 90 % of the whole cost of this fur put on the market by hunting. It is worth mentioning that significant differences in existing ecological conditions have brought about the evolution of local forms with newly created morphological characters. For example, it is found that the dimensions of the body of the muskrat (and hence its skin), the thickness of the leather and the texture of the hair growth have changed. These characteristic features determine the trade value of the skin and thereby its price.

Successful acclimatization of the muskrat in the Soviet Union is mainly due to the fact that the natural conditions of its home country and our country, primarily climatic and feeding conditions, have many common features; and a very favourable ecological niche for muskrat was virtually unoccupied. The only ecologically similar species is the water vole (*Arvicola terrestris* L.), feeding on plants which grow for the most part on the banks or within the shallow littoral zone. Besides that, it feeds mainly on the part of these plants growing above water and, what is more, these rodents live almost entirely out of the water in winter, i.e. during the most difficult season of the year with respect to availability of food. Thus it may be concluded that the water vole can hardly be regarded as a food competitor of the muskrat. Neither can one discover a notable food competition between the muskrat and the beaver (*Castor fiber* L.). As a result of wide-scale settlement by the beaver in the last 30 years in many regions of this country, it has found its way to the same waters as the muskrat. However these rodents very often occupy different waterside habitats and their main feeding plants are different.

The process of acclimatization has brought about more complicated interrelations between the muskrat and the local species of predatory vertebrate animals. In the first years when the number and population density of the introduced rodents were not significant, the predatory activity of the raptorial animals was exhibited relatively weakly. They preyed mostly on the young. As the number of muskrats grew and their range expanded, they began to settle in less protected sections of the reservoirs, and predatory animals of the region gradually acquired experience in pursuing and capturing their new victim. So its enemies grew in number. This can be illustrated by the following examples. At first the fox (*Vulpes vulpes* L.) was not used to digging up the lairs of the muskrat. But later on, especially in the years of crop failure or poor availability of mouse-like rodents, the fox became quite accustomed to breaking into muskrat tunnels. In 1944 the muskrat was released in the delta of the Amu Darya where the most common beast is the jackal (*Canis aureus* L.). In the winter of 1947-1948 the rodent's remains were discovered in 3,8 % of the total sample of this beast of prey analyzed. In the year that followed this index grew to 12.8 %, and in 1960-1961 up to 64.3 %. Little by little many species of birds and beasts began to feed on the muskrat. Among these predators it is worth mentioning the fox, the wolf (*Canis lupus* L.), the raccoon dog (*Nyctereutes procyonoides* Gray), the Alpine and Siberian weasels (*Mustela altaica* Pall, and *Mustela sibiricus* Pall.), the European mink (*Mustela lutreola* L.), the steppe cat (*Felis libyca* Forst.) amongst others. The predatory bird feeding on the muskrat is the marsh harrier (*Circus aeruginosus* L.). It is widely spread in the USSR and has its breeding place in the same habitat as the muskrat. The muskrat has also become an important food stuff for such relatively rare birds as the white-tailed and Pallas's sea-eagles (*Haliaetus albicilla* L. and *H. leucoryphus* Pall.), the lesser and larger spotted eagles (*Aquila pomarina* Brehm. and *A. clanga* Pall.) and the steppe eagle (*Aquila rapax* Temm.). For example, in the delta of the Ili over 80 % of pellets of the white-tailed sea-eagle found during the warm period of the year contained the remains of this rodent. Such a typically fish-preying bird as the osprey (*Pandion haliaetus* L.) has started to feed on the muskrat. It has also been found out experimentally that among birds belonging to species of the owl family the one that hunts the muskrat, although not very often, is the eagle owl (*Bubo bubo* L.). It is worth mentioning that the great black-headed gull (*Larus ichthyaetus* Pall.) has partly started to feed on the young of the muskrat. For instance, on the Alakul'sk Lakes (south-east Kazakhstan), such remains were discovered in 16 % of the crops of this bird examined. Even the crow (*Corvus corone* L.) has started to feed on young muskrats.

We have recorded cases of fishes attacking the muskrat, among them the catfish (*Silurus glanis* L.), the pike (*Esox lucius* L.); while reptilian predators one can mention are the water snake (*Natrix tesselata* Laur.) and *Elaphe dione* Pall...

It is interesting to note that such animals as the wild boar (*Sus scrofa* L.) and the reindeer (*Rangifer tarandus* L.) are now attracted by the dwellings of the muskrat. It is mainly in winter, in search of food (roots, stalks), that they destroy these dwellings, thus making them unavailable for the muskrat, for the alternative passage into the water soon gets frozen.

The results of studies of some parasitic and infectious diseases of the muskrat testify to the fact that in the course of acclimatization of animals new, complicated and multiform biotic bonds are created. Within a relatively short period of time the muskrat became infected by at least 17 species of parasitic worms and about 15 species of ectoparasites which are known to infest animals belonging to such orders as *Carnivora, Rodentia, Lagomorpha* and *Artiodactyla* and a number of birds (*Anseres, Steganopodes, Gressores, Accipitres*).

At the same time it has been noticed that the original parasitic fauna is deteriorating. Only 8 species of parasitic worms and two species of ectoparasites characteristic of the North American population have survived on the muskrat. Certain of these parasites were found on the muskrat in England and Finland.

Close contact between the muskrat and the water vole (the latter being the principal vector of tularaemia infection) is resulting in recurrent outbreaks of tularaemia and Omsk haemorrhagic fever disease among the muskrats.

In addition it is subject to epizootia of hay fever as well as to some other zoonoses. When studying ecological and epizootic bonds of the new and aboriginal species in the wild, we discovered an interesting fact: in some regions the muskrat filled the main ecological niche of the water vole, dislodged it and in the process notably improved the local natural conditions for tularaemia.

After the muskrat was introduced into the fauna and its number grew, the food position of many species of raptorial animals (mink, Siberian weasel, stoat (*Mustela erminea* L.), Alpine weasel, steppe polecat (*Mustela eversmanni* Less.), fox) became more abundant and stable. The dwellings and food stores of the muskrat are used as the basis for the nests of many species of birds inhabiting the same area. On the other hand geese (*Anser* spp.), resting on the dwelling mounds, contaminate them with faeces and compress the walls which forces the animals to abandon them. The fact that in winter the muskrat takes care that the air holes in the ice should be kept open favours aeration of the water and to a certain extent prevents the death of fish from oxygen deficiency in lakes which are without outlets. The habitat conditions for fish are also improving, for coarse vegetation is eaten up by the rodents.

This far from complete list of interspecific bonds concludes this short account of preliminary results of studies carried out in our country. The fact that the indigenous Russian *Desmana moschata* L. and the introduced *Ondatra zibethica* L. live together in the same waters is undoubtedly resulting in a decline of the number of the former species.

NUTRIA OR COYPU (*Myocastor coypus* Moll.)

In 1930, 113 of these animals were brought to the USSR from Argentina with a view to rearing them in captivity as well as carrying out some tests on the acclimatization of this South American rodent in natural conditions. A further 2,500 animals were brought mostly from breeding farms in England and Germany within the two years that followed.

During the period 1930-1941, about 1,100 imported coypus, as well as many others of local origin, were released in the Caucasus and a certain number in Central Asia. After the second World War the settlement of locally bred coypus was carried out on a greater scale. Much attention was paid to the problem of acclimatizing the rodent in the republics of Central Asia. As could well be expected the process of acclimatizing the South American rodent was complicated, difficult and long, despite the fact that the coypu was released in regions situated to the South of 45° N. Lat. There were a lot of failures and disappointments. In Transcaucasia even though winters are less severe one could witness a mass death of coypu, and in some reservoirs it disappeared entirely as a result of cold weather, hunger and the pressure of enemies. This was mainly caused by the fact that the coypu in constrast to the muskrat cannot provide itself with food when underwater parts of plants become unavailable to it. Neither does it build dwellings above ground which would protect it from low temperatures and against enemies. The burrows it digs are primitive, last only for a short time and cannot be easily replicated, because it usually lives in low swampy ground sloping gently into the water.

It was necessary to devise new ways and methods of breeding and keeping coypu to create conditions for ensuring a steady growth in numbers. Use was made of a new so-called semi-free method of breeding. In the warm period of the year the animals live freely in natural conditions. Before their waters get frozen as large a part as possible of the coypu population is caught. Some of the beasts are killed for the sake of their skin, but the young as well as some adults are kept in cages and poultry-yards until the spring. The application of these methods has made it possible to increase greatly the population of coypus and also the production of skins and, in general, the extent of the fur-farming industry's network.

It is important to note the following: under new conditions and in the course of a long period of time the coypu has acquired a number of new economically valuable properties. For example, its moult and reproduction periods have somewhat changed in keeping with the climatic peculiarities of particular regions. The coypu has become notably more frost resistant; its tail, paws and lips are now less often frostbitten even when the temperature of the air is lower than usual. The Argentine beasts released in the waters of the Kuban plavni (semi-permanent flooded areas) in 1932, perished during the very first winter though the temperature of the air did not drop lower than — 11° C. Eighteen years later coypus adapted to natural conditions of this country were released again at the same place. They have survived up to the present in the plavni despite the fact that some of the winters have been hard with much snow and frost, the temperature falling below — 15° C for relatively long periods of time. There is also a second example. In 1931 the Argentine coypu was released in the waters of the Amu Darya river valley (Turkmen SSR). They survived only the first winter which was relatively mild. In 1962 coypus were released in the delta of the same river (about 450 kilometers north of the previous area). The animals left in the area after the autumn catch survived the winter quite satisfactorily. At the present time coypu farms are distributed in the Republics of Central Asia, N. Caucasus, Transcaucasia and the Ukraine.

The economic result of acclimatizing coypu in the USSR is relatively low. After the release of the animals the first crop was taken on varying dates depending on habitat conditions and the number of established coypu. In the Armenian and Abkhazian Republics it was available in two years, in the Georgian Republic after a term of six years, in the Azerbaijan Republic not until after 14 years. The output of skins has risen relatively slowly. In recent years it amounted to 160,000 pieces, including the production from coypu farms where it is kept in captivity all the year round.

When studying the biology of the coypu in some parts of its habitat, it has been discovered that its biotic bonds as well as interspecific contacts are gradually extending. It has attracted new enemies and parasites and got new diseases. At the same time it has adapted itself quite quickly to feeding on local species of plants, thus becoming at least a partial food competitor of certain indigenous animals. For example, in the Tashkent Region the main foodstuff of the coypu all the year round comprises the following species of plants : false, lesser and dwarf bulrush (*Typha latifolia* L., *T. angustifolia* L., *T. minima* L.), floating pondweed (*Potamogeton natans* L.), common reed (*Phragmites communis* L.). In Transcaucasia the main foodstuff of the coypu comprises the following plants : lesser bulrush, reed, water-lily (*Nymphaea alba* L. and *N. candica* Presl.), water-chestnut (*Trapa hyrcana* Woronow and *T. colchica* Albov), fennel pondweed (*Potamogeton pectinatus* L.), tape-grass (*Vallisneria spiralis* L.), Dallis-grass (*Paspalum digitaria*), bur-reed (*Sparganium ramosum* Huds., *S. polyedrum* Asch. and Gr., *S. neglectum* Boely), whorl-grass (*Glyceria aquatica* Presl.), yellow-flag (*Iris pseudocorus* L.), galingale (*Cyperus longus* L.). The animal food of the coypu which it prefers to any other is the mussel (*Anodonta cygnea* L.). Some species of the above-mentioned plants are eaten by wild hogs, brown rats (*Rattus norvegicus* Berk.), bandicoot-rats (*Nesokia indica* Gray) and water voles, as well as by some birds such as the coot (*Fulica atra* L.) and the purple gallinule (*Porphyrio poliocephalus* Latham).

The most dangerous enemy of the coypu is the jackal, which is very common in several parts of the same habitat. It should be noted that at first it did not touch even dead bodies of coypu but later, especially at the season when water is frozen in the wetlands, the coypu became an important addition to the food of this predatory animal. For example, in the Abkhazian Republic remains of coypu were discovered in 26 % of stomachs examined and of droppings collected in the warm period of the year, and after the waterways become frozen the proportion was 89.4 %.

There is reason to believe that the same phenomenon is also becoming characteristic of the behaviour of the fox, wolf and jungle cat, *Felis chaus* Güld. To begin with the fox preyed only on newborn coypu and on ones which had died. As far as could be determined from footprints left on the snow it did not hunt adults. Cases of coypu being attacked by birds of prey, and diurnal ones in particular, are, it seems, infrequent. The fact that coypu remains have sometimes been discovered in the stomach of the marsh harrier could be attributed to its feeding on dead bodies of coypu, as is also the case with the brown rat.

Preliminary helminthological investigation testify to the fact that the coypu has acquired new species of internal parasites. For instance, the coypu settled in Azerbaijan proved to be infected with *Ascaris* sp., *Gastrodiscoides rominis* and *Plagiorchis arvicolae.* The local host of the second of these species are the water vole and the brown rat, the former being also the host of *Plagiorchis arvicolae.* The coypu settled in Armenia proved to be the host of *Fasciola gigantica* Coll. and *Hymenolepididae* gen. sp.

In certain regions the coypu has been exposed to epizootia of a number of diseases characteristic of some local animals. We have recorded outbreaks of such diseases as paratyphoid, pseudotuberculosis, leptospirosis and tularaemia. However up till now coypu have shown comparative immunity to diseases of an infectious nature. Due to its physiological and biological characteristics, as it now appears, it is not an important factor in maintaining foci of infection or spreading epizootias.

It is worth mentioning that as a result of the intense activity of coypu the habitat of many species of local animals is considerably improving. By eating out coarse water vegetation, the coypu raises the efficiency of fishing areas. The old abandoned nests of coypu are used as a foundation for the nests of greylag geese and some other birds. The feeding places and nests of coypu are used by frogs, tortoises, water snakes, marsh birds and waterfowl, birds of prey, water voles and brown rats, for resting and devouring their food. Some of these animals finish off the remains of food brought by coypus to the feeding places.

THE LONG-TAILED CHINCHILLA (*Chinchilla laniger* Mol.)

In 1960, 200 of another South American rodent, the long-tailed chinchilla, were brought to the USSR. At first the animals were kept at the experimental animal-breeding farms of the Moscow and Kirov Regions, but later on they were taken to the Kirghiz, Tajik and Uzbek Republics.

The main tasks in the first stage of acclimatization of the chinchilla in our country included detailed studies of its biology, to discover the best methods for keeping and breeding it in captivity and building up its numbers. Acclimatization of this rodent to natural conditions comprised the second stage of the trial. A small group of chinchillas was first released in the Tajik Republic where the Darvaz mountains slope down to the river Pyandj (28° 30' N. Lat.). Before being released the animals were kept in open-air cages for a whole year, when a number of interesting observations were made. The animals soon grew wild and became cautious. They began to use hollows between stones for refuge and shelter. Some cases were observed of chinchilla perishing from the bite otf he snake *Vipera lebetina* L. By next spring not a single one of the chinchillas could be found in the area where they had been released.

THE RACCOON (*Procyon lotor* L.)

Introduced in 1929, when two animals were brought to the USSR and kept in the Tashkent zoo, work on acclimatization of this species started in 1936. The breeding nucleus was comprised of the 22 animals born in the zoo and a further 21 raccoons were brought from breeding farms in Western Europe. When effecting subsequent releases, beginning in 1949, use was also made of raccoons trapped in Azerbaijan. The total number of raccoons released, for the most part in southern regions of the USSR, that is in the Caucasus, Central Asia, Primorye Territory and Byelorussia, amounted to 1,200 animals.

The main criteria in selecting suitable areas for releases of the raccoon were founded on the knowledge that this species cannot stand cold periods exceeding 265 days in length with sub-zero temperatures. This limit is quite characteristic of natural conditions in its home country, that is the northern parts of its range in Canada. Nor can it survive at temperature below minus 42^0 C. In our country use was made of certain regions in Transcaucasia with most favourable climatic conditions for releasing the raccoon, namely freezing temperatures limited to 125 days in duration and never falling anywhere near as low as the critical point. The greatest density of population of the raccoon has been recorded in the Azerbaijan Republic in the terrain along lower parts of river valleys, in broadleaved forests with many fruit trees where the humidity index is high. In Kirghizia and Byelorussia the raccoon found itself in a somewhat different habitat. In Kirghizia it was released in *Caryocarpus* woods where the climate is much drier and the snow cover is more stable, lasting for a longer period of time. In Byelorussia it was established in comparatively young mixed woods with very limited opportunities for natural refuges. The plant food in this area is rather poor compared to more southerly regions where the raccoon had also been released. It was necessary to build artificial shelters for them, although this in fact provided certain advantages.

The euryphagous characteristics of the raccoon differ from many of those which distinguish local resident species. The raccoon provides itself with food at all levels in the forests from the crowns of tall trees down to the herbaceous soil-covering of wetlands. The list of what it eats comprises over 250 species of animals and plants. Even in years of crop failures, when its preferred food in not available, it has been found that the raccoon can fatten itself by autumn unlike other omnivorous beasts such as the badger (*Meles meles* L.), bear (*Ursus arctos* L.) and wild boar (*Sus scrofa* L.), which were found to have become noticeably emaciated. One of the prominent features characterizing the food habits of the raccoon is that it feeds on many kinds of different foods in small and approximately equal quantities. The number of preferred foods is relatively small. Furthermore in different habitat conditions one kind of fodder can be successfully replaced by another.

For example in Transcaucasia the proportion of plant food in the diet of the raccoon is 63.5 % and of animal food 46.5 %. The most commonly found plant food includes green briar berries (*Stnilax excelsa* L.) 37.8 %, hazel nuts (*Corylus avellana* L.), acorns of *Quercus longipes* Stev., Virgina creeper (*Vitis sylvestris* Gml.), cherries and plums (*Prunus* sp.) and other berries and fruit. The main animal food includes insects (*Insecta*), amphibia (*Amphibia*), molluscs (*Mollusca*) and to a less extent fish (*Pisces*) and birds (*Aves*).

In the North Caucasus the raccoon feeds largely on mouse-like rodents and crawfish (*Decapoda*). In Kirghizia it feeds on reptiles (*Reptilia*) and insects, as well as to a large extent on birds and their eggs. As to plant food, nuts are of primary importance. In Byelorussia its principal food is mouse-like rodents and as plant food—acorns.

In spite of the fact that the areas inhabited by the raccoon also contain stronger rapacious beasts it has very few enemies. Among them we should mention first of all the marten (*Martes flavigula* Bodd.) in the Far East and, in some other areas, wolves and stray dogs.

The jackal and the fox cannot get the upper hand over the raccoon. The lynx (*Lynx lynx* L.) cannot catch it for it can easily climb on thin branches and so beyond reach. The raccoon itself is aggressive only to small rodents, reptilia, amphibia and insects, which for the most part are harmful for fishery, forestry and rural economy. Among preferred species of insect food we should name the following: click beetles (*Elateridae*), weevils (*Curculionidae*), leaf beetles (*Chrysomelidae*), longhorn beetles (*Cerambycidae*), crickets (*Gryllidae*) and water beetles (*Dytiscidae*).

The raccoon is highly resistant against helminth diseases, although analyses of droppings showed the presence of intestinal worms' eggs (*Crenosoma* sp. and

Uncinaria sp.). As it has been proved by a great number of analyses the raccoon is not infected by any kind of specific endoparasite nor have we detected any infectious diseases.

Hibernation of the raccoon should be considered as an important feature of its biology. In the hibernating period the raccoon is removed completely from the complicated chain of its trophic interdependence with the native fauna.

In years of crop failures the raccoon might be regarded as a competitor of a number of species which are less adapted to diverse diets. When the number of amphibia is insufficient, it will be a competitor of the badger. When the crops of the plants food are poor it will be a competitor of the wild boar, bear, Fat Dormouse (*Glis glis* L.) and to a certain extent of the stone marten (*Martes foina*), and when the population of small rodents declines too much it might be a competitor of the fox and so on. At the same time all these species of animal have their own habits of hunting for foodstuff which differ from those characteristic of the raccoon.

In the USSR the raccoon has filled in its own ecological niche and one which is not natural to any other species in spite of the fact that to a great extent it eats the same food as a number of carnivorous beasts and vegetable-feeders.

The American Mink (*Mustela vison* Briss.)

This was introduced into the USSR in 1928. Up to 1933, mink was kept only in cages, for it was necessary to build up the stock. After that date it was decided to start work on acclimatization of the species to natural conditions.

The ecological plasticity of the mink provided conditions for establishment over broad areas in European and Asiatic parts of the USSR. It has spread to different geographical and natural zones beginning with the islands of the Pacific Ocean and Kamchatka and extending to Byelorussia and Transcaucasia. The only regions where it is absent are the northern and southern deserts and high mountain areas. And yet there are only a few parts of its present range where the density of population of the mink has attained the level which makes it available for hunting.

The analysis of results obtained in acclimatization shows that the failure of introduction of the mink in a number of regions is most probably caused by high floods, extremely low temperatures affecting its food supplies, the lack of frost-free open water, and inadequate availability of natural refuges.

The success of *Mustela vison* is to a certain extent affected by such adverse factors as the presence in a number of regions of the European mink occupying a similar ecological niche. The characteristic habitat of the acclimatized species is represented by fluvial plains and inland basins with definite and sometimes high shores covered with woods or shrubs. The large list of food eaten by the mink comprises over 200 items of animal and plant species. Of this, however, in certain parts of its present range, only 5 % consists of the more commonly used and widespread types of food utilized by the mink.

According to the data from different regions the list includes: mouse-like rodents—over 50 % ; the water vole—up to 30 % ; birds—up to 17 % ; fish—up to 55 %; Amphibia and Reptilia—up to 18-20 % ; crawfish—up to 86 %; insects—up to 25 %.

All of the animals mentioned above are very common and widespread in the areas inhabited by the mink. A number of native resident species also feed on the same species of animals though in somewhat different proportion. These local species include: the European mink, the Siberian weasel, the stoat (*Mustela erminea* L.), the weasel (*Mustela nivalis* L.), the pine marten (*Martes martes* L.), the Russian sable (*M. zibellina* L.), the polecat (*Mustela putorius* L.), the otter (*Lutra lutra* L.), the fox, the raccoon dog, the lynx and some others, as well as a number of predatory birds such as the common buzzard (*Buteo buteo* L.), harriers (*Circus* spp.) and several owls.

The euryphagous characteristics of the mink and the abundance of the food prey in natural conditions makes it obvious that even in years when the quantity of rodents becomes low, the mink does not become a serious food competitor of local resident raptorial beasts, whether mammals or birds.

The habitat and prey shared by mink and a number of raptorial animals has created conditions for the presence of the same kind of helminths. For example it has been proved by our studies that a number of minks not infected previously by parasites, when settled in the Tatar and Mordovian Republics, got infected by the following species: *Filaroides bronalis, Scryabingylus nasicola, Capillaria mucronata* and *Pseudamphistomum truncatum.* The above species of helminths were derived from the local European mink and the polecat, whereas the species *Eupariphium melis* and *Calliparia putorii* originated from polecats and the pine marten. In the Far East it has been found that mink is infected by ten species of parasites originating from other species of marten-type animals in the local fauna. In the Altai the " settler " was found to be the bearer of six species of helminths which it got while preying upon terraqueous reptilia, fishes, small rodents and insectivorous animals. Some of the helminths are common to the sable, Siberian weasel, badger (*Meles meles* L.) and otter.

The diffusion among mink of ectoparasites (ticks *Ixodes persulcatus* P. Schreb. and fleas *Ceratophyllus rectangulatus* and *C. penicilliger)* is characteristic of mouse-like rodents, roe deer (*Capreolus capreolus* L.), Siberian weasels and some other beasts.

A number of species of the local fauna attack *Mustela vison* and keep it under a certain control. However the mink is a minor part of their diet for it can be available only by chance. These animals comprise *a*) carnivorous species: lynx, wolverine (*Gulo gulo* L.), yellow-throated marten (*Martes flavigula* Bodd.) and wolf; *b)* birds : the eagle owl and other big raptorial birds; *c)* fishes : large species of pike and cat-fish.

CONCLUSION

Acclimatization of useful animals is an important economic problem for the Soviet Union. Diversity of geographical conditions as well as the social and economical peculiarities provide the necessary opportunities for carrying out extensive work on the enrichment of the fauna by acclimatization of native and foreign species of animals, fur-bearing beasts included.

The similarity between the landscapes of the USSR and the home habitats of the imported animals as well as the presence of comparatively free ecological niches suited to these animals has made the task of acclimatization easier and created opportunities for biological and economic success.

Essentially variable practical results of introduction of these species of animal into the fauna in various parts of the country were to a large extent determined by the abiotic factors, such as the hydrological regime of wetlands, duration of the warm season and of persistent snow cover.

Introduction of new species of animals into the faunal spectrum has not provoked any violation in historically formed biocenoses. As the density of population of the " intruder " increases in keeping with the extent of its range, its biotic bonds and interspecific contacts are enlarging. This entails the appearance of new enemies, parasites, diseases and competitors.

It has been proved by numerous studies that abundance of plant and animal food in the habitat, without very keen interspecific competition, has provided conditions for coexistence which does not cause severe food competition between resident and introduced species.

Different food habits and ways of hunting for food as well as individual adaptation with respect so seasonal qualitative and quantitative changes in food resources have contributed to the maintenance of the resulting equilibrium.

No new infectious diseases are known to have been brought in with the introduced animals but in some cases where the " intruder " is affected by certain diseases it has complicated the epizootic conditions existing in natural nuclei of infection.

The animals introduced into a new habitat have exhibited new qualitative characteristics with respect to unfamiliar species of parasitic fauna. Their former specific parasites both external and internal are disappearing, their place being taken by new species of parasites characteristic of some native animals. Infection of resident species by parasites brought in with the introduced species has never been detected.

The enrichment of biocenoses with new types of rodents has resulted in an improvement of the habitat status of many species of local animals. For example the food supplies of a number of carnivorous fur-bearing beasts have become more abundant and reliable as a result of multiplication of the muskrat.

The reciprocal influence between the introduced species and new habitat conditions entails morphological, physiological and ecological changes. The natural process of evolution of local populations of these species with distinct qualitative differences is steadily proceeding.

SUMMARY

Work on acclimatization of certain economically valuable species assumes an ever increasing importance in the USSR. Results and perspectives are discussed, including re-introduction of indigenous fauna.

Diversity of geographical conditions in the USSR as well as social and economical peculiarities have provided the necessary opportunities for carrying out

work on the enrichment of fauna, and some very interesting results have been achieved on acclimatization of four fur-bearing mammals:

Ondatra zibethica	muskrat
Myocastor coypus	Nutria Coypu
Procyon lotor	raccoon
Mustela vison	American mink

In 1965 the fur crop included an increase to 5 million muskat pelts per annum; about half of the crop of mink in the USSR is derived from the American mink.

Acclimatization is more likely to be successful where there are vacant biological niches, but during the process of the acclimatization of new species, there is always a biological interrelationship with indigenous species. When food was in free supply there was never competition between the two. Introduced rodents were subject to increasing natural predation. Numbers of internal and external parasites have increased from local parasitic infections; the burden of exotic parasites has decreased. The muskrat was subject to certain epizootics. The muskrat dislodged the water vole and expropriated its principal ecological-niche. In some areas the water vole was totally excluded. The muskrat can thus be credited with the elimination of diseases for which the water vole acted as a vector.

The natural expansion of the introduced rodent population has increased the prey species of the indigenous carnivores. On the other hand the presence of the American muskrat has caused the disappearance of the indigenous Russian *Desmana moschata.*

In acclimatized species one can sometimes notice certain morphological, physiological and ecological changes. Subspecific differentiation can then occur.

The paper makes no attempt to describe all these changes. Interrelations between introduced and indigenous species of animals and plants are extremely complex. The results described raise important theoretical and practical issues of interest to all countries who deal in acclimatization of animals.

RÉSUMÉ

Les travaux sur l'acclimatation de certaines espèces de valeur économique prennent une importance toujours croissante en URSS. Les résultats et les promesses de ces expériences sont examinés, y compris ceux de la réintroduction d'espèces de la faune indigène.

La diversité géographique de l'URSS ainsi que ses particularités sociales et économiques ont fourni les facilités nécessaires à l'exécution de travaux sur l'enrichissement de la faune, et quelques résultats très intéressants ont été obtenus dans l'acclimatation de quatre mammifères à fourrure :

Ondatra zibethica	Rat musqué
Myocastor coypus	Coypou nutria (Ragondin)
Procyon lotor	Raton laveur
Mustela vison	Vison d'Amérique

En 1965, la production de fourrure comprenait une augmentation de peaux de rat musqué ayant atteint 5 millions par an ; la moitié environ de la production de peaux de vison de l'URSS provient du vison d'Amérique.

L'acclimatation d'une espèce a plus de chances de réussir dans les endroits où des niches écologiques sont vacantes, mais au cours du processus d'acclimatation des rapports biologiques réciproques existent toujours entre les nouvelles espèces et les espèces indigènes. Lorsque la nourriture était abondante aucune compétition ne régnait entre les deux. Les rongeurs introduits furent l'objet d'une déprédation naturelle croissante. Le nombre de parasites externes et internes, provenant d'infections parasitaires locales, a augmenté ; le nombre de parasites exotiques a diminué. Le rat musqué était sujet à certaines maladies épizootiques. Le rat musqué délogea le rat d'eau et l'expropria de sa niche écologique principale. Dans certaines régions le rat d'eau fut totalement expulsé. On peut donc attribuer au rat musqué l'élimination de maladies dont le rat d'eau était le vecteur.

L'expansion naturelle de la population du rongeur introduit a augmenté les espèces prédatrices des carnivores indigènes. D'un autre côté, la présence du rat musqué d'Amérique a causé la disparition de l'espèce indigène russe *Desmana moschata.*

Certains changements morphologiques, physiologiques et écologiques peuvent parfois être remarqués chez les espèces naturalisées. Une différenciation au niveau de la sous-espèce peut donc se produire.

Le rapport n'essaie pas de décrire tous ces changements. Les rapports réciproques entre les espèces introduites et indigènes d'animaux et de plantes sont extrêmement complexes. Les résultats décrits soulèvent des questions théoriques et pratiques importantes intéressant tous les pays engagés dans des travaux sur l'acclimatation d'animaux.

THE REHABILITATION OF CERTAIN MAMMAL SPECIES IN CIRCUMSTANCES OF ENVIRONMENTAL DEGRADATION

by

Dr. V. G. HEPTNER

Biological Faculty and Zoological Museum
of Moscow University

Introduction of exotic species often achieves unsatisfactory results; whilst re-introductions are normally more successful. In the USSR particular interest in this subject has arisen as a result of research on the sable, European Bison and beaver. I will summarize the more important results concerning the two last named species.

European Bison. The work we are carrying out in the USSR on the European Bison is undertaken in co-operation with Poland. USSR and Poland are in possession of the largest stock, about 60 % of the world population. Poland started operating in 1926, and the material on which we are working was kindly given to us by the Polish Republic. Our co-operation is particularly based on a biennial meeting at which we plan a two year programme.

Before the first World War the USSR possessed almost the only surviving population of European Bison. More than 1,000 existed in Bielowieza and in the Caucasus. In 1920, only 5 pure-bred specimens, plus a number of hybrids, remained at Askania Nova. The possibility of obtaining pure-bred stock was out of the question. The re-establishment of this species was therefore dependent upon back-breeding. Firm success was achieved even before the second World War when the first specimens were introduced into the Caucasus National Park.

After the second World War there remained only a single pure-bred European Bison in the USSR. Due to the new relationship with Poland we were able to obtain 17 pure-bred Bison between 1946-1951. According to a plan drawn up by Dr. Zablocki a comprehensive rehabilitation programme was arranged for the species. Special stud-farms were organized in Bielowieza and in Prioksko-Tierassnoy National Park near Moscow. By January 1966 numbers in the USSR had reached 250 pure-breds (Bielowieza 69, Caucasus 181). This comprises more than one third of the total population. This means that the USSR possesses one of the two largest stocks in the world.

The main areas in which they occur in addition to the above mentioned, are Voroniez, Oka, Khapiersky National Parks and a few other places.

At the present time our principal aim is not only to increase the number of specimens but also to re-establish the species in the wild state. Our experience has shown that the European Bison can thrive under free-living conditions. In this way over 100 wild-bred Bison now exist in Central Russia. The Bison can live in heavily populated areas and is no more dangerous than the moose.

A particularly interesting situation has occurred in the Caucasus National Park, where there is a herd containing a small admixture of American Bison blood. The herd numbers 500 individuals and occupies a range of 30,000 ha: each year the range is extended by a further 1,500 ha.

In the northern part of its range the Bison occupies a region in which environmental conditions have undergone substantial modification during the 1,000 years which have elapsed since the species occurred there in a free living-state. In the Caucasus, on the other hand, the species disappeared only as recently as 50 years ago.

These differing circumstances represent widely contrasting ecological conditions.

Beaver. In ancient times the beaver was of great economic importance and was subject to regular management. During the 14th and 16th centuries traditional management practices were relaxed and from then on the decline accelerated. The animal formerly occupied almost the whole of the European part of the USSR and a part of Siberia. At the beginning of the 20th century only a few hundred remained in Voroniez (Biolorussia) near Kiev and in western Siberia. In the 1920's, National Parks were created in these areas and the beaver population increased rapidly. The most important area was and still is Voroniez National Park. Since 1934 translocations have taken place from Voroniez to other National Parks as well as other unprotected areas. Between 1934 and 1947, 700 beavers were translocated from Voroniez and by the beginning of 1966 the total had reached 2,000. Since 1948 a total of about 3,500 individual Bielorussian beavers have been transplanted. At the same time translocations from the newly established colonies have also taken place. During the last 30 years about 9,500 beavers have been successfully moved in this way. As a result of protection and management there are now 45,000 to 50,000 beavers in the USSR.

In 1963 the population had reached a level at which it was possible to commence cropping. This is being done because the range is now adequately stocked. Moreover, there is an overabundance of beavers and limited food supplies. The new biocenotic relationship shows the need for these measures.

The Centre of all our practical and applied scientific work on the beaver is Voroniez National Park, where there are adequate laboratory facilities and competent scientists such as Dr. Jarkov and Prof. Lavrov.

COMMENTS

(Papers of Lavrov and Pokrovsky, and Heptner)

H. V. Thompson (United Kingdom) drew attention to the different policies of the governments of the USSR and Britain with respect to introduced species. Whereas the USSR very actively encouraged the introduction of many mammal species, Britain has spent a considerable sum of money in exterminating the muskrat and nutria, and is currently attempting to destroy an established population of mink. The statements in the Papers that no adverse reactions from the introductions of furbearing mammals had yet come to notice, was of considerable interest.

A. de Vos (Canada) asked if the meat of such fur-bearers as beaver and musk-rats is of use in the USSR. In Canada beaver populations are locally excessive because of inadequate harvesting and these problems might be eliminated if the animals could be utilised for meat.

Dr. Heptner, replying: beaver meat is not normally eaten in the USSR and it is not anticipated that its consumption would ever be considered desirable.

V. Puscariu (Rumania) stated that he agreed completely with views that had been expressed about the dangers involved when exotic species are introduced into small countries. Despite the results in the USSR, Rumania was one such country and large expenditures had had to be incurred in order to rid the Danube delta of muskrats.

K. R. Ashby (United Kingdom): can any continental vertebrate predators be considered to control prey species ? The contrary is often asserted, yet the evidence from the biological control side would indicate that predatory mammals might be similarly controlling.

A CHANGING AQUATIC FAUNA IN A CHANGING ENVIRONMENT

by

A. DUNBAVIN BUTCHER

Director, Fisheries and Wildlife Department of Victoria,
Australia

INTRODUCTION

The introduction of living fish into a country is a centuries old activity and the earliest importations were doubtless motivated by a need for food. Much later the demands of recreation resulted in the introduction of " sporting " fish and the interest in keeping aquarium fish greatly increased the range of species transported from one place to another. Fish were also introduced for the purpose of mosquito control.

Public or sectional interests have always played a large part in promoting the introductions of fish from one country to another.

In this discussion, our primary concern is with food and sport fishes. Their introduction into a foreign aquatic environment with its associated fauna is usually deliberate; the entry of aquarium species is usually inadvertent.

No consideration was given to the possible implications of acclimatisation in earlier years. In Australia, any acknowledgement and appreciation of the potential ecological significance of exotic fish species dates back little more than two decades.

Special circumstances exist in Australia. Climatically, Australia differs substantially from other large land masses. The first European settlers arrived less than 200 years ago, so that its developmental history is very short.

1. THE AUSTRALIAN ENVIRONMENT [1]

The climatic peculiarities of Australia are such that any discussion on changes in the environment which might have been brought about by introduced fish species must be developed against this background.

Australia is the driest of all continents with an extremely variable climate.

It should be appreciated that the total area of Australia is 2,971,000 square miles which closely approximates the area of the United States of America,

[1] This information is largely taken from *Water in Australia,* M. D. GANGE and W. D. DUNK, 1965. *Cbeshires.* Melbourne.

excluding Alaska and Hawaii. Only about 7 per cent of the area of Australia is above an elevation of 2,000 feet and this is largely confined to the eastern coast, whereas approximately 45 per cent of the United States of America is above 2,000 feet in elevation.

Australia lies mainly in the 15° to 35° latitude belt which is the zone of most of the world's deserts, both in the northern and southern hemispheres. The average rainfall is 17 inches per year compared with 26 inches for all the land areas of the world and the wetter areas are confined to the coastal and mountainous parts of the continent (see Fig. 1).

Australia, north of the Tropic of Capricorn, receives summer rains and the winter is dry. In southern Australia the reverse applies. A great arid area lies approximately between 20^0 and 32^0 south latitude. The Great Dividing Range runs parallel with the eastern coast line and has a marked influence on rainfall which occurs in all seasons and is greatest near the coast (see Fig. 2).

Not only is the rainfall over Australia, as a whole, low but it is very variable from year to year, resulting in droughts in some years and floods in others. The main belt of reliable rainfall lies in the winter rain regions in the south and south-east. The northern fringe is the only area in the tropics which has a rainfall which is as reliable as in the south.

Over most of the mainland, stream flow is intermittent or non-existent and in fact no other continent has such a sparse river system. Perennial streams are confined to a narrow strip along the northern and eastern coasts, and along small stretches of the southern coast.

The average annual discharge of all rivers is approximately 280 million acre feet and this is equivalent to a run-off of 1.8 inches over the whole continent, including Tasmania. The total annual Australian river flow is less than the annual discharge of the Saint Lawrence in North America.

The Murray River and its tributaries form the largest river system with a catchment covering 414,000 square miles which has an average rainfall of 17 inches. The system has an average annual flow of 12 million acre feet.

The situation is even more extreme in that Australian streams are variable, both during each year and over a period of years. This is associated with the variability of the annual rainfall over the catchment areas. Two examples will suffice. The Darling River, the longest tributary of the Murray, has an average annual flow of 2,153,000 acre feet, but flow has been known to vary from 1,000 to 11,000,000 acre feet in different years. The Goulburn River, another tributary of the Murray, and which is one of the most dependable of the larger streams, has an average annual flow of 2,300,000 acre feet but this has varied from 567,000 to 6,000,000 acre feet.

To conclude this brief description of the inland water resources of Australia, the uneveness of the distribution of rainfall is further illustrated by the fact that something like two-thirds of the water flowing in streams is north of the Tropic of Capricorn.

2. The demands on the water resource

The climatic peculiarities of the Australian continent establish basic limits within which changes due to introduced species may develop. However, because of these very peculiarities, the changes brought about in the environment to meet the community's needs are gross and it is within this new framework that the changes due to introduced species must be examined.

It is essential that this further step be taken because the new and radically changed environment must exert its own influences on both the indigenous and non-indigenous aquatic faunas, and on the inter-relationships between these faunas.

The very great man-made changes in the aquatic environment are restricted to that small proportion of the continent which is being developed intensively. This is well illustrated by the situation in Victoria which is the most intensively developed of all the states. The Great Dividing Range runs approximately in an east-west direction across it and three quarters of the available water north of the Range will have been stored and regulated when works already approved have been completed. It is expected by 1980 that all the rivers of northern Victoria will be used to the greatest extent practicable.

In a country such as Australia, water conservation is all important. Variability in stream flow and in annual rainfall, the low flow of rivers and the high evaporation rate require the construction of relatively large storage reservoirs. The amount of storage per irrigated acre has to be much higher than it is in other countries; it is approximately twice as high as in the United States of America and as much as 20 times that of India.

3. CHANGES IN THE AQUATIC ENVIRONMENT BROUGHT ABOUT BY WATER CONSERVATION

Impoundment walls present a physical barrier to fish and this is a serious problem if the species involved are migratory and do not readily utilize a fishway. When water is abundant, it is possible to maintain flow downstream and in a fishway, which will enable fish to negotiate the barrier, but in Australia, water conservation practices rarely allow the discharge of water for fish management.

Impoundments may bring about temperature changes which may be upwards or downwards. In a Victorian storage where the draw-off point is at a depth of 200 feet, the water discharged in the summer months may be as much as 20F^0 cooler than the water in the stream system. In this instance, indigenous fish have been displaced for many miles downstream and their place has been taken by rainbow and brown trout.

Impoundments function as flood control devices and floods (and variability in flow) are a characteristic of Australian streams—they are part of the normal cycle.

Conservation, irrigation, flood control and " improvement " of waters of the Murray - Darling system (see Fig 3) have brought about substantial changes in the total stream environment. Relatively few of the natural characteristics of the uncontrolled river system now remain. The major physical elements contributing to the changes are impoundments (there are more than ten large structures on the whole system); four diversion structures; thirteen locked weirs on the Murray alone and numerous small impoundments and hundreds of miles of levee banks. These structures and their operation have produced very significant physical and chemical changes in the river with concomitant serious biological effects on fishes.

Generally, the uncontrolled river was high, cool, turbid and fast flowing in spring or early summer and these conditions changed gradually until, by the end of summer, the waters were low, warm, slow flowing and relatively clear.

The transition from spring to late summer also brought changes in the chemistry of the water. The full significance of this natural pattern is not yet well understood. However, it is certain that the initiation of breeding in some, if not all, native fishes is greatly influenced by the natural seasonal changes in the water. Sexual development will cease if the changes do not follow their normal patterns fairly closely.

Some of our native fishes may require a pre-spawning migration—probably upstream. Tagging experiments with golden perch have shown that fish moved very considerable distances upstream and migrations of more than 500 miles in five months have been recorded. The time of the year when these movements would normally take place is the very time at which they are prevented by the operation of weirs. It is possible that the locked weirs on the Murray have already had a significant effect on the golden perch population and perhaps on some other species.

Natural river flush is of great importance to fishes. The filling of the elaborate back water system results in the production of food organisms and the quantity produced is undoubtedly the biggest single factor in determining how many fishes the river system will support.

Where the river overflows its banks and floods lower areas, the stage is set for the spawning of a number of native species and, if the flood lasts long enough, the fish spawn so that hatching of the eggs is co-ordinated with the development of many small food organisms in the warm, shallow areas.

River flushes do not occur with the same frequency as they used to, nor does high water last so long. The construction of levee banks has, in some situations, made extensive spawning and nursery areas almost permanently inaccessible to fish.

Sudden rises in river level do occur in a natural system especially in feeder streams, but when a river is highly controlled, rapid rises become fairly common, particularly in areas just below impoundments. The sudden release of water can swirl young fish into an unfavourable environment.

Natural falls in river level tend to be slow whereas the falls produced by irrigation, power generation and water storage demands can be very sudden. They have been known to leave fish eggs high and dry and to strand young fish or empty them back into the river before they are ready to cope with the stream environment. Sudden falls also kill bottom-living food organisms in the newly exposed shallows.

Major diversions may direct young fish which are being carried downstream into a favourable environment but more often they become lost in a maze of irrigation channels.

In eastern Australia water conservation has brought about changes in zoogeographic boundaries and there are at least two instances in which streams have been diverted from one watershed to another, destroying a natural system.

4. The history of introduction

European colonisation of Australia commenced in 1788 and the purpose was to establish a penal settlement. The " First Fleet " carried a number of domestic animals but no fish. However, only sixty-four years after settlement began, the first attempts were made to introduce fish from England.

The introduction of fish presented many problems. The capacity of carp to withstand very unfavourable conditions in transit explains their successful introduction prior to 1860 but success with the salmonids was not achieved until 1864 when viable eggs of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) arrived in Melbourne en route to Tasmania. Some salmon eggs were kept in Melbourne, and the balance of the shipment was taken to Tasmania.

Early acclimatisation activities were essentially those of private citizens, acting independently or through acclimatisation societies which were particularly vigorous in earlier years. The period of greatest acclimatisation activity was between 1850 and 1875 and, from the viewpoint of overcoming the associated problems, it was a remarkable success. The emphasis was on sporting and foodfish and no consideration was given to the broader implications of acclimatisation. In that short period, nine of the twelve species of fish to be discussed were introduced and of these nine species, seven were first introduced into Tasmania and one was introduced into Victoria. The meagre evidence available suggests that the remaining species may have been taken into Tasmania. It is a matter of considerable interest that, although the greater proportion of introductions was made into Tasmania, the present distribution of the fish in that State, with the exception of the salmonids, is extremely limited. Active acclimatisation was taken further in the south-eastern corner of the mainland and this was due, as has been stated already, to the very great interest of the acclimatisation societies.

After 1875, there was little further activity in making introductions until governments began to take interest in the 1890's. They concerned themselves almost exclusively with the salmonids.

Of the twelve species of fish referred to above, five are members of the carp family, five are salmonids and the two remaining species are European perch (*Perca fluviatilis*) and the mosquito fish or top minnow (*Gambusia affinis*).

In the early years three carp species, the goldfish (*Carassius auratus*), the Crucian carp (C. *carassius)* and the European carp (*Cyprinus carpio*), may each have been imported as separate species but little attempt was made to segregate them in the records. Even today the situation is confused, particularly in reference to the goldfish and Crucian carp and little attempt is made to differentiate between them. They are widespread in Victoria and in New South Wales with the exception of the fast-flowing higher altitude streams; they occur in South Australia; their distribution appears to be limited to one water in Tasmania; carp are abundant in waters west of the Great Dividing Range and in some coastal streams in south-east Queensland and, although there is a record of their release in Western Australia, they are not listed in that State today. The European carp is today recorded from only New South Wales and Victoria.

Special legislation has been enacted in Victoria requiring the destruction of all European carp as a noxious fish but their illegal release in several localities and subsequent escape into nearby rivers has made their destruction impracticable.

The tench (*Tinca tinca*) thrives in sluggish or still waters and is fairly widespread in Victoria; it is limited to a few western streams in New South Wales and attains a high population in sluggish waters only; it is found in the Murray River and associated lakes in South Australia; the Tasmanian distribution is limited to slow-flowing streams and lagoons in the south of the State; the one acclimatisation attempt in Queensland failed.

The record of the introduction of the roach (*Leuciscus rutilis*) is obscure but it is believed that it was imported into Tasmania about the same time as the other carp. It was then introduced into New South Wales, Victoria and Western Australia but the only contemporary records of this fish are from two very limited areas in Victoria.

A consignment of eleven European perch (*Perca fluviatilis*) was imported into Tasmania in 1862 and a further consignment of ten fish into Victoria in 1868. This species is widespread in Victoria; it is common in the western rivers of New South Wales; it occurs in Tasmania, particularly in the Midlands area; it has had a limited success in Western Australia; it is found in all fresh water streams in South Australia but although an attempt was made to acclimatise it in Queensland, the species is not recorded from that State today.

The eggs of brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) were successfully shipped from England to Tasmania in 1864. Today Tasmania, Victoria, and New South Wales are the " trout states " of Australia. Early attempts to introduce the brown trout to Western Australia failed but more recent efforts have been successful in the few suitable streams. South Australia has established trout but Queensland had no success and only recently further tests have been initiated. The history of the Atlantic salmon is very different. Hopeful reports have been received from Tasmania from time to time but there is no evidence that the species survived. New South Wales has imported eggs during the last few years and has stocked one water system, but it is too soon as yet to assess this experiment.

A Victorian citizen imported the eggs of Quinnat salmon (*Onchorhynchus tschawytscha*) from California in 1874 but the venture was not a success. A further shipment in 1877 was successful but an attempt to acclimatise the fish in coastal streams failed. Tasmania imported eggs in 1901 and in 1910 but attempts to establish stream populations failed. Further importations were commenced in 1931, and a lake stocking produced angling results. Victoria has imported eggs at intervals since 1936 and has developed a spectacular fishery in one land-locked lake but this is essentially a management project. No reproduction takes place.

New South Wales imported brook trout (*Salvelinus fontinalis*) eggs from New Zealand some time around 1890 but the project was unsuccessful. Tasmania's early endeavour in 1905 was also unsuccessful, but the experiment was resumed in 1962 and a small start has been made in stocking selected waters.

The history of the rainbow trout (*Salmo gairdneri*) is strangely obscure. New Zealand obtained the first consignment of eggs from the United States of America in 1883 and New South Wales obtained eggs from New Zealand in 1894. Trout are now found in the Tablelands of New South Wales especially above 2,000 feet altitude. Queensland obtained eggs in 1897 and succeeded in one stream only. As with brown trout, a new programme has been initiated recently. Rainbow trout are widespread in Victoria and are found in Tasmania, Western Australia and in South Australia.

The last introduction to be discussed is that of the mosquito fish or top minnow (*Gambusia affinis*). The full account of its spread will probably never be known. It was brought to Sydney in 1925 and to Brisbane in 1929 but its spread was accelerated during World War II when Service camps throughout the country used the fish for mosquito control. It is now found in all the mainland states and it is probable that the pattern is similar to that in New South Wales where it is not found in streams at the higher elevations.

The total spread of introduced fish in relation to the area of the continent is not great. However, the widest possible distribution of some of these species in eastern Australia, and particularly south-eastern Australia, has been virtually achieved. In these areas acclimatisation has advanced and may be regarded as " highly successful " in respect to brown and rainbow trout, carp (goldfish and/or Crucian carp), European perch and mosquito fish. Possibly this applies also to tench within the environmental range which is acceptable to it. The tench does not appear to have " extended its frontiers " greatly.

Fishery administrations in Australia are now confronted with growing demands in support of further introductions. Frequent requests are made for the importation of American bass and these come from anglers and angling organizations. Australia is an affluent society; outdoor recreation is increasing in popularity very rapidly and there is the continual stimulus provided by North American sporting journals.

From the anglers' viewpoint the history of acclimatisation is the introduction of fish into waters which contained no fish which might be regarded as " sporting fish ". Current thinking is perhaps directed simply toward providing " better fishing ".

5. Indigenous fish

The importance of the indigenous fish of Australia's inland water system in the context of this paper is that a discussion of the " changes due to introduced species " requires consideration of the inter-relationship between four things : the enrivonment, the man-made changes in that environment, the introduced species and the indigenous fauna.

Australia has more than 2,200 species of fish but only a small proportion of these is found in the inland water system. This is not surprising as, compared with other large countries, the fresh water environment is not only limited but it is rigorous. The fish which have adapted themselves to this environment are, in many ways, unusual.

Although conflict between introduced and indigenous fish is probably limited to a few species of indigenous fish, these include the most important in the south-eastern part of the continent. They are the lowland " warm water species " —Murray cod (*Maccullochella macquariensis*), golden perch (*Plectroplites ambiguus*) and silver perch (*Therapon bidyana*); the Macquarie perch (*Macquaria australasicd*) and black fish (*Gadopsis marmoratus*) which occur in the highland and colder waters and the Australian bass (*Percolates colonorum*) of the coastal streams and estuaries.

6. The impact of introduced species

Studies of the environment, of the changed environment, of the indigenous aquatic fauna, and of introduced species have been entirely inadequate and it is only now that these subjects are receiving serious attention.

The introduced fishes are to be found in the areas of greatest environmental change consequent on settlement, yet there are many people who claim that any apparent adverse changes in the indigenous fauna are brought about by the introduced species. This is obviously a gross over-simplification.

Control exercised by the environment

Climate and natural environmental conditions have had a marked influence over the initial acclimatisation of fishes within the regions into which they have been introduced. The effective distribution of trout, both brown and rainbow, has probably been determined by temperature levels, both prevailing and extreme, and by the availability of suitable spawning areas. The deliberate endeavours to establish trout have been more intensive than for any other species and have covered a far wider area. They could be established possibly in some of the streams in the higher country in the north of the continent and certainly in more lakes and storages if this was determined to be desirable.

The European perch, widespread in south-eastern Australia, has a somewhat surprising distribution. It thrives in north-western Victoria in an eight to twelve inch rainfall belt, with high summer temperatures. This habitat is very different from that occupied by this species in its country of origin. It does not occur generally in the tableland country streams but is found in some water storages at the same elevation. This species has become adapted to a wide range of habitat.

A striking feature of the acclimatisation of European perch in Australia is the recorded introduction of only two consignments of fish—eleven in one instance and ten in the other.

The situation in respect to the roach is puzzling. Records indicate its initial distribution in Tasmania, Victoria, Western Australia and New South Wales. Today it is found in only two areas in Victoria and these differ greatly in character; one is a stream system and the second a water storage. It could have been reasonably expected that this species would become established in a number of localities.

The tench is limited to slow-flowing, sluggish streams or to lakes and ponds and is rarely found in other environments.

The carps are widespread, in both natural and artificial water systems. They are widespread in farm water supplies and survive very adverse conditions. They are not commonly found in the faster flowing streams. These and *Gambusia* are the only introduced fishes successfully acclimatised in Queensland.

Conflict: indigenous and non-indigenous fish

Table 1 summarises the scanty knowledge about three direct and simple conflicts between the more important of the indigenous and non-indigenous fishes. No attempt can be made to discuss the more complex inter-relationships.

TABLE 1

Introduced species	*Competes for food with*	*Competes for space with*	*Eats*	*Is eaten by*	*Other comments*
Trout (both species).	Macquarie perch.	Macquarie perch, trout-cod, blackfish.	Macquarie perch, trout-cod, blackfish.	Trout-cod, blackfish.	
European perch.	Murray cod, golden perch.	Murray cod, golden perch.	Murray cod, golden perch.	Murray cod, golden perch.	
Carassius carassius, C. auratus.	Silver perch, Macquarie perch	Silver perch, Macquarie perch	Macquarie perch, Murray cod	Murray cod, golden perch.	
Tench.	Silver perch.	Silver perch, Macquarie perch.			
European carp (very restricted range as yet).	?	?	?		Commencing to roil certain waters.

The table may suggest that the range of inter-action between the introduced species and the native species is great but the actual degree of inter-action has not been studied intensively. The conflicts listed are not all of equal significance. For example, trout are found associated with trout-cod in only a few localities. However, where they do occur together trout may have a significant effect on small trout-cod, very small Macquarie perch and small blackfish.

The effect of European perch on Murray cod, and golden perch is probably significant in certain areas.

Conflict: between introduced species

The Tasmanian authorities believe that there is significant conflict between European perch and trout, to the detriment of the latter, in that State. There is also some evidence however that brown trout eat the perch.

Trout and European perch are found associated in many localities in Victoria but the inter-relationship has received casual investigation only. Trout certainly consume large quantities of perch and there is satisfactory fishing for both species in many localities. Carps, European perch and trout occur in one well-known lake and fishing for both trout and perch is good. Even in the absence of adequate data, lakes containing populations of perch are stocked with yearling or larger trout as a precautionary measure.

In the majority of Australian trout waters where hatchery raised trout of both species have been released over a period of years angling results show that the rainbow trout are more readily taken than the brown trout. Eventually, this appears to result in a residual population of large brown trout and these are difficult to angle. Tasmania has taken active steps to meet this problem and large quantities of adult brown trout are removed, spawning of brown trout is limited or prevented and spawning facilities for rainbow trout are improved.

The relative ease with which rainbow trout may be angled, and the tendency for brown trout to establish territories would help to explain this ability of the brown trout to predominate in all Victorian waters. On the other hand, brown trout are known to be more selective feeders than rainbow trout and the later spawning of the rainbow trout can result in serious disturbance of the redds of brown trout.

Environmental change favours certain species

Impoundments result in additional and changed environments. Generally, impounded waters, apart from the question of their influence on a particular water system, favour the introduced species of fish. At best, residual populations of indigenous fish are found in impounded waters. Impoundments throughout south-eastern Australia have provided additional trout waters and a number support flourishing fisheries. These fisheries follow the normal pattern of a high growth and catch rate in early years with a subsequent decline to a more or less stable situation in which fishing is relatively poor. The majority of impounded waters have received their fish stocks from the stream system on which the impoundment is built.

European perch also thrive in a number of the impounded waters and provide excellent fishing, even at altitudes at which the species does not do well in the streams. Perch have been introduced into some of these waters when they have been used as live bait.

Goldfish and Crucian carp are also established in many impounded waters but do not provide a fishery.

There is some reason to believe that one indigenous species might be favoured by impoundments. The Australian bass (*Percolates colonorum*) may find a suitable and extended habitat in waters to be created by the proposed impoundment of some coastal streams.

The prevailing water temperatures downstream from an impoundment are frequently lower than the normal temperature pattern for the system as a whole. This again has in nearly every instance favoured introduced fish. Indigenous fish are displaced, not by the introduced fish, but by the radical changes in the environment. Several of the most famous trout fisheries in Australia are located in tail waters.

The extensive irrigation channel system has created another new environment and one which again favours the introduced species. Indigenous fish may make limited use of some of the major channels but this habitat is insignificant. The European perch is widely spread through the channel system and in some localities it has provided fishing for the first time.

Impoundments have adversely and seriously affected the fresh water catfish (*Tandanus tandanus*). European perch and the carps are frequently held responsible for the decline of the catfish but almost certainly the significant factor is the loss of habitat. The great anabranch or backwater system of the Murray and its tributaries has been progressively eliminated or made unavailable by water control works.

Other environmental changes

Discussion on changes in the environment has been limited to those brought about by water conservation activities. Other environmental changes have taken place and have had an adverse effect on indigenous fish.

The southern blackfish (*Gadopsis marmoratus*) appears to be intolerant of environmental change. A typical blackfish water is a stream with dense bank cover, shaded, fallen timber in the water and with quiet pools. The undue clearing of coastal hills and the coastal belt has destroyed these features. Table I demonstrates some conflict between trout and blackfish but the blackfish has fallen back also in areas where the only change has been in the environment.

The clearing of foot-hills in unstable country for primary production leads to the siltation of streams and this may be gross. The character of a stream may be changed through this one activity.

Stream improvement or channelisation as it is practised by water conservation bodies in various parts of the world also results in gross change. These changes may include the loss of bank cover, the deviation of currents, the loss of pools, the loss of gravel beds and so on.

Environmental change brought about by clearing of foot-hills, or by stream improvement has its effect on both indigenous and non-indigenous fishes.

Environmental change, in its many forms, favours introduced fish species over all. This may be direct, in the creation of new conditions which are favourable to introduced species; it may be indirect in that it creates conditions which are unfavourable to indigenous fish. In the case of the latter, introduced fishes may occupy the changed environment by default, if the conditions are particularly suited to their requirements, or they occupy the changed environment because they can tolerate the conditions provided.

7. ANIMAL INTRODUCTIONS - BENEFITS - DANGERS

This is simply a catalogue of the benefits and dangers which may be associated with the introduction of animals, and of fish in particular. This list is submitted without comment or judgement and, as a consequence, the items do not appear in any particular order.

" *Greater food production* "

Introduced fish may, for a number of reasons, contribute a greater protein output per unit area than the indigenous species. This may apply to natural water systems or it may be limited to some form of fish culture, for example, production under controlled conditions of trout and carp.

Within certain limits, fish production may be increased as the number of species present increases.

" *Greater variety* "

Recreational fishermen, as a group, seek a number of different species of fish. This may be for the sake of variety itself; it may be to provide angling under different conditions such as in streams, lakes, ponds, and so on; it may be to provide a range of fish which may be taken by different types of lures and baits and it may be to provide " all year round " fishing. Trout and European perch have met some or all of these requirements in south-eastern Australia.

" *Better sporting* fish "

Recreational fishermen place considerable emphasis on " fighting quality " or " gameness ", and trout satisfy many anglers.

" *Fish for new environments* "

Water conservation produces changed and new environments. Non-indigenous fish such as trout and European perch have been used successfully to stock impoundments, the stream immediately below them, irrigation channels and " improved " streams.

" *Filling empty spaces* "

Introduced fish may fill some habitats which have not been occupied by indigenous fish. In Australia lakes and ponds are notable examples and these have been stocked with trout, European perch and Quinnat salmon.

" *Biological control* "

Fish such as the mosquito fish or top minnow (*Gambusia affinis*) have been introduced for the specific purpose of mosquito control. The grass carp (*Ctenopharyngodon idellus*) is currently receiving attention in a number of countries as a possible means for controlling unwanted aquatic plants.

" *General ecology* "

Any introduction is, per se, a potential threat to the equilibrium of the system into which it is introduced.

" *Conflict* "

More specifically, the introduced species may displace the indigenous vertebrate fauna through direct competition. There may also be direct competition between two or more species of non-indigenous fish to the detriment of the more highly regarded species. The areas of conflict have been summarised in Table 1.

" *Environmental change* "

Introduced species such as the carps, and more particularly the European carp (*Cyprinus carpio*), may bring about marked environmental changes. These changes may affect the aquatic fauna and the quality and use of water for domestic and industrial purposes.

" *Disease* "

The introduction of fish may result in the introduction of new diseases which may threaten existing fish stocks, both indigenous and non-indigenous. A reservoir of disease organisms may be created, which, even though of no immediate concern, may pose a threat to whatever fish stocks might be encouraged in the future.

" *Behaviour* "

The behaviour of an introduced species in its new environment is largely unpredictable. This may create or add to management problems.

" *Difficulties in limiting distribution* "

It is in fact virtually impossible to limit or confine the distribution of an introduced species. Even if man's activities can be restrained, there remains the problem of dispersal by birds and other animals, and the transfer of water from one river system to another by water conservation activities. Outstanding examples of uncontrolled distribution are provided by the carps, European perch and *Gambusia.*

" *Predatory Fishes* "

Predatory fish may be introduced and in a country such as Australia this would present a particular problem.

" *Predation* "

The introduction of fish may encourage a build up in the population of an indigenous predator. This may result in greater predation on indigenous fish if the numbers of non-indigenous fish fluctuate markedly.

" *Forage Fish* "

Little or no attention has been paid to the species of small fish, many, if not all, of which form part of the food chain for larger species. There is evidence of decline in forage fish populations (*Galaxia* spp., *Retropinna* spp.).

" *Invertebrates* "

Even less attention has been given to the invertebrate aquatic fauna. There is circumstantial evidence of the decline of a number of invertebrates in waters into which fish have been introduced.

" *Acceptability* "

Some anglers have strong views on the need for adequate management of indigenous fish and many believe that non-indigenous species receive an undue share of attention.

8. CONTROLS EXERCISED ON THE IMPORTATION AND DISTRIBUTION OF NON-INDIGENOUS FISH IN AUSTRALIA

Importation into Australia

It is significant that the fishery authorities of Australia, both state and federal, have reached general agreement on the question of the importation of live fishes and their eggs. The authorities are associated in a body known as the (Australian) Commonwealth/States Fisheries Conference which has a permanent secretariat and which meets at least once a year. The members of Conference are the senior fishery personnel from the appropriate government departments. Matters which are determined by Conference and which are designated as policy matters are referred to the Meeting of Fishery Ministers which meets immediately after the Conference.

Conference has decided that live fish shall not be imported into Australia without its authority and this decision reflects the firmly held view of Conference members that importations, particularly of new species of fish, should be rigidly controlled. Conference is advised by an Advisory Committee on Importation of

Exotic Food and Sport Fishes and an Advisory Committee on Importation of Exotic (Aquarium) Fishes.

The two Committees have been active, meeting jointly, and independently. The recommendations of the Committees are considered by Conference where they may or may not be upheld. To date, all recommendations have been adopted.

In recent years, the import of living salmonid eggs has been permitted but the number of requests which has been cleared has been small and each has been from a Governmental agency. The importations have been made subject to conditions recommended by a Committee and approved by Conference.

Aquarium fish have been placed in four classes and the free importation, subject to quarantine controls, of a number of species is permitted. There is still considerable discussion on the whole question of the aquarium fishes.

Distribution of fishes within Australia

The degree of control over the distribution of non-indigenous fish may vary between states and territories but generally there is restriction on the release of non-indigenous fish. In Victoria the relevant section of the Fisheries Act states that:

> " Any person who without the written permission of the Minister releases or puts any non-indigenous fish or eggs of such fish into any Victorian waters shall be liable to a penalty of not less than Forty dollars nor more than Two hundred dollars. "

It is important that, by definition, the only water excluded from this provision is the indoor aquarium.

Under permit from the Victorian Fisheries and Wildlife Department, many land holders stock their farm water supplies with non-indigenous fish and are encouraged to do so. The limitations placed on the release of fish are not regarded as restrictive by the public.

The European carp (*Cyprinus carpio*) has been proclaimed by legislation to be a " noxious fish " and the keeping and/or release of this species is prohibited. Provision is made for proclaiming any species of fish as " noxious fish ".

9. Discussion

In retrospect, the effects of introductions, whether good or bad, may be listed and various hypotheses may be advanced to explain them; but the real issue which will affect future action is the question " are introductions of animals required? ".

The advantages and dangers associated with the introduction of animals are meaningless unless there is a measuring stick. The biologist and the ecologist may object on fundamental grounds but any judgement as to whether an introduction has been, or may be, beneficial or harmful must be tempered by a recognition and an acceptance of the *total demands* of a growing community—the local or national community initially, the world community ultimately. This requires that the person with appropriate training and experience should advise how community needs are to be determined and how benefits and dangers are to be assessed against these established needs.

Having made the assessment, the decision may be made that the dangers are acceptable.

The administrator must look beyond the immediate policy decision which determines the framework within which his immediate work is to be undertaken. He is confronted with what is possibly the greatest problem in the utilisation and management of the natural resources—that is, gaining public acceptance of measures which are designed to provide safeguards for the future. A minor example of this is the control exercised by the Australian authorities over the importation of live fish.

A number of people, including N.W. Moore, in England, have discussed the problem. Food supply and the human population are so much part of conservation that what we are concerned with is, in fact, the conservation of man. Economic motives for conservation are recognised and accepted; aesthetic motives are yet to receive the same wide recognition. If we are to consider the conservation of man, we must plan on a broad basis.

If fish are to be introduced into a country, it should be for a specific purpose. The production of protein might well be the over-riding consideration. A preliminary investigation is still essential and the diversion of a great deal of effort to the study is warranted. The end result should be a positive net gain if the project is to be given official support.

There may be degrees of need for additional protein (over-riding, primary, secondary) and as these diminish, the prerequisites for approval to import should be more carefully scrutinized.

It is suggested that the ecological implications of introductions cannot be ignored. The European carp in North America provides a gross example of environmental change. Whatever changes in the environment were brought about following the introduction of this fish into Europe have been lost apparently in antiquity. There must have been changes but these have long become part of the European aquatic scene.

The history of this species in North America is short and great changes have been brought about. The most obvious is the great increase in turbidity in many waters—an environmental change with many consequences. There have been changes, brought about directly and indirectly, in the aquatic flora and again the consequences have been many. These, taken together, represent major changes in the habitat of aquatic fauna—fish, mammals, birds and associated forms of life.

It is less than 10 years since the re-introduction of the European carp into Victoria. Changes in turbidity became apparent in less than 12 months.

The significance of environmental change has been discussed at length and particularly those changes which have some bearing on the inter-relationship of indigenous and non-indigenous fishes. Passing reference has been made to pollution and now the matter is again relevant because consideration is being given to man's total needs. Is pollution to be opposed because it is fundamentally wrong? Do we accept aesthetic despoliation on the grounds that the situation can be rectified, at least in so far as domestic and industrial water uses are concerned, by processing the water, maybe time and time again ? Fish production for protein can be entirely limited to production under controlled conditions.

The angler is really not of great importance in the total scheme of things (the role of angling in the great unsolved problem of use of leisure time is of importance but this is not the place to develop the subject). However, the angler has been of very considerable importance historically during the relatively short period in which the acclimatisation of fishes has become practicable and he has had a very marked influence on the directed movement of fish across the world.

Reference has been made to instances where non-indigenous fish have proved uniquely suitable to new and changed environments. If there is a public demand for such fish and if that demand can be met and the fish concerned confined to that particular environment because of its specific habitat requirements, can there be any valid objection to the introduction of that fish ? Possibly the answer lies largely in the specificity of the habitat requirements because it is, in fact, not possible to ensure that there will be no transfer of fish.

The pond culture of fish is a particular example of an artificial environment but the fish species are unlikely to be selected for quite the same reasons as those intended for the new environments which man created in the course of other developments. The measure here must surely be simply the total benefit to be gained.

Countries with active immigration programmes such as Australia have a special first generation problem as the migrant brings with him a traditional taste for many things, including certain fresh water fish. This can result in strong pressure for the introduction of certain species and there is still another problem that, the fish having been introduced, the second generation migrant has little or no interest in it. Even the population check of harvesting the fish is removed.

The roles of the biologist and of the ecologist are difficult. The case they have to make is clear but it cannot be sustained and it is here that much of our teaching fails. The student must be taught certain fundamentals but he must also be taught how to apply them.

The introduction of animals spells change and it has been suggested that, in the light of demonstrable needs of the community, these modifications should be assessed. If the real needs of the community can be met by introductions, then presumably introductions will take place. Is it not the role of " applied science " to determine how compromise might be achieved? Applied science must be granted a new status.

It is only by a full investigation of the potential effects of an introduction and a full assessment of the community's needs that any foundation can be provided for a rational compromise. It will provide for the protection of the indigenous fauna and flora and this will require the setting aside, difficult as this may be, of aquatic environment reserves which must be complete in themselves, for example, a section of a watershed.

The significance of a reserve goes far beyond the protection of certain representatives of the indigenous fauna. Each of the ecosystems selected as reserves will provide reference areas which will be of inestimable value to those responsible for the proper utilisation of the natural resources in the years to come. Matters which are of intense sectional interest at present may well become matters of national significance.

10. CONCLUSIONS

1. Any natural environment, particularly one influenced by an extremely variable climate, has a marked effect on the history of introduced fishes.

2. As a corollary to 1., man-made changes to the environment, under the conditions of an extremely variable climate, further influence the history of introduced fishes:

a) Artificially contrived stability in a stream of greatly variable flow brings about radical changes in the aquatic environment.
b) Indigenous fish are more adversely affected under these circumstances than fishes in a naturally more stable situation.
c) Conversely, because of the wide range of environmental conditions which are made available, there is a high probability of suitable habitat being provided for a non-indigenous fish.

3. The introduction of even small numbers of individuals has, under Australian conditions, led to the successful acclimatisation of a surprisingly high proportion of the species involved.

4. In an active acclimatisation programme the greater part of the final distribution of the species involved is determined early in the project by climatic and other environmental factors.

5. The influence of introduced species on the indigenous must be investigated within the limits set by
a) the natural environment, and
b) man-made changes in that environment.

6. Environmental changes may be the primary, or the only, factor influencing the welfare of a fish species. This influence may be favourable or adverse.

7. Predation is not regarded as a significant problem in fishery management in Australia.

8. There is a number of benefits to be obtained from the introduction of fishes; greater food production, better angling, the stocking of new and old environments which are not suitable for indigenous fish and so on.

9. On the other hand, there are inherent risks associated with introduction; unpredictability of behaviour, disease, conflict with indigenous fauna, difficulty in limiting distribution, general ecological changes and so on.

10. Australia has established machinery and procedures, on a co-operative basis, to limit and control the importation of live fishes and fish eggs.

11. An introduction should be authorised only if
a) it is for a specific purpose,
b) it will satisfy a real need of the community,
c) the need is long term and
d) there has been a complete assessment of the benefits and dangers which may arise from such an introduction.

12. The question of introductions should be a matter of national policy and, where there are common borders between nations, a matter of international policy.

13. The approach to teaching must be modified in many places to equip effectively trained persons to play their part in achieving the compromise which is a prerequisite to meeting a community's total need.

14. A significant facet of compromise is the setting aside of adequate reserves, preferably ecosystems, to provide a bank of reference areas.

ACKNOWLEDGEMENTS

I am indebted to Messrs. F. W. Cheshire, Publishers, for permission to use figures 1-3 which have been taken from " Water in Australia " by M. D. Gange and W. P. Dunk. I also wish to thank the authors for their readily granted permission to use these illustrations.

Mr. T. S. Pearce and Mr. J. K. Dempster of the Fisheries and Wildlife Department assisted greatly in checking the manuscript.

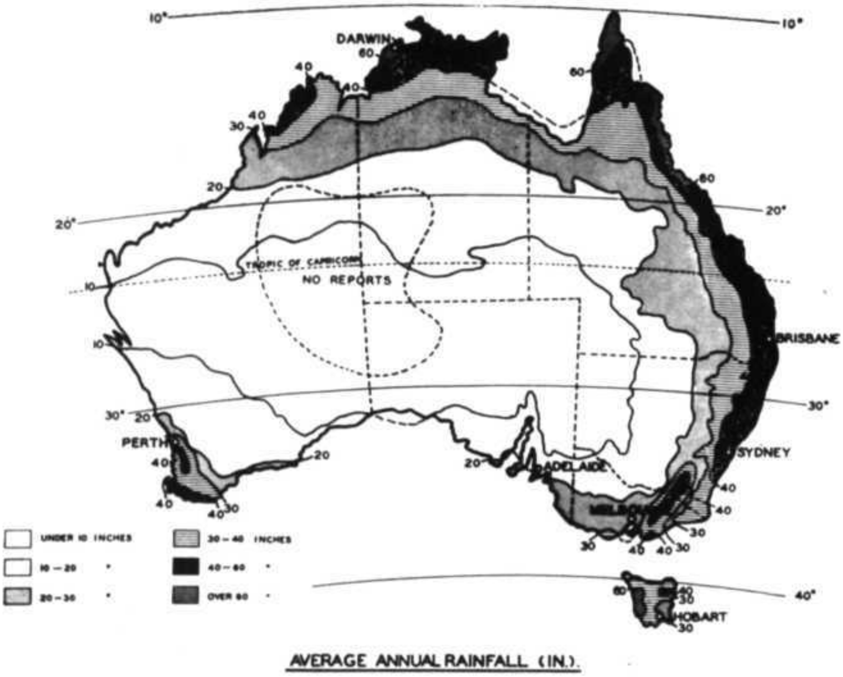

Fig. 1. Average annual rainfall (inches). Identification of *Stales* and *Territories* by their capitals : *Western Australia,* Perth; *South Australia,* Adelaide; *Victoria,* Melbourne; *Tasmania,* Hobart; *New South Wales,* Sydney; *Queensland,* Brisbane; *Northern Territory,* Darwin.

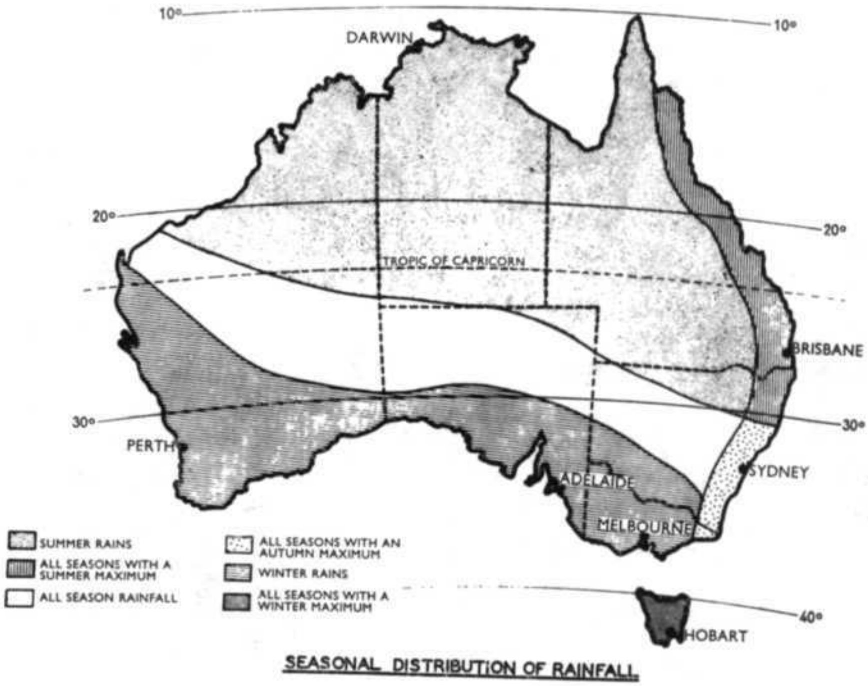

Fig. 2. Seasonal distribution of rainfall.

Fig. 3. River Murray Catchment.

LIST OF SELECTED REFERENCES

COMMISSIONERS OF FISHERIES (1922). *Report for the Tear 1920-21.* Parliament of Tasmania, Hobart.

— (1923). *Report for the Tear 1921-22.* Parliament of Tasmania, Hobart.

INLAND FISHERIES COMMISSION (1962). *Report for the Tear Ended 30th June 1962.* Government Printer, Hobart.

LAKE, JOHN, S. (1959). *The Freshwater Fishes of New South Wales.* State Fisheries Res. Bull. No. 5 Government Printer, Sydney.

MCCAUSLAND, M. E. (1958). *Fly Fishing in Australia and New Zealand,* 2nd ed. Lothian, Melbourne.

MCCULLOCH, ALLAN, R. (1922). *Check List of the Fishes of New South Wales,* Royal Zool. Soc. N. S. W., Sydney.

MACLEAY, WILLIAM (1881). *Descriptive Catalogue of Australian Fishes,* F. W. White, Sydney.

MUNRO, IAN, S. E. (1956 *et seq.) Handbook of Australian Fishes.* Published in parts in *Fisheries Newsletter,* Dept. Prim. Industry, Canberra.

NICOLS, ARTHUR, (1882). *The Acclimatization of the Salmonidae at the Antipodes.* Sampson Low, Marston, Searle, & Rivington, London.

ROUGHLEY, T. C. (1951). *Fish and Fisheries of Australia.* Angus and Robertson, Sydney.

SALMON COMMISSION (1873). *Salmon - History of its Introduction; and Distribution of Ova, 1869-1872.* House of Assembly, Tasmania.

SALMON AND FRESHWATER FISHERIES COMMISSION (1933). *Report for the Tear Ending 30th June 1933.* Parliament of Tasmania, Hobart.

SCOTT, TREVOR D. (1962). *The Marine and Fresh Water Fishes of South Australia.* Government Printer, Adelaide.

STEAD, DAVID G. (1906). *Fishes of Australia,* William Brooks, Sydney.

— (1910). *A Brief Review of the Fisheries of New South Wales.* Government Printer, Sydney.

THOMPSON, LINDSAY, G. (1893). *History of the Fisheries of New South Wales.* Government Printer, Sydney.

WEATHERLEY, A. H. (1962). Notes on Distribution, Taxonomy and Behaviour of Tench *Tinca tinca* (L.) in Tasmania. *Annals and Magazine of Nat. Hist.* Ser. 13, IV, p. 713.

— (1963). Zoogeography of *Perca fluviatilis* (Linnaeus) and *Perca flavescens* (Mitchill) with special reference to the effects of High Temperature. *Proc. Zool. Soc. Lond.* 141 : 3, p. 557-76.

WHITLEY, GILBERT, P. (1948). *A List of the Fishes of Western Australia.* Fisheries Bull. No. 2 Chief Insp. Fisheries, Perth.

— (1951)- Introduced Fishes (Parts 1 & 2). *Aust. Mus. Mag.X:* 6, 198-200 & X: 7,234-238.

— (1960). *Native Freshwater Fishes of Australia.* Jacaranda Press, Brisbane.

WILSON, SAMUEL (1878). *The Californian Salmon.* Sands and McDougall, Melbourne.

— (1879). *Salmon at the Antipodes.* Edward Stanford, London.

ECOLOGICAL CHANGES IN NEW ZEALAND DUE TO INTRODUCED MAMMALS

by

WALTER E. HOWARD

Department of Animal Physiology,
University of California,
Davis, California 95616, U.S.A.

INTRODUCTION

" When a species is introduced into an area where it has not lived before it is almost impossible to foretell the consequences, although it is quite probable that it will either succeed gloriously or eventually fail entirely " (Graham, 1944). Throughout the world man has transplanted animals from one place to another for a variety of reasons. Sometimes the introduced forms fail to acclimatize, although too often they cause undesirable ecological changes. When the habitat is altered by introduced mammals, it creates a change in the balance of nature, and the resulting disturbances require new animal-plant-soil adjustments before any new equilibrium with stable habitats can be re-established. The world-wide evidence indicates that the introduction of mammals, in particular, compared to that of fish and birds, may be a hazardous undertaking (De Vos *et al.,* 1956). However, and I cannot emphasize this point too strongly, the ecological consequences of all mammalian introductions are not, *ipso facto,* going to be deleterious. This is even true in New Zealand and many other oceanic islands where the inherent hazards of undesirable ecological changes are much greater than on continents.

The reason New Zealand is vulnerable to disastrous side effects from mammalian introductions is due to the presence of many species of highly palatable plants, which evolved in the complete absence of a mammalian fauna, that cannot withstand the selective browsing pressure of the exotic mammals. Two other significant factors partly responsible for the dramatic habitat modifications resulting from mammalian introductions into New Zealand are that some of the soils are highly susceptible to erosion once the vegetative cover is removed, and the mountainous country often gets high intensity rainfall, with annual totals ranging from 40 to 300 inches or more in some areas.

In addition to reporting on the ecological changes in New Zealand due to introduced mammals, I also will make a few comments about (1) some ecobehavioral principles that concern transplanted mammalian populations, (2) some related aspects of the population dynamics of introduced mammals, and (3) some general considerations that are necessary before attempting to predict what the ecological changes will be as a consequence of any particular mammalian liberation.

As background for this paper, I have been privileged to make two surveys of mammal populations in New Zealand, which I would like to acknowledge. The first trip was a Fulbright research grant in 1957 to study the rabbit problem (Howard, 1957 and 1958). At that time I also participated in an ecological expedition into the Cameron Mountains of Fiordland National Park (Riney *et al.*, 19S9). The second trip (1962-1963) was a grant-in-aid and a travel grant, respectively, from the Division of Animal Ecology of the New Zealand Department of Scientific and Industrial Research and the New Zealand Forest Service (Howard, 1964 a and b; 1965 a). Also, at the International Union of Biological Sciences Symposium on " The Genetics of Colonizing Species " I had the opportunity of discussing the role genetics may play concerning mammalian introductions in New Zealand (Baker and Stebbins, 1965).

THE NEW ZEALAND SCENE

New Zealand has been called the social laboratory of the world, and it may equally appropriately be regarded as the acclimatization laboratory of the world, the reason being that in no other country have so many importations of foreign animals and plants been made (Westerskov, 1953). Early in the settlement of New Zealand, which began about 1840, there was a strong demand to introduce from England and other parts of the world many kinds of animals, primarily for sport and nostalgic reasons, but also as a fur resource, for food, and as predators of the earlier introduced rabbits. This practice prevailed until the beginning of the twentieth century.

The early settlers of New Zealand had a better reason than people of most other places in the world for introducing so many mammals, for New Zealand was almost devoid of native mammals and had a very small vertebrate fauna. The only land mammals present when the European settlers arrived were feral goats and pigs, and black rats introduced by Captain Cook and by sealers and whalers, the kiore or Maori rat (*Rattus exulans*), and two kinds of bats (*Chalinobus* and *Mystacina*). The Maori dog was probably extinct by then, and no fossils of other land mammals have ever been found.

According to Allan (1937), " The remarkable diversityof plant forms and of plant communities is due to the interaction of many factors—*e.g.* the very varied topography and climate, the wide range of edaphic conditions, the intermingling of elements from very distinct floristic groups, the long isolation from other lands coupled with a kaleidoscopic geological history—all this, too, in an area under 270,000 square kilometres. Within a short distance of each other can be found dense, wet, many-specied forest and true desert, closed herbifield and open fell-field, tree-fern groves and ice-planed rock...

" The primitive vegetation arose in the absence of grazing and browsing animals, while since the advent of the white man and his animals, domesticated or introduced for sport, we have witnessed the incoming of a new flora and a new vegetation, so that the appearance of great stretches of country has been completely transformed. An outstanding feature is the great measure of success that has attended man's efforts to transform forest of various classes into grassland and to maintain this by skilled management. Equally important are his failures, where, owing to lack of ecological knowledge, he has attempted the transformation on areas that have persisted in returning towards forest by way of various induced communities ", *e.g.* manuka, fern, gorse, broom, and blackberry.

Godley (1961), discussing the vegetation of New Zealand, pointed out that all 20 species of gymnosperms (*e.g.* Kauri and rimu), 83 percent of the flowering plants, and 35 percent of the species of fern are found only in this country. Some of these endemic plants have little innate resistance to heavy browsing or grazing; during the evolution of the New Zealand flora there were virtually no browsing or grazing pressures acting to favor and select for the evolution of unpalatable and browse-resistant vegetation (Holloway, 1960). " The success of weeds and animal pests in New Zealand... reflects the general ecological poverty and low competitive ability of the native flora and fauna " (Costin, 1963).

To understand New Zealand's unique fauna and flora, it is necessary to realize how isolated these islands are from other land masses. New Zealand is about 1,230 miles from Australia, 1,600 miles from the Antarctic continent, 2,500 miles from New Guinea, and 4,500 miles from South America. There is no evidence for any direct trans-Tasman connection with Australia nor the Antarctic continent, but the latest land connection with New Caledonia to the north-west could have extended into the Cretaceous; hence New Zealand's isolation has existed for at least 70 million years (Fleming, 1962). The native flora and fauna of New Zealand, therefore, consist largely of forms that have evolved during this long isolation. The small number of survivors from late Cretaceous land connections include a few species of fresh water fish, *e.g. Galaxias* whose marine ancestors no longer survive according to Fleming (*ibid.*), the tuatara (*Sphenodon*), and perhaps some of the endemic geckos (Fleming, 1957). There are no snakes. Native land birds consisted of about 150 species. The now extinct moas may have been browsers as well as grazers, but they obviously could not have provided either the variety or intensity of browsing pressure on the indigenous vegetation that was inflicted by the introduced opossums, red deer, and other big-game species.

According to Wodzicki (1965), a total of 207 vertebrates (15 fishes, 5 amphibians, 3 reptiles, 130 birds, and 54 mammals including 2 species of self-introduced rats and the house mouse) were liberated in New Zealand during the last 125 years. Of these 91 became permanently established. These comprise 13 fishes, 3 frogs, 43 birds, and 32 mammals (26 wild and 6 feral species). Of this adventive mammalian fauna (Table 1), Wodzicki considers only 12 species to be true colonizers, as the remainder still have only restricted distributions. It is of interest to note that the percentage of successful establishment among mammals (32 out of 54) is almost twice as great as that of the introduced birds (43 out of 130), probably due to the fact that there are about 150 native species of birds, whereas native mammals consist of only two species of bats. Consequently, there may be fewer vacant niches for birds in the natural habitats. Wodzicki (*ibid.*) points out that none of the established bird species live only in undisturbed habitats, that one-quarter of them occupy both natural and modified habitats, and that three-quarters of the introduced birds are restricted to modified habitats. In contrast, the mammals were more successful in adapting to natural habitats; one-fifth of them are able to inhabit the natural habitats; three-fifths are equally at home in both types, and only one-fifth are restricted to the modified habitats.

The ecology, origin, history of introduction, present distribution and management problems of the main species of mammals established in New Zealand have been well documented by Anderson and Henderson (1961), Batcheler (1962), Donne (1924), Howard (1958 and 1965 a), Kiddie (1962), Logan (1956), McKinnon and Coughlan (1960-64), Marshall (1963), Pracy and Kean (1949), Pracy (1962), Riney (1955 and 1957), Riney *et al.* (1959), Shennan (1960), Thomson (1922), and Wodzicki (1950, 1961, 1963, and 1965).

ECOLOGICAL CHANGES IN NEW ZEALAND

The selective browsing and grazing pressure of the introduced mammals have been the main factor responsible for the ecological changes that have occurred on the " wild " lands in New Zealand during the past century. Many of the highly palatable indigenous plants are not able to withstand heavy browsing and grazing and their densities have been materially depleted (Table 2). The seven most important wild animals that caused marked ecological changes in the forests and grasslands are red deer, European rabbit, brushtailed opossum, European hare, feral goat, chamois, and feral pig (Table 1). Of these, the red deer deserves the dubious honor of being the most troublesome species. It and the feral pig and goat are widespread. Other species of deer such as the wapiti, Japanese, fallow, and white-tailed, also have considerably modified the composition of the vegetation, but only in restricted areas because of their limited distribution. The hare, rather than the rabbit, is the principal lagomorph grazier of alpine grasslands. Feral horses are no longer important, and the axis deer that were released in Fiordland National Park presumably have died out. The moose, with its limited range in Fiordland, seems likely to follow the same fate as the axis deer.

Prior to the liberation of deer, goats, opossums, and the other animals, the forests of New Zealand were multilayered and usually had a " spongy " ground cover. Even the tussock-grassland communities often assumed a two-layered effect. With the trampling, feeding, and rooting of introduced animals the ground surface loses its spongy character, and the lower tiers of vegetation are destroyed (thus exposing bare soil), even though most of the canopy species still remain. " In dense-canopied, mixed forests, low light intensity so reduces the rate of growth that plant production is too slow to produce a sustained yield of browse; so that once the under-growth was browsed it was permanently damaged and no longer impeded the movement of animals " (Davidson and Kean, 1960). A forest whose canopy may look undamaged when seen from the air, may actually be considerably modified and even in critical condition.

By selective browsing, some animals have not only thinned and opened-up many of the native forests, but they have completely denuded some sites, thereby accelerating soil erosion. They have also compacted the soil, thus retarding water infiltration and root development. This has increased the amount of run-off, hence augmenting flood peaks following periods of high intensity rainfall. The main problem of deer in forests is their prevention of adequate regeneration of the principal crown plants, but to what extent this will persist once the canopy trees begin to die and more light gets through is really not known. Deer have also been responsible for considerable erosion within many indigenous forests, especially when assisted by opossums, and feral cattle, goats, and pigs. Opossums usually do not cause soil erosion by themselves, but they frequently assist other animals in doing so.

That the " problem areas " in New Zealand are not as they were prior to the arrival of Europeans is clearly borne out by forest floors of scree, lack of under-story vegetation, large numbers of dead or dying plants that are heavily browsed, striking browse lines, dead, pedestalled vegetation, compacted subsoil, abundant animal trails, exposure of fresh subsoil, recently formed slips and gullies, charred stumps and burned-out tussock, discolored water in streams following rain, and the too common overall character of grazed-out, browsed-out vegetation. However, in some situations it is not easy to know accurately where to lay the blame for these conditions—whether it is mostly due to the misuse of fire and merino sheep, the introduced wild mammals, or various combinations of these causes.

" The introduction of fire and animals in the steeplands... upset the natural stability of the soil over large areas... with consequent disastrous effects on the water regime of rivers " (Cuttler, 1962). A vegetated soil mantle is essential because the weather is harsh in many of the problem areas, alternating between dry, high winds and torrential rains, and frequent night frosts followed by warm, dry winds leading to severe wind erosion. As the high country erodes away, the masses of displaced soil, rock, and trees washed down raises the level of river bottoms. The problems in river stability, flooding and erosion control differ from those of most other countries (Campbell, 1961). Due to erosion trout can no longer propagate in some New Zealand rivers where they once thrived. Many expensive stop-banks have already been constructed to counteract the channel aggradation of rivers. The water-holding capacity of most New Zealand soils is only 2-3 inches of rainfall (Campbell, 1963), and since most of the soils are usually damp, it is no wonder that most of the water must run off following torrential rains. To prevent erosion in river catchments is often a land-use matter, not just an engineering problem. Local Catchment Boards have the authority to reduce burning and withdraw livestock from critical areas in the upper reaches of catchments where erosion is usually initiated, but most Boards seem to need more courage to enforce their convictions.

There have been marked changes in the lower tussock grasslands during the period they have been grazed by sheep. Barbara Hercus (1964) finds that this is mainly a quantitative change in vegetative growth and that the combined effects of fire and sheep have served to open up the community and allow invasion of exotic species leading to a richer or more varied inter-tussock flora than the original. Much erosion has also occurred.

There is little doubt, at least for much of the eastern side of the mountain ranges in the South Island, that man's use of fire and sheep are the chief factors responsible for well over half of the current erosion problems. Nevertheless, the red deer has been responsible for opening up many of the beech forests that have had no sheep or fire, and for preventing regeneration within them. Also, it is the year-round activities of deer, chamois, hare, and the other wild animals that have been responsible for additional erosion, especially above the timber line.

The presence of domestic animals and fires have often made it difficult to ascertain the true role of deer and other introduced animals in depleting vegetation and causing soil erosion. Moore and Cranwell (1934) showed how feral cattle, pigs, and goats had converted a rain-forest on the Coromandel Peninsula to grassland. Feral goats established for over half a century on Cuvier Island, Hauraki Gulf, eliminated a number of species, altered the forest succession in many places, and destroyed an entire coastal scrub community while allowing an induced grassland to develop in its place (Atkinson, 1964). Holloway (1959) and McKelvey (1959) have given very good descriptions of the ecological changes due to animals in a number of localities in South Island and North Island, respectively. Batcheler (1962) has briefly reviewed the writings of Turbott (1948), Baylis (1948 and 1951), and Holdsworth (1951) on the role of feral goats in forest depletion and soil erosion on Great Island of the Three Kings Group, 35 miles north-west of the North Island. Goats were liberated there in 1889 and exterminated by shooting in 1946. Without goats from 1946 to 1951, luxuriant and floristically rich plant communities developed. The number of known vascular plants increased from 118 to 151, in the absence of goats. The " new " species apparently were so scarce in 1946 that they were not observed.

The interaction between introduced plants and animals can produce interesting phenomena. Sweet brier (*Rosa rubiginosa*), which was probably introduced into New Zealand by the early missionaries, has long been a serious weed in many parts of the country but, since the introduced rabbit has been controlled, it has increased and spread so rapidly in the tussock country of South Island that it has become a serious menace to production on thousands of acres of pastoral land and threatens hundreds of thousands more.

The manner in which the introduced mammals may have affected the native fauna, in particular the native birds, is obscure and not easily interpreted empirically. Marshall (1963) probably sums up the subject as well as can be done in his statement that " the effects of mustelids [stoat, weasel, and ferret] on native birds appear to have been of relatively small significance in relation to the extensive changes in both quantity and quality of forest habitats " brought about by man. The opossum and other introduced mammals certainly have locally destroyed the food supply of many native birds and in other ways have made the habitats less suitable to the native fauna. Some research has been done on the preference for native seeds by the introduced rodents (Beveridge, 1964). But, as Bull and Falla (1951) point out, many factors may have caused the reduction or disappearance of different species of native birds, including competition and diseases from the introduced birds. Much more knowledge is required before these factors can be properly understood.

Other good accounts of how certain species of mammals have both damaged and altered New Zealand vegetation are Christie (1964), Conway (1949), Davidson and Kean (1960), Davis (1953), Druce and Atkinson (1959), Elder (1956), Grant (1956), Hercus (1964), Hobbs (1954), Holloway (1948, 1950, 1951, 1954, and 1956), Holloway and Naylor (1959), Kean (1951 a and b), Kean and Pracy (1949), Kiddie (1962), McKelvey (1960 and 1963), Packard (1947), Poole (1959), Poole and Holloway (1951), Poppelwell (1929), Riney (1956), Riney and Caughley (1959), Riney and Dunbar (1956), Riney *et al.* (1959), Silvester (1964), Walsh (1893), Wardle (1961), Widdowson (1960), Wraight (1960 and 1964), and Zotov *et al.* (1939).

The fact that the species composition of much of the vegetation in New Zealand has been altered permanently warrants special emphasis. One way this happens is that when opossums kill certain palatable trees, the canopies of adjacent non-palatable species quickly fill the light gap, which prevents any regeneration of the palatable plants, thereby altering irreversibly the species composition of the forest. Since the introduced mammals cannot be eradicated, in some localities the highly palatable and easily killed species can persist only in sites that are inaccessible to the browsing species concerned. When light reaches the ground through breaks in the canopies, many of the eroded places become colonized by fairly unpalatable grasses, such as *Microlaena* and *Uncinia* (also, kikuyu grass in Tangihua Range, North Auckland). Whether these situations will remain in grassland is not known.

The subalpine shrub (*Olcaria colensoi),* where accessible to deer, has been nearly eliminated in many places, *e.g.* at Lake Monk, Fiordland (Riney *et al.* 1959), and in the Tararua Range. In the latter area Wardle (1961) stated that in wind-throw gaps that normally would be quickly filled by thickets of young beech, nearly all the beech seedlings had been killed, as had the shrub story, *Nothopanax, Coprosma,* and *Olcaria colensoi.* According to Wardle, it seems likely that most of the wind-damaged subalpine forest is destined to be replaced by grassland or parkland, in which the dominant species will be *Danthonia cunninghamii.* He thinks there is no doubt that deer must bear the ultimate blame, yet the research team had only limited success when they searched during the summer of 1958-59 for direct evidence of browsing by deer. By far the greatest amount of damage was caused by a native caterpillar (*Agriophara caricopa* Meyr.) that destroys the buds of *Olcaria colensoi.* " The total evidence indicates that stands of *Olcaria colensoi* are normally in equilibrium with a number of destructive factors, and that the introduction of deer into the habitat is sufficient to cause the system to overbalance " (Wardle *ibid.).*

DISCUSSION

The true test of a theory is its predictive power, but it is often difficult to do more than speculate about the consequent changes that may occur as concomitants of such zoogeographic events as introducing a mammalian species into a new ecosystem. Such enrichment of fauna by this means increases diversity, resulting in new balances between the flora and fauna, but not enough is known about the factors that regulate productivity and stability in modified ecological communities to accurately predict what the consequences of introductions will be, as has been pointed out by Howard (1965 b). However, before much light can be shed on the underlying causal principles and processes determining how well an introduced species will succeed in any new set of conditions, more insight about its ecobehavioral, physiological, and other properties will be required. Only then will it be prudent to attempt to predict the optimum habitat requirements and ecobehavioral responses of any proposed introduction of an exotic species.

All biotas, but some more than others, apparently have vacant niches, even in what otherwise are well-balanced faunas. The irregular pattern of success and failure of mammalian introductions throughout the world bears out this. Vertebrates often are acclimatized without any apparent reduction in the densities of other species of vertebrate animals. And the wider the tolerance of an animal, the greater will be the number of suitable niches available for its survival without any immediate genetic differentiation being required.

When a farmer replaces native vegetation with non-native plants that have been developed by breeding experiments in which such factors as natural selection by native animals has been ignored, he alters the habitat to such an extent that sometimes the native wild animals no longer can exist there. In other instances, the alien forage or crop may be as palatable and sensitive as some of the New Zealand vegetation with the result that native mammals become so numerous that locally they may completely destroy the crop. The introduction of alien mammals likewise results in destruction of certain types of native vegetation. The probability that introduced mammals will disrupt the natural stability of their new habitats depends upon many factors. If native animals closely related to those being introduced are present, the chances that the stability of the habitats will be weakened are much less. This is why any species of big game ungulates introduced into the United States have not upset the stability of habitats as has occurred in New Zealand.

It seems likely that the most important reason why so many species did so well in New Zealand is that they found good habitats (vacant niches) that contained an ample supply of year-round shelter and food. Many of the habitats had a dense understory of palatable and apparently nutritious broadleaved plants that remain green the year round. The open grasslands along rivers and on many of the mountain tops also helped provide an adequate food supply, even during periods of adverse weather in winter. As mentioned by Wodzicki (1963), New Zealand forests provide a habitat different in many ways from the deciduous and needle-leaved forests of the North Temperate Zone. He points out that too little attention has been paid to the contribution ample winter browse can make towards a rapid, initial build-up of numbers of herbivorous mammals, and to how evergreen forest, such as found in New Zealand, can maintain the population until all the acceptable plant species vanish. There have been deer die-offs in New Zealand but they differ in pattern and predictability from those in North America, where in winter deer are often trapped in limited areas by deep snow and die of starvation.

In many areas of virgin forest, according to Holloway (1950), after the immigration or liberation of deer the population rises rapidly; browsing is highly selective and the preferred food plants are eaten out; in time the level of population overtakes that of available food supply; a period of overpopulation follows, with food habits of the deer changing; plants previously untouched are now browsed and the forest is opened up; through semi-starvation of herds and emigration, the population falls; and the final level of population becomes adjusted to the renewal rate of the preferred food plants, the degree to which deer can utilize alternative and less attractive browse, and to the proximity of alternative or seasonal browsing range such as is found above the timber line or in valley grasslands.

The time required for newly established deer herds to reach peak density often appears to have required from 20 to 30 years. The next period of overpopulation and severe habitat destruction by animals living under conditions of malnutrition yet struggling to keep alive seems to have lasted from 5 to 10 years, depending on a number of circumstances. Destruction of the sensitive, palatable plants usually produces an irreversible change in the floristic composition of such forests. The carrying capacity for introduced animals is then permanently lowered, and some of the plants avidly eaten during the initial peak population are mostly ignored thereafter.

The recovery of severely eaten-out forests, and the amount of scree formation and soil erosion resulting from devegetation depends largely upon the rate of establishment of other types of vegetation that can withstand browsing or are unpalatable. In some localities man must keep the number of deer and other browsing and grazing animals extremely low until the vegetation and animals can reach a new stable equilibrium. In some catchments where such an equilibrium has not yet been fully reached, deer, opossums and other species are still being intensively controlled over vast areas to protect the remaining small, unstable sites. In other localities the present degree of habitat stability is not known. However, it is apparent that many will require for sometime either intensive control of the mammals, the practice of modern game-management principles, reseeding with exotic plants if native species cannot withstand the new environmental conditions, or a combination of these procedures.

Since adequate regeneration to replace the canopy is often lacking, the future of such forests is of concern. A browse-resistant shrub is not the most desirable replacement of a high forest canopy, but even this or introduced grasses should be used in some areas if there is nothing better. On drier slopes without a forest canopy, seedlings may die as much from summer drought as from animal browsing. Once a forest becomes damaged by animals, a chain reaction of other effects may be started, *e.g.* plagues of bark beetles (*Nascioides enysii*) and other insects or diseases, which further decimate the vegetation.

Damage to vegetation done by one kind of mammal may trigger subsequent damage by another species that finds the new conditions beneficial. Opossums are helped if deer or other browsing animals first remove the lush, dense ground cover so prevalent in indigenous forests, for opossums do not thrive well in the damp, cold conditions of dense native bush (Kean, 1951 b; Kean and Pracy, 1949). These authors point out that opossums seldom do serious damage where there are dense thickets of vegetation at ground level. In their avoidance of dense vegetation, opossums have much in common with the European rabbit in New Zealand, which does not thrive in lush grass growth (Howard, 1958). "The rabbit problem in tussock grassland has probably arisen because grazing disturbance (and fire) has created a favorable habitat, and the most effective permanent control may well be to provide a cover—*e.g.* a forest or snow-tussock grassland—which is unsuitable for rabbits " (Costin, 1963). There is every likelihood that the present deterioriation evident in the alpine grasslands may be caused in large part by insects that feed on the leaves, seeds, and roots of the plants. If so, it is also possible that the grazing animals have created a favorable habitat for these insects. As yet little is known of techniques for distinguishing damage done to alpine grasslands by sheep, chamois, thar, deer, and hare from that of grasshopper or other insects.

Animal populations have considerable powers of self-limitation which prevent severe overpopulations that otherwise would destroy the species. Self-limitation counteracts their innate ability to produce a surplus of offspring. This compensatory mortality tends to increase, percentagewise, as density increases above a certain equilibrium point, and to decrease as density falls below this point (Nicholson, 1954; Morris, 1963). As Nicholson (1957) points out, a species automatically adjusts its " density in different places, and in the same place at different times, in relation to the prevailing environmental conditions; and it maintains a state of stability under all conditions which are not inherently intolerable. "

Not only do undesirable ecological changes sometimes result from liberating exotic mammals into new ecosystems, but even attempts at maintaining inviolate sanctuaries and refuges have at times failed in the perpetuation of specific animal communities, because the species to be protected managed to unbalance the ecosystem by deteriorating their own habitats. It is axiomatic that man will come into various degrees of conflict with the environment around him when he modifies the ecosystems through interruption of ecological succession and the substitution of simple plant communities for natural diversity, but too often it is not appreciated that all wild animals also find numerous other species pests to them.

It has been my observation that the combined predation pressure by hawks, owls, snakes, and carnivores usually perpetuates a greater, not lesser, seasonal and annual density of species of vertebrate prey than would otherwise exist. The suitability of other aspects of the habitat and self-limitation resulting from intraspecific stresses used in the broad sense (psychological, competition for food or mates, territoriality, weather, disease, or other vicissitudes of life), not interspecific relationships between predators and their prey, largely determine the magnitude of the natural vertebrate densities that have been in existence for long periods of time over large areas. The ecology of predators of vertebrates has been discussed more fully by Howard (1965 b and in press).

The intentional introduction of predators to control troublesome species of vertebrates obviously should not be undertaken until after all potential ecological consequences have been carefully scrutinized. The introduction of a predator onto a very small island or other isolated locality might result in the complete extermination of a certain kind of vertebrate prey, but in most situations the introduction of alien predators into a new ecosystem cannot only be perilous, but may prove to be catastrophic, because the predators of vertebrate pests are not host-specific. Tragic examples include the introduction of the mongoose in Hawaii to control rats, the fox into Australia to check the rabbits, and New Zealand's introduction of weasels, stoats, and ferrets in the mistaken belief that they would control the rabbit. All of these introduced predators not only failed to accomplish their mission, but they have become troublesome predators as well.

The thesis of this meeting inherently places an undue emphasis on undesirable ecological changes due to introduced animals, hence also my unfair weighting in this paper by using the dramatic ecological changes that occurred in New

Zealand as my main examples. Consequently, both the degree and the desirability of how adventive mammals can modify the continuum of complex interactions existing amongst living things has not been brought into proper perspective in this paper. The benefits accruing to man from many mammalian liberations often makes even the undesirable portions of the resulting ecological changes seem insignificant. In other words, there is no scientific basis for saying categorically that all mammalian introductions are going to produce undesirable ecological changes, unless one defines any man-caused ecological change as being undesirable. Ecosystems are kaleidoscopic in nature and the " success" or ' failure " from an ecological basis of mammalian introductions often will hinge on how successfully man can deal with the resulting changes in the biota.

Extreme caution, however, should be employed when attempting to artificially modify a habitat to assist in the acclimatization of an exotic mammal, for there is little doubt that any modification of the physical nature of a habitat will produce more pronounced interactions with other native species of animals than usually results as a consequence of population reductions of native mammals by selective means of control. " Observations indicate that natural biomes have a well-established, stable, animal-soil-vegetation complex which is *not* delicately balanced. A natural change (*e.g.* by disease) or man-caused change (*e.g.* by shooting), in the density of a native species of browsing, grazing, seed-eating, or predatory mammal does not precipitate a dramatic " balance-of-nature " type chain reaction of responses by other components of the community. Such chain reactions usually are the consequences of the introduction of alien plants or animals, farming, grazing, logging, man's use of fire, or natural catastrophic events " (Howard, 1965 b), all of which cause habitats to be modified. And the main way that our native biotas have been degraded and fragmented is by the alteration of habitats. Take the coyote as an example. The coyote started out as a lonely predator of prairie dogs and rabbits in the Great Plains and other western parts of the United States, excluding Alaska. Then man came along with lambs and chickens, and while he spread his civilization into the coyote's habitat, the coyote backtracked along man's trail to where now the coyote can make a living almost anywhere from California to Maine and also Alaska.

The effective management of mammalian populations is the translation of ecology into policy. With intentional mammalian introductions, the objective is to promote new but tolerable balances, *i.e.,* to create new but largely self-regulatory ecological units. With care and finesse, and a sound ecological background, newly liberated mammals can often be artificially provided with certain ecological advantages over competing native species to ameliorate certain acclimatization difficulties. And there are many ways man can assist in the development of a new stable equilibrium of the animal-vegetation-soil complex (Howard, 1965 a). That stable habitats often can be perpetuated following the liberation of exotic mammals is perhaps best illustrated by the success of various species of livestock and game animals. Perhaps the most important demographic phenomenon with introduced mammals needing management is to lessen the population-increase momentum new populations attain upon that precipitous slope of the classical sigmoid growth curve. Various types of management procedures can be implemented to help regulate the biotic factors that nurture the high natality and survival which produces initial population peak densities.

As a general rule, the extent of ecological changes resulting from mammalian introductions into a new biota containing only a sparse fauna, especially if there are no near ecological counterparts to the exotic species, is likely to be much greater than if the fauna was rich and it contained ecological equivalents. Faunal diversity provides a natural sustaining force, a homeostatic control on density. It increases the capacity for continuous self-regulation of species with respect to their environment. When there is considerable diversity of fauna and flora, living things and systems then appear to be endowed with a self-regulating feedback mechanism that guarantees their sustenance, adaptiveness, and perpetuation in a dynamic continuum. Just how social behavior and bioenergetics of species control population density is not well understood, but individual animals as well as populations are dynamic in structure and behavior, not static units.

A crucial factor affecting the success of colonizing species is the degree of saturation of the fauna and the availability of suitable, vacant niches, into which the species is entering plus also its plasticity and adaptability to the existing ecological counterparts of its inherent niche requirements. As Dice (1952) points out, the process of adaptation (acclimation) of introduced individuals to a new environment is not to be confused with acclimatization. Only the transplants, which can successfully acclimate (adapt) to the new environmental conditions will survive to breed. This process of acclimatization (production of ecotypes), which is a genetic change resulting mostly from the selection of favorable hereditary variations already present in the population, requires several generations rather than happening rapidly within an animal's life span as is the case with acclimation.

As Waddington (1965) has pointed out, introduced species have, in effect, been a series of experiments in evolution, since the transplanted organisms have been faced with a whole new ecological system in which they have had to find a niche for themselves. " The natural selective pressures acting on an organism are not simply given by the circumstances, but depend to some extent (particularly in animals) on the activities of the organism themselves, *i.e.*, natural selection forms part of a ' feedback ' loop, with ' position in the ecological system ' as the other link. An organism must be regarded with many potentialities, that has to make its way by fitting, in some way or another, into an ecological system composed of other pluripotential organisms and a diverse collection of available physical factors... Presumably once any new evolutionary path begins to be followed successfully, the ' inertia ' produced by selection of many genes will tend to direct further advance along the same line... It seems to me that what is needed, at the present stage of our understanding of evolution, is not so much a greater elaboration of formal theories of quantitative and population genetics of the kind we have been producing for the last 20 or 30 years, or even more analyses of wild populations in terms of genetics divorced from their ecology—what we need is more knowledge about the ways in which populations, in fact, meet evolutionary challenges. What intensities of natural selection can they put up with, how far and how fast can they modify their phenotype (including their habits) ? Colonizing species are ones which we know to have been confronted by a challenge—that of their new location; and we often know, even quite precisely, how long they have been facing it. "

In a lucid paper on "The Challenge from Related Species", Wilson (1965) predicts that the class of species " termed ' fugitive species ' by Hutchinson (1951) produces the bulk of the colonizers of new regions. ...As the habitats are altered serally, or competitor species begin to infiltrate the area, the fugitive species disappear. They are able to survive by the relatively quick and temporary occupancy of suitable new habitats as these first become available; in contrast, other species specialize in more persistent tenancy of relatively stable habitats. The fugitive species are characterized by superior dispersal and reproductive powers. The fugitive strategy enables a minority of species to survive indefinitely within the kaleidoscopically changing environments of single regions. It also preadapts species to colonize neighboring regions, such as offshore islands or adjacent continents. "

Many species of mammals seem to have a high degree of natural, ecobehavioral plasticity within relatively wide genetic parimeters; most mammals inherit a fairly wide range of tolerance for changes in the physical and chemical factors of their environments. This is why these species exhibit considerable capacity to adapt themselves phenotypically to new biotypes created by man and to any new natural environments that they may have the opportunity of colonizing. The large genetic plasticity of mammals is evidenced by the ability of individuals of so many species to readily adjust within their lifetime—hence no genetic change—to considerable social environmental change. Perhaps some day someone will adequately classify or cateragorize this phenomenon with respect to the different species of mammals, localities, and specific situations to help create suitable concepts. This meeting on ecological changes due to introduced species is certainly a step in the right direction.

SUMMARY

Few places in the world equal New Zealand in the magnitude of ecological changes resulting from introduced mammals. The principal reason that they caused such extensive erosion and have markedly alterated the species composition of the vegetation, sometimes irreversibly, is because many of the endemic plants, which evolved in the absence of grazing and browsing mammals, are highly palatable but have little innate resistance to heavy, selective browsing or grazing. Also, some of the soils are highly susceptible to erosion, once the vegetative cover is removed, and torrential rainfall is common. A new and stable equilibrium of the animal-vegetation-soil complex has developed where browse-resistant and unpalatable plants have replaced the sensitive plants that were killed by the introduced mammals. The improper handling of fire and merino sheep has also been responsible for extensive areas of erosion.

Observations indicate that natural biomes have a well-established, stable, animal-soil-vegetation complex which is not delicately balanced. A natural change (e.g. by disease) or man-caused change (*e.g.* by shooting) in the density of a native species of browsing, grazing, seed-eating, or predatory mammal does not precipitate a dramatic " balance-of-nature "-type chain reaction of responses by other components of the community. Such chain reactions usually are the consequence of the introduction of alien plants or animals, farming, grazing, logging, man's use of fire, or natural catastrophic events.

It is proposed that mammalian densities are determined primarily by the suitability of the habitat and the self-limitations owing to intraspecific stress factors (psychological, competition for food or mates, territoriality, weather, disease, or other vicissitudes of life), and that interspecific competition, especially between mammalian predators and their prey, often is only of minor significance.

RÉSUMÉ

Peu d'endroits au monde égalent la Nouvelle-Zélande pour l'ampleur des changements écologiques résultant de mammifères introduits. La principale raison pour laquelle ils causèrent une érosion tellement étendue et modifièrent profondément, et parfois irrévocablement, la composition des espèces végétales réside dans le fait que beaucoup de plantes endémiques, qui évoluèrent en l'absence de mammifères pâturants et broutants, sont extrêmement savoureuses mais ont peu de résistance innée au broutage ou au pâturage intensif et sélectif. En outre, certains sols sont extrêmement sensibles à l'érosion une fois que la couverture végétale a disparu et les précipitations torrentielles sont courantes. Un équilibre nouveau et stable du complexe animal-végétation-sol s'est développé là où des plantes résistantes au broutage et désagréables au goût ont remplacé les plantes sensibles détruites par les mammifères. L'usage abusif du feu et les moutons mérinos sont aussi responsables de l'érosion dans de vastes régions.

Les observations indiquent que les écosystèmes naturels ont un complexe animal-sol-végétation bien établi et stable, ayant un équilibre solide. Un changement naturel (dû à la maladie, par exemple) ou un changement provoqué par l'homme (la chasse, par exemple) dans la densité d'une espèce indigène de mammifère brouteur, pâturant, granivore ou prédateur ne précipite pas un « équilibre naturel » dramatique - du type réaction en chaîne des autres composants de l'association. De telles réactions en chaîne sont généralement la conséquence de l'introduction de plantes ou d'animaux exotiques, de l'agriculture, du pâturage de l'abattage des forêts, de l'utilisation du feu par l'homme ou de phénomènes naturels catastrophiques.

Il est suggéré que les densités de mammifères sont déterminées principalement par la convenance de l'habitat et par les auto-limitations dues aux facteurs de résistance intraspécifique (psychologique, compétition pour la nourriture et l'accouplement, territorialité, temps, maladie et autres vicissitudes de la vie) et que la compétition intraspécifique, spécialement entre les prédateurs mammifères et leurs proies, est souvent d'importance minime.

Table 1. INTRODUCED MAMMALS ESTABLISHED IN NEW ZEALAND. ADAPTED FROM WODZICKI (1965).

Order and species	Date introduced	Distribution — Abundance	Ecological changes
MARSUPIALIA			
* Brush-tailed Opossum *Trichosurus vulpecula*	1858	Widespread and abundant, North, South, and Stewart Islands	Acute
* Common Scrub Wallaby *Wallabia rufogrisea*	1870	Restricted but common, South Island	Moderate
Swamp Wallaby *W. ualabatus*	1870	Restricted but common, North Island	Minor
Black-striped Wallaby *W. dorsalis*	1870	Restricted but common, North Island	Minor
* Dama Wallaby *Thylogale eugenii*	1870	Restricted but common, North Island	Moderate
Black-tailed Rock Wallaby *Petrogale penicillata*	1870	Restricted and rare	Minor
INSECTIVORA			
Hedgehog *Erinaceus europaeus*	1892?	Widespread and abundant, North and South Islands	Minor
CARNIVORA			
* Stoat *Mustela erminea*	1885	Widespread and common, North and South Islands	?
Weasel *M. nivalis*	1885	Restricted and rare, North and South Islands	?
Ferret *M. putorius*	1882	Widespread and common, North and South Islands	?
Feral Cat *Felis canis*	Early 19th Century	Widespread and common, North, South and Auckland Islands	?

Table 1. Continued

Order and species	Date introduced	Distribution — Abundance	Ecological changes
RODENTIA			
Kiore or Maori Rat *Rattus exulans*	14th Century	Restricted but common, North, South, Stewart, *et al.* Islands	Minor
* Ship Rat *R. rattus*	18th Century	Widespread and common, North, South, and Stewart Islands	?
* Norway Rat *R. norvegicus*	Early 19th Century	Widespread and common, North, South, Stewart & Campbell Islands	?
* House Mouse *Mus musculus*	Early 19th Century	Widespread and abundant, North, South, Stewart & Auckland Islands	?
LAGOMORPHA			
* European Hare *Lepus europaeus*	1867	Widespread and abundant, North and South Islands	Acute
* European Rabbit *Oryctolagus Cuniculus*	1838	Widespread and abundant, North, South, and Auckland Islands	Acute
ARTIODACTYLA			
* Feral Cattle *Bos taurus*	Early 19th Century	Restricted but common, North, South, Auckland & Campbell Islands	Acute
* Feral Sheep *Ovis aries*	Early 19th Century	Restricted but common, North, South, and Campbell Islands	Acute
* Feral Goat *Capra hircus*	18th Century	Widespread and abundant, North and South Islands	Acute
* Chamois *Rupicapra rupicapra*	1907	Widespread and common, South Island	Acute
* Thar *Hemitragus jemlahicus*	1904	Restricted but common, South Island	Acute

* Red Deer *Cervus elaphus*	1851	Widespread and abundant, North, South, and Stewart Island	Acute
Sambar Deer *C. unicolor*	1895	Restricted but common, North Island	Moderate
Javan Rusa Deer *C. timoriensis*	1907	Restricted and rare, North Island	Moderate
Wapiti *C. canadensis*	1905	Restricted but common, South Island	Acute
* Japanese Deer *C. nippon*	1885	Restricted but common, North Island	Acute
* Fallow Deer *Dama dama*	1864	Restricted but common, North and South Island	Acute
Moose *Alces americana*	1900	Restricted. Extinct? South Island	?
Virginia Deer *Odocoileus virginianus*	1901	Restricted but common, South and Stewart Islands	Acute
* Feral Pig *Sus scrofa*	18th Century	Widespread and common, North and South Islands	Acute
PERISSODACTYLA			
Feral horse *Equus caballus*	Early 19th Century	Restricted and rare, North Island	Minor

* Indicates species considered to be locally important " noxious " animals.

Table 2. A SMALL SAMPLE OF THE KINDS OF NEW ZEALAND FLORA THAT HAVE BEEN MATERIALLY DEPLETED LOCALLY BY INTRODUCED MAMMALS. FROM HOWARE (1964 a).

Family	Genus Species	Common name
ASPIDIACEAE	*Polystichum vestitum* Presi.	
GRAMINEAE	*Chionochloa cunninghamii* (Hook f.) Zotov	Snow tussock
FAGACEAE	*Nothofagus* spp.	Beech
RANUNCULACEAE	*Ranunculus lyallii* Hook f.	
CUNONIACEAE	*Weinmannia racemosa* Linn. f.	Kamahi
ELAEOCARPACEAE	*Aristotelia serrata* Forst. f.	Wineberry
MALVACEAE	*Plagianthus* spp.	Ribbonwood
	Hoheria sexstylosa Col.	Lacebark
VIOLACEAE	*Melicytus ramiflorus* Forst.	Mahoe
MYRTACEAE	*Metrosideros* spp.	Rata
ONAGRACEAE	*Fuchsia excorticata* Linn. f.	Konini or tree-fuchsia
ARALIACEAE	*Neopanax* spp.	Five finger
UMBELLIFERAE	*Aciphylla* spp.	
	Anisotome spp.	
	Angelica spp.	
CORNACEAE	*Griselinia littorallis* Raoul	Broadleaf
RUBIACEAE	*Coprosma* spp.	
COMPOSITAE	*Olearia* spp.	Scrub
	Senecio elaeagnifolius Hook f.	Leatherwood

REFERENCES

ALLAN, H. H. (1937). Some ecological features of the main islands. *Handbook, Auckland meeting A.N.Z.A.A.S.* 1937: 36-42.

ANDERSON, J. A., and HENDERSON, J. B. (1961). *Himalayan thar in New Zealand. Aspects of life history and assessment of management problems.* N.Z. Deerstalkers Assoc, Special Publ. 2, 37 p.

ATKINSON, I. A. E. (1964). Relations between feral goats and vegetation in New Zealand. *N.Z. Ecological Soc. Proc.* 11 : 39-44.

BAKER, H. G., and STEBBINS, G. L. Eds. 1965. *The genetics of colonizing species.* Proc. 1st IUBS Symposia on General Biol., Academic Press, New York, 588 p.

BATCHELER, C. L. (1962). Record and perspective of *The proceedings of the meeting to discuss the noxious-animals problem in New Zealand* 1958. *N.Z.* For. Serv., 50 p.

BAYLIS, G. T. S. (1948). Vegetation of Great Island, Three Kings Group. *Rec. Auckland Inst. Mus.,* 3 : 239-252.

— (1951). Incipient forest regeneration on Great Island, Three Kings Group. *Rec. Auckland Inst. Mus.* 4: 103-110.

BEVERIDGE, A. E. (1964). Dispersal and destruction of seed in central North Island podocarp forests. *Ecological Soc. Proc.* 11 : 48-55.

BULL, P. C, and FALLA, R. A. (1951). Observations on birds. In *Preliminary Reports of the New Zealand-American Fiordland Expedition* (A. L. Poole, cd.) p. 76-92. N.Z. Dept. Industr. Res. Bull. 103, 99 p.

CAMPBELL, A. P. (1961). Hydrology in New Zealand. *N.Z. Engineering* 15 (8): 281-287.

— (1963). Flood estimation and channel scour. In *Proc. Tech. Symposium on Hydrol. and Land Mgmt. 14-16 May, 1962,* p. 94-101. Soil Conserv. and Rivers Control Council, Christchurch.

CHRISTIE, A. H. C. (1964). A note on the chamois in New Zealand. *N.Z. Ecological Soc. Proc.* 11 : 32-36.

CONWAY, M. J. (1949). Deer damage in a Nelson beech forest. *N.Z. J. For.* 6 (1) : 66-67.

COSTIN, A. B. (1963). *Some impressions of a visit to parts of the South Island, June, 1962.* Tussock Grasslands and Mtn. Lands Inst. Spec. Publ. 2, 16 p.

CUTTLER, E. J. B. (1962). Stability of steepland soils of South Island, New Zealand, International Soil Conf. New Zealand 1962. *N.Z. Dept. Sci. Industr. Res., Soil Bur. Publ.* 280 : 3-7.

DAVIDSON, M. M., and KEAN, R. I. (1960). Establishment of red-deer range in the Tararua Mountains. *N.Z. J. For.* 8 (2): 293-324.

DAVIS, J. H. (1953). Biotic change in New Zealand. *Sci. Monthly* 76: 109-111.

DE VOS, A., MANVILLE, R. H. and VAN GELDER, R. G. (1956). Introduced Mammals and their influence on native biota. *New York Zool. Soc. Zoological.* 41 (Part 4): 163-194.

DICE, L. R. (1952). *Natural communities.* Univ. Mich. Press, 547 p.

DONNE, T. E. (1924). *The game animals of New Zealand.* John Murray, London, 322 p.

DRUCE, A. P., and ATKINSON, I. A. E. (1959). Forest variation in the Hutt Catchment. *N.Z. J. For.* 62 (2): 21-28.

ELDER, N. L. (1956). North Island protection forests. *N.Z. J. For.* 7: 96-103.

FLEMING, C. A. (1957). Trans-Tasman relationship in natural history. In *Science in New Zealand* (F. R. Callaghan, ed.), p. 228-246. A. H. & A. W. Reed, Wellington.

— (1962). New Zealand biogeography—a paleontologist's approach. *Tuatara* 10 (2): 53-108.

GODLEY, E. J. (1961). Fauna and flora. In *Distance looks our way—The effects of remoteness on New Zealand* (Keith Sinclair, ed.), Univ. Auckland and Oxford Univ. Press, 120 p.

GRAHAM, E. H. (1944). *Natural principles of land use.* Oxford Univ. Press, London, New York, and Toronto.

GRANT, P. J. (1956). Opossum damage in beech forests Ruahine Range, Hawke's Bay. *N.Z. J. For.* 7 (3): 111-112.

HERCUS, B. H. (1964). Sheep in the tussock grasslands. *N.Z. Ecological Soc. Proc.* 11 : 36-39

HOBBS, D. F. (1954). Do newly introduced species present a separate problem. *N.Z. Ecological Soc. Proc.* 2 : 12-14.

HOLDSWORTH, M. (1951). Effects of goats on Great Island, Three Kings: the permanent quadrats resurveyed. *Rec. Auckland Inst. Mus.* 4 (2): 113-122.

HOLLOWAY, J. T. (1948). Ecological investigations in the Nothofagus forests in New Zealand. *N.Z. J. For.* 5 (5): 401-410.

— (1950). Deer and the forests of western Southland. *N.Z. J. For.* 6 (2): 123-137.

— (1951). Forests and forest animals. *N.Z. Sci. Rev.* 9: 143-145.

— (1954). Forests and climates in the South Island of New Zealand. *Trans. Roy. Soc. N.Z.* 82: 329-410.

— (1956). The national forest survey and the watershed protection forests. *N.Z. J. For.* 7 (3) : 61-67.

— (1959). Noxious-animal problems of the South Island alpine watersheds. *N.Z. Sci. Rev.* 17 (2): 21-28.

— (1960). Research in mountain-land management: New Zealand problems in the light of overseas experience. *N.Z. J. For.* 8 (2) : 275-292.

— and NAYLOR, R. (1959). Protection forest problems in Nelson-Marlborough. *N.Z. J. For.* 8 (1) : 121-132.

HOWARD, W. E. (1957). Ecology of rabbits in New Zealand compared with California rodents. *Proc. N.Z. Ecological Soc.* 5: 13-14.

— (1958). The rabbit problem in New Zealand. *N.Z. Dept. Sci. Industr. Res. Inform.* Series 16, 47 p.

— (1964 a). Introduced browsing mammals and habitat stability in New Zealand. *J. Wildl. Mgmt.* 28 (3): 421-429.

— (1964 b). Modification of New Zealand's flora by introduced mammals. *N.Z. Ecological Soc. Proc.* 11 : 59-62.

— (1965 a). Control of introduced mammals in New Zealand. *N.Z. Dept. Sci. Industr. Res. Inform.* Series 45, 96 p.

— (1965 b). Interaction of behavior, ecology, and genetics of introduced mammals. In *The Genetics of Colonizing Species* (H. G. Baker and G. L. Stebbins, eds.), p. 461-484. Proc. 1st. IUBS Symposia on General Biol., Academic Press, New York, 588 p.

— (In press). Vertebrates : Biocontrol and chemosterilants. In *Ecological, Physical, and Advanced Chemical Methods of Control* (W. W. Kilgore and R. L. Doutt, eds). Academic Press, New York.

HUTCHINSON, G. E. (1951). Copepodology for the ornithologist. *Ecology* 32: 571-577.

KEAN, R. I. (1951 a). Deer and the vegetation; (d) carrying capacity of Fiordland. N.Z.-Amer. Fiordland Exped., *N.Z. Dept. Sci. Industr. Res. Bull.* 103 : 34-37.

— (1951 b). Estimation of the effects of deer and opossums in high country. *N.Z. Sci. Rev.* 9 (8) : 146-149.

— and PRACY, L. T. (1949). Effects of the Australian opossum (*Trichosurus vulpecula* Kerr) on indigenous vegetation in New Zealand. *Proc. 7th Pacific Sci. Congr.* 4 : 696-715.

KIDDIE, D. C. (1962). The sika deer (*Cervus nippon*) in New Zealand. *N.Z. For. Serv. Inform.* Series 44, 37 p.

LOGAN, P. C. (1956). Some problems in the control of wild and domestic animals in a critical hydro-electric catchment. *N.Z. J. For.* 7 (3): 68-75.

MARSHALL, W. H. (1963). The ecology of mustelids in New Zealand. *N.Z. Dept. Sci. Industr. Res. Inform.* Series 38, 32 p.

MCKELVEY, P. J. (1959). Animal damage in North Island protection forests. *N.Z. Sci. Rev.* 17 (2): 28-34.

— (1960). Condition assessment of protection forests. *N.Z. J. For.* 8: 325-334.

— (1963). The synecology of the West Taupo indigenous forest. *N.Z. For. Serv. Bull.* 14, 127 p.

McKinnon, A. D., and Coughlan, L. (1960-1964). *Data on the establishment of some introduced animals in New Zealand forests.* Extracts from Annual Reports of ... 1960: Vol. 1, 26 p., Agriculture Department 1901 and 1905, Tourist and Health Resorts Department 1902-1931; vol. II, 53 p., Lands and Survey Department 1896-1919, State Forest Service 1920-1949, New Zealand Forest Service 1950-1960. 1961 : Vol. III, 83 p., Department of Internal Affairs 1916-1957. 1962: Vol. IV, 67 p., Wellington and Wairarapa District Acclimatisation Society 1885-1960; Vol. V, 57 p., Auckland Acclimatisation Society 1907-1946, Nelson Acclimatisation Society 1903-1949, North Canterbury Acclimatisation Society 1902-1949, South Canterbury Acclimatisation Society 1902-1932; Vol. VI, 50 p., Southland Acclimatisation Society 1896-1940, Otago Acclimatisation Society 1888-1947. 1963 : Vol. VII, 37 p., Animal protection acts and amendments 1861-1903. 1964: Vol. VIII, 96 p., Animal protection acts and amendments 1907-1962.

Moore, L. B., and Cranwell, L. M. (1934). Induced dominance of *Microlaena avenacea* (Raoul) Hook, f., in a New Zealand rain-forest area. *Rec. Auckland Inst. Mus.* 1 : 219-230.

Morris, R. F. (1963). Part V. Resume. In *The Dynamics of Epidemic Spruce Budworm Populations,* p. 311-320. Entom. Soc. Canada Mem. 31, 332 p.

Nicholson, A. J. (1954). An outline of the dynamics of animal populations. *Australian J. Zool.* 2 : 9-65.

— (1957). The self-adjustment of populations to change. *Cold Spring Harbor Symp. Quant. Biol.* 22 : 153-173.

Packard, W. P. (1947). Lake Coleridge catchment: a geographical survey of its problems. *N.Z. Geographer,* 3 : 19-40.

Poole, A. L. (1959). The noxious animal problem. *N.Z. Sci. Rev.* 17 (2): 18-20.

Poole, A. L., and HOLLOWAY, J. T. (1951). Deer and the vegetation; (a) field evidence. In *Preliminary Reports of the New Zealand-American Fiordland Expedition* (A. L. Poole, ed.), p. 27-29. N.Z. Dept. Sci. Industr. Res. Bull. 103, 99 p.

Poppelwell, D. L. (1929). Some ecological effects of acclimatisation in New Zealand. *N.Z. J. Sci. and Tech.* 11 : 125-127.

Pracy, L. T. (1962). Introduction and liberation of the opossum (*Tricbosurus vulpecula*) into New Zealand. *N.Z. For. Serv. Inform.* Series 45, 28 p.

— and Kean, R. I. (1949). *The opossum in New Zealand.* Int. Aff. Dept. Wildl. Publ. 1, 19 p. Reprinted 1963 as N.Z. For. Serv. Publ. Item 40, 19 p.

Riney, T. (1955). *Identification of big game animals in New Zealand.* N.Z. Dominion Mus. Handbook 4, 26 p.

— (1956). Comparison of occurrence of introduced animals with critical conservation areas to determine priorities for control. *N.Z. J. Sci. and Tech.* 38B (1) : 1-18.

— (1957). Sambar (*Cervus unicolor*) in sand hill country. *N.Z. Ecological Soc. Proc.* 5 : 26-27.

— and Caughley, G. (1959). A study of home range in a feral goat herd. *N.Z. J. Sci.* 2 (2): 157-170.

— and Dunbar, G. A. (1956). *Criteria for determining status and trend of high country grazing lands in the South Island of New Zealand.* Soil Conserv. and Rivers Control Council, Wellington, N.Z., 33 p.

— Watson, J. S., Bassett, C, Turbott, E. G., and Howard, W. E. (1959). Lake Monk expedition, an ecological study in southern Fiordland. *N.Z. Dept. Sci. Industr. Res. Bull.* 135, 75 p.

Shennan, J. P. (1960). " Journals " 50 years' war on animal pests. *N.Z. J. Agr.* 101(2): 145, 147, 149, 151, 153, 155, 157 and 159.

Silvester, W. B. (1964). Forest regeneration problems in the Hunua Range, *Auckland. N. Z. Ecological Soc. Proc.* 11 : 1-5.

Thomson, G. M. (1922). *The naturalization of animals and plants in New Zealand.* Cambridge Univ. Press, 607 p.

Turbott, E. G. (1948). Effect of goats on Great Island, Three Kings, with description of vegetative quadrats. *Rec. Auckland Inst. and Mus.* 3 : 253-272.

WADDINGTON, C. H. (1965). Introduction to the symposium. In *The Genetics of Colonizing Species* (H. G. Baker and G. L. Stebbins, eds.), p. 1-6. Proc. 1st IUBS Symposia on General Biol., Academic Press, New York, 588 p.

WALSH, P. (1893). The effect of deer on the New Zealand bush : a plea for the protection of our Forest reserves. *Trans. N.Z. Inst.* 25: 435-439.

WARDLE, P. (1961). The effect of deer on subalpine forest and scrub. *N.Z. Ecol. Soc. Proc.* 8: 52-54.

WESTERSKOV, K. (1953). Acclimatisation of new game species. *N.Z. Dept. Internal Affairs, Wildl. Publ.* 17: 1-8.

WIDDOWSON, D. (1960). Beech regeneration and deer in the north-eastern Ruahine Range. *N.Z. J. For.* 8 (2) : 335-336.

WILSON, E. O. (1965). The challenge from related species. In *The Genetics of Colonizing Species* (H. G. Baker and G. L. Stebbins, eds.), p. 7-27. Proc. 1st IUBS Symposia on General Biol., Academic Press, New York, 588 *p.*

WODZICKI, K. A. (1950). Introduced mammals of New Zealand. *N.Z. Dept. Sci. Industr. Res. Bull.* 98, 250 p.

— (1961). Ecology and management of introduced ungulates in New Zealand. *La Terre et la Vie* N° 1 (1961): 130-157.

— (1963). Introduced mammals in New Zealand forests. *Acta Biol. Cracovinsia Ser. Zool.* 6: 111-134.

— (1965). The status of some exotic vertebrates in the ecology of New Zealand. In *The Genetics of Colonizing Species* (H. G. Baker and G. L. Stebbins, eds.), p. 425-460. Proc. 1st IUBS Symposia on General Biol., Academic Press, New York, 588 p.

WRAIGHT, M. J. (1960). The alpine grasslands of the Hokitika River catchment, Westland. *N.Z. J. Sci.* 3 : 306-332.

— (1964). Modification of grasslands by grazing animals. *N.Z. Ecological Soc. Proc.* 11 : 27-32.

ZOTOV, V. D., ELDER, N. L., BEDDIE, A. D., SAINSBURY, G. O. K., and HODGSON, E. A. (1939). An outline of the vegetation and flora of the Tararua Mountains. *Trans. Roy. Soc. N.Z.* 68 : 259-324.

UNGULATE INTRODUCTIONS AS A SPECIAL SOURCE OF RESEARCH OPPORTUNITIES

by

T. RINEY

Wildlife Officer,
Forestry and Forest Products Division,
Food and Agriculture Organization of the United Nations,
Rome, Italy

INTRODUCTION

Populations of animals existing in an area because they were placed there by man are said to be introduced species. They may be exotic or native, introduced or re-introduced.

This paper is restricted in scope to large wild or feral ungulates, for although some generalizations apply equally to other taxonomic groups, others do not.

The principal thesis is that, while we are often involved with one aspect of field biology and are interested in discovering more facts and principles to increase understanding of ungulate ecology, we frequently overlook the wonderful opportunities for research arising from introductions. The following discussion tries to emphasize this point.

Because of personal acquaintance with ungulate introductions in New Zealand (nearly 8 years) and in Africa (5 years), nearly all of the examples and references are drawn from these two parts of the world. In New Zealand all animals introduced were exotic, while in Southern Africa nearly all were indigenous and re-introduced, an important difference in cross-checking generalizations about large ungulate introductions.

THE HISTORICAL SETTING

Well before the time of Christ the technique of capture and transporting wild animals was advanced enough to permit a wide variety of African game to be used as meat on the tables of Roman emperors, in their menageries and in their amphitheatres.

Between one and two thousand years ago the Maori brought the Polynesian rat and Maori dog to the remote pacific islands of New Zealand and, judging from the strange distribution of sika and other deer in the Pacific region south and east of the Philippines, introductions of deer by various islanders have been widespread for hundreds of years. Polynesian introductions seem an excellent subject for future study.

Within the last hundred years tremendous development of facilities for transportation have taken place along with large scale efforts at colonization and in this period a trend started toward the liberation of large ungulates that eventually involved thousands of animals. In the Pacific introductions of deer ranged from tropical islands of Hawaii and New Caledonia to Tasmania and Stewart Island, New Zealand. The southernmost ungulate liberation was on the island of South Georgia where reindeer were released; they still exist, providing an accessory source of meat for whaling ships.

The eleven successful and two unsuccessful introductions of ungulates into New Zealand mainly occurred between 1850 and 1914. Actual numbers of liberations were in the hundreds, there being over 150 liberations of red deer alone in the North Island. At the present time most of these species can be found in all stages of acclimatization ranging from populations that are fully adjusted and stable to others in which deer are still spreading into previously unoccupied habitat.

While human colonization brought large mammals into New Zealand habitats devoid of mammals, in Southern Africa colonization combined direct destruction of large mammals by shooting, with indirect but even more effective destruction of habitat through drastic changes in the pattern of land use.

Recent introductions of animals in Southern Africa are thus largely re-introductions to re-establish ungulates on private and public lands to ensure the survival of the various species. In the past thirty years over three dozen species of large mammals were re-introduced in thousands of liberations. At present several well known game reserves and many private, lands hold thriving populations of re-introduced ungulates.

Facilities and techniques for transport and for capture are improving. It is clear that in the last ten years more ungulates have been introduced than in any previous similar period in history. If this is a long term trend, then we have only just started. In any event it may be useful at this point to review some research opportunities associated with introductions and the acclimatization process and to give examples of research results already in hand or now being produced.

RESEARCH OPPORTUNITIES ASSOCIATED WITH THE INTRODUCTION PROCESS

Research in simplified ecosystems

The New Zealand environment, uncomplicated by previous history of animal use, and with the human history and impact rather precisely known, offers comparatively simplified ecosystems for studies of introductions and acclimatization. The islands permit a laboratory-like opportunity for field observations and a rapid accumulation of evidence that, obtained under other more normal conditions, would be time consuming, difficult and expensive. This in no way implies a monotony of environment; far from it. Over the thousand miles of latitude the climate changes from mediterranean to sub-antarctic; topography, from flat coastal plains to precipitous mountains over 10,000 feet high; rainfall varies between 15 inches to well over 400 inches per year. Nevertheless, except where complicated by a history of agricultural land use, ecosystems in which introduced ungulates occur are, comparatively, remarkably uncomplicated in the sense that environmental controls are few in number. Since the available environments are remarkably varied, the islands lend themselves to a type of comparative study between ecosystems that if exploited can quickly and considerably increase our understanding of comparative ungulate ecology. The following examples may be illustrative.

Habitat selection

From known points of liberation in New Zealand it is possible to trace the spread of various species of deer through a variety of habitats. In some of these areas, nearly one hundred years later, after the populations have long been stabilized in the new environment, deer in adjacent valleys and coming from the same liberation are occupying very different environments and quick comparative studies are easy.

Similar opportunities are present in South Africa; for example, in three days in the Transvaal comparisons were made between nine species of ungulate, introduced into two different game reserves at about the same time, approximately ten years earlier. In one reserve the species (zebra, sable, wildebeest, blesbuck, impala, ostrich, common duiker, nyala, eland, kudu and klipspringer) had occupied preferred sections of the reserve and with very little overlapping. In this reserve the differences in preferred habitat were easily described as differences in rock, slope, vegetation type, proximity to water, edge between forest and grassland, forest alone and so on.

In the second reserve some of the same species were present (zebra, eland, wildebeest, blesbuck, duiker, etc) but, instead of a variety of habitat types, this reserve consisted of a level plane of grassland, with a few short scattered trees. Nevertheless the various species occupied the area for nearly the same length of time with but little or no overlap between species, the separation being mainly on a sociological basis based on intolerance or tolerance between different species (Riney and Kettlitz, 1964).

In some cases it is clearly easier to learn the essential requirements of the species by study of an introduction into a " strange " environment than by study of the species in its natural environment. This is the case of the sambar (*Cervus unicolor*) in New Zealand (Riney, 1957). In India the sambar is a creature of the forest, occurring from the foothills up to elevations as high as 9,000 feet in the Himalayas. In New Zealand in one of the areas of introduction, they occur on sand dunes and do not penetrate the forest clad mountains. Rather they remain on the coastal plain. The search for a common element between these two environments (so different that one might feel that there was an excellent example of quick and great adaptation to a new environment) revealed that in both cases the deer were closely associated with broad leafed sedges and grasses, which in India grew along the streams that ran through the forest and in New Zealand in the swampy areas between the dunes.

Lupines and small scattered (introduced) conifer plantations suffice as cover in New Zealand, while in India nearly the entire environment was under cover, which precluded cover as a limiting factor. Cross-checking with other introductions in New Zealand confirmed that the broad leafed grasses and sedges associated with swampy areas were always an important element of the sambar habitat.

EXAMPLES OF RESPONSE OF AN INTRODUCED SPECIES TO DIFFERENT HABITATS

Evidence of population response to environment has been used as evidence of suitability of habitat. This is a useful procedure if certain precautions are taken, for example:

The population should have passed its initial eruptive oscillation and have become stabilized with the consequently modified environment before making even general comparisons with other areas. Comparing one population as it approaches the peak of even a mild initial oscillation (Riney, 1964) with another population past the peak by four or five years would be meaningless as evidence of population response to different habitats.

Examples of other precautions are included below, with examples of differences in population response.

Types of evidence of population response

Types of evidence of population response readily obtained in New Zealand and African populations are size of animal, age ratios, sex ratios, population density, and physical condition. Examples of the usefulness of these different kinds of evidence are given below.

From a single liberation near Bluff, in the South Island of New Zealand, red deer were liberated in 1901 and 1904. Since then they have gradually dispersed (1) over a small range of hills, (2) across a low, densely-forested valley, and (3) up and over the next mountain range. Deer living in the densely forested intermediate area are considerably smaller in size, and fewer in number, than either of the two adjoining populations in spite of the fact that the forest population came from one and in turn gave rise to the other. The almost complete absence of open grassland in the forested area is the major habitat differencee between the three areas, the first and third areas being similar in having a good interspersion of grassland and forest. The last of these populations (3) had passed its initial oscillation by 14 years (Riney *et al.,* 1959) at the time the above observations were made.

Differences in ratios between fawns and adult hinds in different environments taken in New Zealand when the fawns were three to four months of age showed differences between different areas ranging between 28 to 70 fawns per hundred hinds. Since the average of all these areas was 41/100, approximately the same as comparable figures taken from Jutland (38/100), one of the northernmost extensions of red deer in its natural range, this evidence has contributed to the conclusion that many New Zealand environments are in general less suited to red deer than the original natural environment. On the other hand, a few New Zealand populations produce fawn-hind ratios of 70/100 and are thus comparable to good red deer habitat in Europe.

Indices to fat reserves in ungulate populations or segments of these populations can provide important data for comparing two environments. Three of the New Zealand Avoca and Monowai areas containing red deer have been compared in this respect. It has been suggested that the Avoca population can recover more quickly from the influences of decimating environmental factors with, for example, a kidney index rating in adult females averaging 31 (± 6) than either Monowai one or Monowai two, where kidney fat ratings averaged 13 (± 6) and 18 (± 5), respectively. (This technique has been described by Riney, 1955). Comparable figures for adult males, taken at the same time of year in the same areas were Avoca: 81 (± 11), Monowai one: 12 (± 11), and Monowai two: 27 (± 9). Even more important are condition indices taken from younger elements of the population. Comparable figures for yearlings in the above areas were: Avoca: 26 (± 4), Monowai one: 11 (± 4), and Monowai two: 9 (± 4) (Riney, 1955). This kind of evidence is consistent with the notion that the Avoca area is a better environment for red deer than either Monowai one or Monowai two.

In a similar way, a more rapid field technique to record physical condition has been used in other New Zealand environments (e.g. Riney *et al.*, 1959, and Riney, 1960) and in African environments, to assess the extent to which the habitat was suitable for holding even greater numbers of introduced animals than were present at the time of the study (Riney and Kettlitz, 1964).

Testing and expanding the concept of home range

The concept of home range, or the area in which an individual lives (usually considered on a yearly basis) is of obvious importance in considering relations between populations and environment, for it is within the home range that all the necessary requirements for an individual's existence are met.

Twenty-five to thirty years ago home range was expressed as a linear distance, indicating the diameter or radius of the area occupied. It was recognized that some species had greater ranges than others and home range was normally regarded simply as a characteristic of a species that might be described along with numbers of young, weight, measurements, nesting habits, and food predilections. In 1950, in a study of mule deer (Riney, 1950), emphasis was given to the importance of learning the shape of the individual home ranges as a means of thinking more critically about essential habitat requirements. Many other recent workers have emphasized the influence of the environment on home range. This was carried a step further in New Zealand when, within a precisely defined home range of a long-established herd of feral goats, areas of high use connected by trails and areas of complete unuse were described (Riney and Caughley, 1959).

Studies of home ranges of introduced populations can contribute in an important way to an understanding of the biology of a species, for in various areas the size and shape of home ranges markedly differ. In the case of red deer in New Zealand, where the various major elements of the habitat, such as edible shrubs, grass, water, and shelter from the elements, are closely interspersed, home ranges are small, often under a mile in greatest diameter. On the other hand, where these elements are widely spaced home ranges are considerably larger.

In this connection it may be noted that differences in condition indices can be used as indirect evidence of restricted home ranges, that is, restricted enough to delineate populations for study purposes. Thus, the areas Monowai one and two, mentioned above, were contiguous areas separated only by a small shallow stream, across which deer whose home ranges included both sides of the stream freely crossed daily. Nevertheless, differences in fat reserves of numbers of animals shot on both sides of the stream, in obviously different habitats, were great enough to be used as indirect evidence of restricted ranges.

New light on the origins of migration

Migration is here used to refer to movements between seasonal home ranges. For deer of temperate climates the yearly home range normally involves a winter range and a summer range, connected by a migratory route. In Africa, where migrations occur, the yearly range includes often a dry season and a wet season range, and sometimes consists of repetitive seasonal shifting over a wide area without any clear seasonal ranges being established.

There are many examples in New Zealand of deer occupying areas and establishing yearly home ranges without migratory behavior even fifty years after introduction. In other areas, clear patterns of migration have been established shortly after introduction. In some areas, from a single liberation, deer moving into one area migrate while those dispersing into a nearby but differing environment do not migrate.

Here the explanation is simply an extension of our knowledge on home range. Where the population finds all of its yearly requirements for existence within a small area, it does not leave the area (even under rather severe hunting pressure) but resides there throughout the year and does not migrate. Where it has been necessary to migrate, migrations have become established.

Because in temperate regions it is most difficult critically to examine the origins of migration without a great deal of speculation (usually involving gradually receding ice-caps), it should be clear that there is great opportunity for further study of the origins and development of migration by exploiting unique opportunities associated with introduced ungulates.

Patterns of dispersal, an important field for future study

Dispersal, as used here, is the movement of an ungulate away from the home range of its parents or family group to a home range of its own. In large ungulates this normally takes places as the young animal reaches breeding age and the home range is maintained, normally with only slight yearly shifts, for the breeding life of the individual. Wandering of old individuals and their temporary association with first one then another family group is not included in the present definition.

W. E. Howard (1960) introduced the hypothesis that there were two different patterns of dispersal, environmental and innate.

Because of their size and known history of introduction, large ungulates in New Zealand and in Africa provided ideal opportunities for testing and elaborating this hypothesis, and the following remarks summarize largely my unpublished findings on the subject of large ungulate dispersal in New Zealand and in Africa.

The New Zealand findings based on 15 species of introduced ungulate entirely confirm Howard's hypothesis that patterns of innate as well as environmental dispersal exist in ungulate populations although the precise definitions used are somewhat different.

I define environmental dispersal as the movement of young members of the population into a suitable habitat within, adjacent to, or near the parental home range.

Innate dispersal, as here used, indicates the type of dispersal occurring entirely independent of the suitability of the environment. It consists of certain young individuals, more commonly males, moving long distances across suitable or unsuitable environments before finally establishing a new home range. As Howard (1960) notes: " Possession of the innate dispersal trait implies that such an animal is predisposed at birth to leave home at puberty and make one dispersal into surroundings beyond the confines of its parental home range. Such density-independent individuals have inherited an urge to leave home voluntarily. They often pass up available and suitable niches and venture into unfavourable habitats ".

It is clear from the New Zealand observations that each species has its own characteristic pattern of dispersal and that, among the fifteen species introduced, the pattern ranges from species like the sika deer, whose dispersal pattern is almost entirely environmental, to chamois and red deer, which have strong innate dispersal characteristics in addition to the basic environmental type dispersal shared by all ungulates.

The most frequently encountered evidence of innate dispersal is the sudden appearance of a young animal in a place considerably removed from the nearest known population. Red deer have suddenly appeared in patches of forest twenty to thirty miles from the nearest known populations. The wanderings of some of these young individuals become well known as various neighbours exchange news of their progress.

A good example of species differences in this respect is the introduction of red deer and sika deer at the same time and on the same North Island farm. The forest behind the farm consisted of podocarp and beech forest interspersed infrequently with small clearings bordering streams. In front of the farm was a very large area of grassland, as much as a mile wide in parts and extending for several miles in either direction. Red deer spread across this clearing within the first few years after introduction, then gradually spread northward, while the sika deer took over sixty years to cross the same clearing to the opposite side. Even so, the sika dispersal was of the environmental type only; that is, by gradually dispersing around the clearing through the forest to a point opposite the initial liberation point. The large area of grassland was enough of a barrier to contain the sika deer and innate dispersal was apparently lacking.

Judging by the infrequency of records coming to hand, the proportion of young that disperses innately varies greatly between species. For example, more records were obtained of young chamois than comparable records for Himalayan thar.

Information on dispersal patterns of African mammals was obtained in a similar way by alerting wardens in game reserves where introductions had taken place to the importance of recording dispersal patterns in such a way that comparable information could accumulate for comparison with New Zealand records.

Some information is already in hand for about thirty African ungulates (largely bovids), providing a basis for comparison with the cervids of the Northern Hemisphere.

Among African introductions one can find a comparable range of dispersal pattern as is present in cervids. Records of innately dispersing kudu are obtained with about the same frequency in Rhodesia, Zambia, and the Transvaal as are records of red deer in New Zealand. Bushbuck, on the other hand, resemble more the sika deer which disperses almost exclusively environmentally.

In addition to the parallels that can be drawn between African and temperate species, certain African mammals have a dispersal pattern that is to my knowledge, unknown in cervids. While dispersal as thus far discussed involves the separation of an individual from the family group and the establishment of a home range for that individual, in Africa certain species disperse in mixed groups. Groups of twenty waterbuck, over a hundred wildebeest, of sixty to seventy giraffe, predominately young individuals, have suddenly appeared in various areas where they have been previously unknown.

The hypothesis is here presented that group dispersal of certain African ungulates may be part of the explanation for the present day survival of a Pleistocene African fauna. Although there are bones of cervids in various parts of Africa south of the Sahara, in the drier areas without dependable water supplies present day species of cervids might temporarily establish themselves but would ultimately die, lacking the two main mechanisms that have allowed African ungulates to survive : either a physiological adaptation to allow survival for months without access to surface water, or a mechanism for dispersal that permits at least small groups to be present in areas where water is still available.

A knowledge of dispersal patterns has obvious practical implications for management, as, for example, when cropping schemes wish to reduce dispersal of unwanted ungulates into nearby farming or ranching areas.

Selective shooting at the right time of the year, and emphasizing certain sex and age groups, can help contain populations. On the other hand, there is some evidence both from New Zealand control operations and from African tsetse fly control operations that when dispersal patterns are ignored, shooting also takes place at the time of the year when young are naturally dispersing and thus accelerates the rate of dispersal.

Howard (1960) observes that all dispersal of whatever type is a mechanism for mixing genes and permitting species to occupy a new habitat as it becomes available through changing climates or large-scale activities of man.

Exploitation of situations surrounding introductions allows us to see this mechanism in operation quickly and clearly without long-term, expensive marking campaigns. For example, consider the record of a single male thar suddenly appearing and taking up residence in a mountain valley, several valleys removed from the nearest New Zealand thar population, and living his entire adult life alone on the small home range he established. In a hundred years' time when thar occur normally in the new valley, only expensive marking studies could permit a similar observation.

SEVERAL CONTRIBUTIONS TO THE CAUSE EFFECT INTER-ACTIONS BETWEEN ANIMALS AND THEIR ENVIRONMENT

Environmental controls and the simplified ecosystem

One of the most attractive aspects of the New Zealand environment for the study of ungulate ecology is that it provides a variety of comparatively simple ecosystems for study. It is still possible to find areas seldom if ever disturbed by hunters and without other forms of predation, where there are few ecto- or endo-parasites, and where there is no other ungulate in the watershed to compete. Under these circumstances it is hard to imagine more ideal conditions for the study of environmental controls.

Studies over a period of seven years have shown that in areas of low populations, held rigidly in check by environmental controls, there are usually several factors that combine and these various factors differ area by area. In most areas the extent of interspersion of various habitat requirements is a major factor determining potential carrying capacity; a close second is the extremely rigorous climate in many of the mountainous areas supporting deer. Examples of special controls in local areas are: deer falling off cliffs or being blown from ridges or precipices (seventy five percent of deer shot in one study area had broken bones and at the base of nearly every cliff were skeletons); torrential rains, sleet and snow are normal in some areas during the weeks of calving; limestone pot holes form natural pit traps for deer in some areas; the normal rise and fall of rivers in some Fiordland areas is between 10 and 20 feet and it is not uncommon for entire valleys to flood to a depth of five feet and more. Thus it is relatively easy in these extreme environments to be certain about the importance of environmental controls and to observe their influence as populations spread.

But what environmental factors control populations under the most favourable habitat conditions, where the potential for numbers is high and where potential productivity is high ? There are study areas in New Zealand where such conditions exist, where environmental control must in some way play the dominant role, for other potential controls are absent; such is the value of the simple ecosystem. In such cases, we can suggest two different contributing mechanisms. First, it was noted that, at the time of the year when deer should be in top physical condition (late summer and early autumn), the average physical condition of females measured was not much better in the best than in the worst deer areas. In the worst environments a high proportion of fawns was lost early and the poor condition of females was due to stresses imposed by weather, while in the better environments with better initial survival of young, stresses on adult females were probably due to lactation.

The second factor is thought to relate to the variability in quality of individual home ranges. In poor environments home ranges are in large proportion poor and this is reflected in the general poor condition of deer. In good environments, while a much higher proportion of home ranges for individual family groups are good, nevertheless many individual home ranges are as poor as those of poor environments and the deer remain in these individual home ranges even though surrounded by more suitable environment, as has been demonstrated in an area of similar topography in California (Leopold *et al.,* 1951).

It should be clear that the question of environmental controls is by no means exhausted. The extent to which social factors such as intolerance of nearby family groups, or territorialism (as suggested by Graff, 1956) operate and contribute to maintain a stable population is not known. I feel exploitation of study opportunities associated with introductions is one of the quickest roads to a better understanding of these questions.

Patterns of population growth

The predictable eruptions or initial oscillations of large ungulates following introductions have been described in a paper presented at a previous IUCN Technical session (Riney, 1964) and needs no elaboration here as a research opportunity associated with introductions.

It is, however, relevant to re-emphasize the importance of knowing the present state of a study population in relation to its initial oscillation for it has obvious importance in the ecological definition of animal problems: the interpretation of data taken from vegetation, in the form of percentage use of annual production, regeneration of certain plant species or in the interpretation of animal sex and age ratios, condition indices and censuses or density indices of various types. In New Zealand, an understanding of the time necessary for the initial oscillation in an undisturbed population is knowledge of the potential minimum time required for conversion of a unique environment without ungulates, into an environment similar to that found in other parts of the world that have supported ungulates since the pleistocene.

The significance of predation on ungulate populations

Most New Zealand areas with deer have no predators although man serves this function as a private hunter or as a government-paid deer culler. After twenty years shooting there were more deer than ever in the vicinity of the very first deer destruction camps established in the South Island (Riney, 1956 a) and the negligible effects of hunting in other areas has been documented (Riney, 1957).

In certain New Zealand areas, as for example in certain parts of the Urewera mountains in North Island, predators exist in the form of completely feral dog populations. The effectiveness of this predation can best be judged by comparison with adjacent areas of similar habitat but without dog packs where there is no significant difference in age structure or in density of animals, the density being clearly governed by environmental controls and not by predation. I have some evidence (still unpublished) to suggest that the deaths of red deer fawns occur sooner after birth in the areas of predation than in the areas without such predators. But at the age of five or six months, the number of young per 100 females is equal in areas with and without predators, either man or feral dog.

Re-examination of the significance of food habits studies

In New Zealand back country, away from the influence of introduced plant species on improved paddocks, no individual deer has, in the last hundred years, eaten one species that its ancestors ate in their country of origin. Nevertheless, deer thrive, or do poorly, in habitats of varying suitability just as they do in their native countries.

There are several ways of commenting on this simple observation. One common reaction is to say this proves how wonderfully quickly or how terribly aggressively (depending on one's attitude) the deer have adapted. Another, and from the standpoint of research opportunity, more profitable view is to re-examine the extent that our traditional food habits studies are really contributing to an understanding of ungulate ecosystems. The definition of good red deer habitat is the same in New Zealand as in Europe if one uses general terms like a higher proportion of shrubs and trees for winter, more grass for summer and spring, available water, protection from predators, hunters, or the weather. These are the things that count for red deer; not the individual plant species. It is suggested that if these were taken as a basis for study some very important comparative food habits studies could be organized between, for example, English, German, Scandinavian and New Zealand biologists.

Re-examination of the significance of parasites as a factor controlling populations

This subject is still little studied in New Zealand. Several internal parasites were lost in transit from England or Europe to New Zealand because of the lengthy time needed to make a sea voyage in the latter half of the 19th century. We know that the few parasites that were brought with the deer and some of those shared in common with sheep, become more prominent and are probably a contributing cause to population control once an animal has reached a certain low level in physical condition. But most of this work is yet to be done and presents a fine opportunity for study of parasitism as a factor in population control.

Understanding the process of extinction

For the 214 species introduced into New Zealand, about two thirds of the introductions failed for various reasons (Riney, 1958). Although success has been much higher in Africa, here too there are failures. If we are looking for important simple ways of documenting the process of extinction, introductions provide us with almost test-tube-like opportunities for documenting this process. This seems a particularly important kind of research for those interested in developing greater ability to manage an ecosystem to achieve the survival of a species.

Other subjects associated with introductions

Development of animal problems

Animals become a problem when their normal activities conflict with human interests. Elephants destroy valuable timber trees, deer eat cabbage, retard forest growth, reduce the value of timber by altering tree shape, and some wild ungulates compete with some domestic ungulates for living requirements.

Consequences of introductions should be predictable. As long as we see introductions of ungulates as a hit and miss affair, we betray the inadequacy of our ecological understanding of the animal in question. The confident prediction of consequences following an introduction is a natural and worthwhile aim of the student of ungulate ecology. We can, for many ungulates, already predict certain types of consequences, for others we need more knowledge and this knowledge can best be gained through study of the introductions around us.

Introductions do not necessarily imply trouble [1]. Most ungulate introductions have in fact been successful and have not caused serious problems. This applies even to the deer in New Zealand judging from a study made in 1956 which showed that the areas of highest deer density were not necessarily the areas that were troublesome from the standpoint of accelerated erosion, or regeneration of native forest (see Riney, 1956 a and 1956 b). And even the notorious red deer is not necessarily bad in all New Zealand areas (Riney *et al.*, 1959; Riney, 1957).

With the above considerations in mind there is good motivation for research to analyse and more clearly define problems associated with introduced animals. The field of investigation within disturbed ecosystems is only just developing and exploitation of opportunities arising from introductions can make an important catalytic contribution.

The following questions may be asked about the desirability of introducing an ungulate species:

a) What is its potential eruptive curve under ideal conditions ?

b) Would over-population of the species interfere with the major form of land use to which the area is now or will be devoted?

c) Is the population controllable?

d) What are its habitat requirements, even in general terms ? (How adaptable to a wide range of conditions, how restricted to a narrow range?)

e) What is the pattern of dispersal, and at what time of the year does dispersal take place?

Capture and transport of animals

The capture and transport of animals presents special opportunities for research. The use of tranquilizers for capture and during transport to the new site of liberation has become a specialized field in itself with a feedback into the studies of social behaviour and animal movements. In this connection it is important to recognize that, in our present state of knowledge, mechanical methods are still more effective for many large ungulates than are tranquilizers; the knowledge gained from developing and successfully applying mechanical methods of capture is another bonus to our understanding.

In the same way we are learning more of the effect of various stress factors on animals being moved or recently moved. Recent experience in Africa points to the increasing significance of this subject if we are to maximize our chances for consistently successful introductions (Riney and Kettlitz, 1964).

DISCUSSION AND CONCLUSIONS

Charles Elton has noted that " man is continuing to change the species network of the world " and he raises questions that will help us on our way if we will but understand their significance and get to work. " What is the full ecosystem... how many species can get along together in one place ? What is the nature of the balance amongst them? Can we combine the simple culture of crops with the natural complexity of nature, especially when there is an almost inexhaustible reservoir of... species that may send new colonists to disturb the scene? All these

[1] This point, as well as several others here discussed, has been made by FITTER (1959) for introductions into the United Kingdom.

questions, are much nearer than the horizon, though most ecologists have not looked at them with any enthusiasm, or if they have glanced at them, shuddered and turned away towards the already tedious and difficult task of understanding the biology of a single species, dead or alive " (Elton, 1958).

In general, future studies of large wild mammals throughout the world, and in particular management of wild and domestic ungulates, must trend increasingly toward assessing the environmental potential of the land on the one hand and the potential range of response of the animals in question on the other hand. Progress in this direction will be facilitated as we understand more details, especially of those mechanisms of animal environment inter-adjustments which result in homeostatic trends within ecosystems. This should increase our skill at managing an ecosystem in order to ensure maintenance of maximum production and conservation values.

As indicated in the above discussion, exploitation of research opportunities associated with introductions can make significant contributions in this direction.

Although little has been said about the motivation for future introductions, this is a subject well worth studying in more detail.

In the past, motivation for introducing a species has been varied. For example, rats and dogs, as potential sources of food, were taken along with humans who colonized previously uninhabited Pacific Islands; ungulates were introduced into New Zealand both as a source of sport and as a psychological link with the homeland of the remote British Isles. In South Africa, ungulates were re-introduced as a means of saving species from extinction and, later, developed as a profitable form of land-use.

The future rests with us and those who follow. In a meeting devoted to conservation of nature and natural resources the concept of introductions may relate closest to the development of acceptable patterns of land-use on a national and international basis. The historical setting of our problem provides the greatest motivation for seriously considering the uses and limitations of introductions for, at present, we find the marginal lands of the world steadily being whittled away, put out of production by unsuitable forms of land-management. The net result is that not only are species becoming extinct with shameful rapidity but that an increasing area of the world is becoming unproductive for any form of land-use.

A logical and practical aim for those interested in the long-term future of man is to achieve a stabilization of the marginal lands of the world and a trend toward an increasing productivity on those areas that become more critical as one moves out into deserts, or swamps, or up the slopes of mountains.

Under these circumstances we may re-examine and expand the concept of multiple land-use already accepted in certain agricultural and forest lands and expand and develop the similar concept of diversified pastoralism, using various combinations of wild and domestic animals.

In many African National Parks there are about thirty species of mammals, fox-size or larger, each species occupying the environment, utilizing a somewhat different part of the primary production than even its closest relative species. Already we know that this type of secondary productivity is possible in other continents where, for various historical, biological and bio-climatalogical reasons, the post-pleistocene ungulate populations have dwindled to a half dozen species or less.

In practical terms, combinations of wild animals can be developed and managed in marginal lands unsuited to present forms of land-use. It is possible, through careful selection of species, to construct a productive ecosystem which allows a gradual recovery of the environment while still maintaining some form of economic use from the land. For example, on areas where grassland has been destroyed by cattle and sheep, wild animals such as eland, oryx and addax can be used as they can thrive on plants unused by domestic animals. The oryx is nearly and the addax is completely independent of surface water. Eventually, as the country improves, other species may be introduced when appropriate.

This in no way means we should start a campaign for indiscriminate introductions. Mistakes of the past are giving enough warning that we should remain on guard. But to worry about walking for fear of tripping places us nearly in the category of vegetables or invertebrates and our expanding activities in other directions gives the lie to this line of thought. We must understand more of the potential uses and the limitations of introductions as a part of our own, so far rather feeble, efforts to live within the capacity of the environments we are given to ensure our own survival.

REFERENCES

ELTON, C. S. (1958). *The Ecology of Invasions.* Methuen and Co. Ltd., London: 181 p.

FITTER, R. S. R. (1959). *The Ark in Our Midst.* Collins, London: 320 p.

GRAF, W. (1956). Territorialism in Deer. *Journ. of Mammalogy* 37 (2): 165-170.

HOWARD, W. E. (1960). Innate and Environmental Dispersal of Individual Vertebrates. *The American Midland Naturalist* 63 (1) : 152-161.

LEOPOLD, A. S., RINEY, T., MCCAIN, R., and TEVIS, L., Jr. (1951). *The Jawbone Deer Herd.* Calif. Div. of Fish and Game — Game Bull. n° 4 : 139 p.

RINEY, T. (1950). *Home Range and Seasonal Movement in a Sierra Deer Herd.* Univ. Calif. M. A. Thesis (filed Univ. Calif. Lib.): 1-42.

— (1955). Evaluating Conditions of Free-ranging Red Deer (*Cervus elaphus*) with Special Reference to New Zealand. Part I: Description of Techniques for determination of Condition of Red Deer. Part II: Application of Condition Indices to Deer Ecology and Management Research. *N.Z. Journ. Sci. and Tech.* 36, Sec. B (5): 429-463.

— (1956 a). A Comparison of Occurrence of Introduced Animals with Critical Conservation Areas to Determine Priorities for Control. *New Zealand Journal of Science and Technology* 38, B (1): 1-18.

— (1956 b). A Zooecological Approach to the Study of Ecosystems that Include Tussock Grassland and Browsing and Grazing Animals. *New Zealand Journal of Science and Technology* 37 B (4) : 455-472.

— (1957). The Use of Faeces Counts in Studies of Several Free-ranging Mammals in New Zealand. *New Zealand Journal of Science and Technology* 38, B (6): 507-532.

— (1958). Opportunities for Land Vertebrate Research in New Zealand. *Amer. Inst. Biol. Sci. Bull.* 8 (2): 21-23.

— (1960). A Field Technique for Assessing Physical Condition of Some Ungulates. *Journ. Wildl. Mgt.*, 24 (1) : 83-84.

— (1964). *The Impact of Introductions of Large Herbivores on the Tropical Environment.* 1UCN Publications new series n° 4, Pt. III: 261-273.

— and CAUGHLEY, G. (1959). A Study of Home Range in a Feral Goat Herd. *New Zealand Journal of Science* 2 (2): 157-170.

— and KETTLITZ, W. L. (1964). Management of Large Mammals in the Transvaal. *Mammalia* 28 (2): 189-248.

— WATSON, J. S., BASETT, C, TURBOTT, E. G., and HOWARD, W. E. (1959). *Lake Monk Expedition: An Ecological Study in Southern Fiordland.* New Zealand Department of Scientific and Industrial Research Bulletin 135 : 75 p.

L. W. Mc Caskill (New Zealand): from the point of view of the *ecological effects* of introduced animal species and the conservation of nature, especially in New Zealand Parks and Reserves, I endorse Dr. Howard's clear exposition of the disastrous effects of the introduction of mammals.

In the Reserves the complications of fire, sheep and cattle do not arise and the National Parks Authority has adopted a policy of exterminating introduced mammals as the only hope of fulfilling the basic aim of preservation of the *natural* fauna and flora. Some 1600 transects and plots are analysed at regular intervals in the forest and mountain lands and show conclusively the effect of deer and other animal destruction on vegetation recovery. Mr. Riney has, however, thrown doubt on the relationship between deer and erosion, and states that areas of high deer density are not necessarily the areas where there is an erosion problem. In fact our higher priority areas for deer extermination are those which have few deer; where country is in critical balance because of soil type, climate, earthquakes and so on, a few deer can reduce vegetation to such an extent that erosion can develop on a vast scale.

It has been suggested that unoccupied lands can be made available for deer, thar and chamois for recreational hunting, but, for the rehabilitation of high-level eroded areas, it is probable that tree or shrub-planting is the best hope, so that the risk of deer, thar and chamois destroying plantations is unacceptable, nor are the farmers who are voluntarily destocking land to assist erosion control likely to agree to the land being used as deer park.

Finally, with reference to the plea of the New Zealand Deerstalkers' Association that the herd of wapiti in the Fiordland National Park should be maintained, the Association which has had control of the herd since 1952 has failed to meet the condition that wapiti numbers should be kept at a level at which the vegetation does not suffer unduly; nearly 500 000 acres is in danger and, in parts, in critical condition. The Park Board has had to resume control and intends to follow a policy of severe reduction in the number of wapiti for the next five year period. It is worth noting that the wapiti are apparently hybrids between pure wapiti and red deer. Probably more important, however, than the wapiti problem is the fact that even some of the small New Zealand islands are in danger, due to recent invasion by rats, which constitutes a threat to several rare species of birds. Full IUCN support will be needed in dealing with all these problems.

Dr. H. H. Roth (FAO, Rome): Although one should always be fully aware of the dangers inherent in introductions, as well as reintroductions, these may offer very definite benefits to nations through abilities to increase food production, to enhance recreation, or to regulate the abundance of less-desirable species, and therefore it may be desirable under certain conditions to gain one or more of these benefits. A very critical, but nonetheless more constructive, attitude should be adopted by biologists who are challenged with the ultimate responsibility in respect of introductions of wild species. In international work there is a great need for some generally accepted criteria in this respect.

A CONCLUDING NOTE

by

GEORGE A. PETRIDES

Following the presentation of the formal papers contributed to Part III of IUCN's 10th Technical Meeting, it was felt to be desirable to summarize the advantages and disadvantages of species introductions and to bring the entire topic into full range for open discussion. Consequently, a preliminary draft resolution covering a proposed international policy for introduced plant and animal species was placed before the Meeting.

The discussion which followed was stimulating indeed. The range of experience with introduced species, however, was wide. It was recognized, for instance, that without certain imported species such as commercial grains, livestock, and ornamental plants, most human societies would find existence difficult or impossible. On the other hand, the imported pests in some parts of the world included the thistles, elm virus, and potato beetle. There was agreement that introduced species should be excluded from natural areas, but there was doubt that this always could effectively be accomplished. Otherwise, however, it proved impossible at this one session to attain a general comprehensive statement which might reflect IUCN policy toward introduced species.

Several successive draft statements were prepared for consideration by the participants. They are printed here as a record of the deliberations, giving evidence of an evolution toward simplicity of statement, and as an indication of the great range of both benefits and dangers which are possible as a result of species introduction. As indicated in these drafts it was felt that the IUCN should be prepared to give useful advice on plant and animal introductions, but it was clear that if such a statement of general policy is to be developed, it will have to be an outgrowth of continuing discussion.

THE DRAFT RESOLUTIONS

DRAFT A (proposed by G. A. PETRIDES)

It is recognized that non-native plants and animals in new habitats may offer benefits to mankind through special abilities to increase food production, to enhance recreation through harvest or observation, or to regulate the abundance of less desirable species. The desire to gain one or more of these benefits, or to enable the preservation of the species in an improved habitat, or to undertake research under controlled conditions is a suitable motive in transplantation efforts.

It is further recognized, however, that the introduction of exotic species holds dangers in that foreign organisms may interact unfavorably with native species through predation, parasite and disease transmission, toxic reactions, foraging, competition or otherwise. They also may become overabundant and comprise a nuisance, or they may be scientifically undesirable in natural areas, or be esthetically objectionable. Furthermore, they may spread beyond the boundaries of the area intended for their occupation.

Therefore be it resolved that the introduction of new species should be effectively restricted by each nation through practical and enforced legal procedures.

It is agreed that introductions may properly be advocated where there is evidence that all of the following conditions are met:

1. The introduced species offers qualities superior to those of native species or no native species has similar characteristics.
2. The introduced species would not endanger the lives of either humans or livestock by direct attack or by otherwise causing unhealthful conditions.
3. The introduced species would not compete to a significant degree with man or his valued resource species or become so abundant as to be annoying.
4. The overall values of the introduced species would be greater than any harm which it would cause to important native wild animals or plants through predation, competition, interbreeding, serving as a disease or parasite vector, or otherwise.
5. Public esthetic values are not violated.

To insure that these conditions are met, the following procedures are to be followed:

1. A study in the native habitat of the species to be introduced will first be made to ascertain its behavioral, physiological, and ecological characteristics with respect to its resource needs and its potential for undesirable species interactions (such as predation, parasitism, interbreeding, competition) and for unwanted population growth.
2. A study in the new habitat will be undertaken to appraise the suitability of the environment for the new species and the probable effects of the introduction on native forms.

3. Approval of the proposal to introduce the new species will be secured from a sub-committee of the IUCN Commission on Ecology which would also consult with appropriate organizations such as FAO and UNESCO.
4. Preliminary test introductions on islands or other isolated areas will be made wherever possible and the results of such tests be made available to IUCN.
5. Approval of plans for final species' introductions into non-native environments will be secured from the IUCN Commission on Ecology prior to the undertaking of the plan on a full-scale basis.

Nothing in this resolution shall be interpreted to affect the restocking and reestablishment of species which, as based on adequate scientific evidence, are being restored to a native habitat.

DRAFT B (proposed by H. H. ROTH, A. DE VOS & W. E. HOWARD)

It is recognized that vertebrate wildlife either introduced into areas in which they are non-indigenous or re-introduced into changed habitats may offer benefits to mankind through special abilities to increase food production, to enhance recreation, or to regulate the abundance of less desirable species. The desire to gain one or more of these benefits, or to enable the utilization of the species in a modified habitat is a suitable motive in translocation efforts.

It is further recognized, however, that the introduction or re-introduction of wild vertebrate species holds dangers in that they may interact unfavorably with the indigenous biotic community through predation, parasite and disease transmission, toxic reactions, competition or other adverse affects on native communities. They may also become over-abundant and a nuisance, or they may be scientifically undesirable in natural areas, or may be esthetically or economically objectionable. Furthermore they may spread beyond the boundaries of the area intended for their occupation. It does not seem possible to conduct experiments in the habitats of origin, which give completely satisfactory answers about the behaviour of a species in its new environment after its introduction.

Therefore be it resolved that introductions or re-introductions of wild vertebrates be considered only:

1) if the introduction can reasonably be expected to add extra aesthetic and/or economic value to an area without being inconsistent with the overall policy of land use for the area;
2) if after research it is likely that the spread of the introduced species can be eliminated or satisfactorily controlled in areas where it is not wanted;
3) if the various stages of acclimatization of the species and its impact on the habitat can be studied.

If introducing of vertebrate wildlife can be recommended in these general terms there is still certain knowledge required about the species to be introduced :

a) the habitat requirements for the species in relation to the intended habitat of introduction or re-introduction;
b) the dispersal pattern of the species (even in general terms);
c) the potential eruptive population growth;
d) the potential of the species for interfering with various forms of agriculture or forest use;
e) the potential of the species as a carrier of unwanted pathogens;
f) the potential contribution to the area of introduction or re-introduction as balanced against potential problems.

DRAFT C (as proposed in the General Assembly Resolutions Committee)

Recognizing that the total effects of introducing any exotic species into a wild environment are difficult to forecast and that such introductions have more often than not proved deleterious to man's overall interests and *further recognizing* that introduction policies should reflect a careful balance between different and sometimes conflicting human interests— aesthetic, scientific and economic...

The 9th General Assembly of IUCN meeting in June at Lucerne *recommends* that the introduction of animal and plant species into wild habitats be strongly discouraged unless:

1) the introduction can reasonably be expected to be of overall benefit to man,
2) it can reasonably be expected not to threaten native species or distinctive populations except those which are pests,
3) the spread of the introduced species can be controlled, and unwanted sections of the population eliminated,
4) the process of introduction can be fully studied,

and *urges* Governments to ensure that natural ecosystems are conserved by the establishment of nature reserves from which exotic fauna and flora are as far as possible excluded.

DRAFT D (proposed by H. H. ROTH, A. DE VOS, W. E. HOWARD, L. M. TALBOT & G. A. PETRIDES)

Recognizing that plants and animals either introduced into areas in which they are non-indigenous or re-introduced into changed habitats may offer benefits to mankind through special abilities to increase food production, to enhance recreation or aesthetic enjoyment, or to regulate the abundance of less desirable species, and that the desire to gain one or more of these benefits, or to enable the utilization of the species in a modified habitat is a suitable motive in translocation efforts,

and recognizing that the introduction or re-introduction of plant and animal species holds dangers in that they may interact unfavorably with the indigenous biotic community through predation, parasite and disease transmission, toxic reactions, competition or other adverse effects on native communities, and that they may also become overabundant and a nuisance, or may be scientifically undesirable in natural areas, aesthetically or economically objectionable, or may spread beyond the boundaries of the area intended for their occupation,

and further recognizing that it does not seem possible to conduct experiments in the habitats of origin, which give completely satisfactory answers about the behaviour of a species in its new environment after its introduction,

The 9th General Assembly of IUCN meeting in Lucerne in June 1966 *recommends* that introductions or re-introductions of plants and animals be strongly discouraged unless:

1) the introduction can reasonably be expected on balance to add extra aesthetic and/or economic value to an area without being inconsistent with the overall policy of land use of the area;
2) the introduction does not threaten the continued existence and abundance of any native plant or animal species or distinctive population;
3) it can be shown by research to be likely that the spread of the introduced species can be eliminated or satisfactorily controlled in areas where it is not wanted; and
4) the various stages of acclimatization of the species and its impact on the habitat are studied.

Printed in Great Britain by
Unwin Brothers Limited,
The Gresham Press, Old Woking, Surrey, England
A member of the Staples Printing Group