Spatial ecology of the Ethiopian wolf, *Canis simensis*

A thesis submitted for the degree

Doctor of Philosophy

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To my father, from whom I learnt to observe nature,

and to Claudio, who introduced me to Bale and the wolves.

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ABSTRACT

Ethiopian wolves (*Canis simensis*) have developed a refined specialization to prey upon the rich rodent fauna of the Afroalpine ecosystem, a once widespread habitat persisting in mountain relicts. I applied a multi-level approach to investigate ways in which wolves respond to their environments at various scales of Afroalpine patchiness and heterogeneity. I focused on Afroalpine rodents as the critical resource and on the ecological constraints in their use at various scales, interpreting ecological patterns in terms of wolf behaviour and life-history traits.

Extensive field surveys showed that high habitat specificity and a specialized diet confine wolves at present to Afroalpine islands at the top of the highest mountains, mostly limited on the lower end by the extent of subsistence agriculture. While wolves persist in almost every Afroalpine range in Ethiopia, habitat loss has resulted in local extinctions in two small Afroalpine patches and all seven extant populations are small (ranging from 10 to 250 wolves) and virtually isolated from each other. The Ethiopian wolf's specialization seems to have appeared early in the short evolutionary history of the species. Mitochondrial DNA phylogeography showed strong links between the genetic structuring of populations and the dynamical biogeography of Afroalpine ecosystems during the late glacial-interglacial period. The genetic data showed that Ethiopian wolves originated around 100,000 years ago, when Afroalpine habitats were widespread across Ethiopia. After an initial population expansion, the subsequent partition of haplotypes reflected random fixation of alleles in isolated populations as the climate warmed, matching the reconstructed pattern of Afroalpine reduction and fragmentation at the onset of the deglaciation ca. 15,000 years ago.

The dynamics of local populations in the Bale Mountains showed that, in the absence of infectious diseases, Ethiopian wolf numbers were relatively stable and resilient to livestock grazing and human disturbance, but disease epizootics severely affected wolves living at high densities in rodent-rich areas. A stable environment and a stable prey resource, combined with the high adult survivorship observed, may facilitate the long-term persistence of populations in spite of small numbers and isolation. In saturated environments, the production of ‘surplus’ adult wolves led to philopatry via delayed dispersal, and some long-distance female dispersal. At low densities resulting from an epizootic, these surplus animals participated in the recovery via pack augmentation and the formation of new breeding units. However, the surviving packs initially expanded to incorporate vacated areas and augmented via delayed dispersal, so that new breeding units only formed once a pack was large enough to allow for splitting, or when sufficient numbers of dispersers coalesced to ensure the successful defence of a new territory. In consequence, reproduction at the lowest densities was initially limited to the few surviving breeding units, leading to inverse density dependence in the rate of population growth. This natural experiment unveiled intrinsic mechanisms of regulation, mediated by territoriality, delayed dispersal and reproductive suppression, operating at the levels of packs but expressed at the population level. The prevalence of expansionism at reduced densities, and the lack of evidence of direct benefits from cooperative breeding in larger groups, strengthens the prevailing thesis that long-term food security and the inheritance of a high quality territory may be the main selective pressures behind sociality in the Ethiopian wolf.

The ecological conditions for sociality and expansionism, however, were constrained by the local pattern of resource availability within populations. In an area with overall low prey density, neighbouring pairs with large territories defended similar amounts of rodent-rich habitats than larger groups with smaller territories in the more productive areas. This contradicts the prediction that animals will defend the minimum territory necessary to fulfil the metabolic requirements of its owners. In one case, group augmentation and territorial expansion appeared to be favoured by the high aggregation of prey, such that larger territories showed proportional increments in the areas of rodent-rich habitats. In the other, patches of high quality habitat existed within a matrix of poor habitat, so that the costs of expanding an already large territory to include more rich patches may be too high, and the benefits for the primary pair nil or minimal. High aggregation of resources may shift the balance of costs and benefits towards sociality in an arm’s race to secure a portion of a very rich area.

This thesis exemplifies the utility of combining studies of a species’ biology at various levels of biological organization and of the spatial distribution of a critical resource to understand better the effects of constraints in their use, and how these affect habitat selection, the dynamics of populations and ultimately the adaptive value of behavioural strategies. The implications for the conservation of this highly threatened canid are discussed in relation to the spatial scale at which threats take place and possible solutions may be implemented.

AKNOWLEDGEMENTS

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A young wolf bitch reaches the rim of the valley wall. She stands there for a moment and drops down towards the barley fields at a speedy trot. She is keeping good pace and hoping for a dark night, long enough for her to reach a safe place, another mountain haven. There are too many people, too many dogs, too many risks in this foreign land.

Is she following a primeval instinct leading her to the nearest mountain, just visible in the farthest horizon? Or is she tentatively exploring, continuously searching for clues signalling to her a place, hopefully not very far, where she may find enough food and a companion to mate?

This same event must have happened many times before, probably throughout the history of the she-wolf ancestors in the Ethiopian highlands. Many other times other wolves would have left home, because it was too crowded, it had been ploughed, or because every other wolf was dying of rabies. Hers is an individual decision, yet shaped by generation upon generation of trials and errors, some winning, some losing.

Today, in an era dominated by peoples' needs, when every inch of the land in these tired highlands is so valuable for the Ethiopian farmers, we want to learn the lessons wolves learnt in a thousand generations to stay alive in a landscape dotted with montane "islands", and find a way to ensure they survive in a treasured handful of the highest mountains.

J.M.

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CHAPTER I

General introduction

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1.1 Prologue

Until recently, the Ethiopian wolf or Simien jackal (*Canis simensis*) was notable simply for its precarious status at the verge of extinction (Harper 1945; Brown 1964; Gottelli & Sillero-Zubiri 1990; Ginsberg & Macdonald 1990). Detailed studies then revealed that it also deserved attention because its behavioural ecology was unexpected. Ethiopian wolves are solitary foragers with a social organization intricately adapted to distinctive features of the Afroalpine ecosystem (Sillero-Zubiri 1994; Sillero-Zubiri *et al.* in press). During the colder times of the late Pleistocene the wolves seemingly specialized to exploit an emerging habitat, feeding on the presumably abundant Afroalpine fossorial fauna (Kingdon 1990). But with specialization came isolation and dependence on a restricted habitat, with concomitant small population sizes that rendered them susceptible to habitat loss and stochastic hazards.

During several expeditions to Afroalpine ranges in northern Ethiopia I marvelled at the wolves' ability to survive in small habitat 'islands' encapsulated within a sea of barley fields and human settlements. While we realized that the wolves' prospects for long-term persistence were undoubtedly jeopardized, I conjectured that the adaptations that once made wolves successful at exploiting the Afroalpine rodent fauna were still successful at ensuring their survival in a warmer, human dominated world. Understanding the wolves' adaptations and their role in population persistence can help answer the questions we face in our quest to secure the species' long-term survival. Under which ecological conditions do Ethiopian wolves survive today? Which factors limit and regulate their populations? What are their chances of persistence in a highland landscape fragmented by densely populated farmland?

These and other related questions could be dealt with in isolation, but answering only one of them while ignoring the others would provide only a dissatisfyingly incomplete picture. My study aims at combining the strength of ecological theories to understand the many ways in which the spatial pattern of rodent availability may influence Ethiopian wolf distribution, the structure and dynamics of populations, and the social and spatial organization of individuals. It is at the level of individuals that the ultimate causes of adaptive behaviours may be fully interpreted, but ecological explanations exist at all hierarchical organisational levels. Changing the magnifying power of the lens through which wolves are observed allowed me to encompass the network of relationships of which the wolves are part. We may thereby enhance our chances of converting scientific knowledge into successful conservation actions.

1.2 The spatial dimension in Ethiopian wolf ecology: a model species

Only one large canid has become extinct in recent times. The Malvinas zorro, or Falkland Island wolf (*Dusicyon australis*), went extinct in 1876 (Allen 1942). The Malvinas zorro lived in the treeless South Atlantic archipelago, and preyed on geese, penguins and seals. Its extermination resulted from the activity of fur traders and poisoning by settlers to control sheep predation (Novak & Paradiso 1983). Although the Ethiopian wolf differs in habitat requirements and is not subject to the same threats, the biogeography of both species converge at one point: at least part of the reason for *D. australis*' extinction was linked to its living in small oceanic islands, while the Ethiopian wolf is threatened with extinction due to a fragmented distribution, restricted to a few '*islands*' of Afroalpine habitat.

The Ethiopian wolf's feeding specialization, and its dependence on a food resource that is highly structured in space, makes it a special case for the application of theoretical concepts in spatial ecology, to understand more completely the evolution and persistence of adaptive behaviours, and the dynamics and resilience of its extant populations. This section presents a brief review of the known ways in which Ethiopian wolves respond to their environment over spatial scales and levels of organisation. This provides the bases for the subsequent definition of the study objectives, set in a theoretical framework relevant for the questions asked at each hierarchical organisational level.

1.2.1 Specialization

The family Canidae is composed of 36 living species of dogs (wolves, jackals, coyote) and foxes (Clutton-Brock *et al.* 1976; Ginsberg & Macdonald 1990; Macdonald & Sillero-Zubiri in press; Sillero-Zubiri *et al.* in press b). It is a family characterized by the adaptability and widespread distribution of most of its species (Ewer 1973; Macdonald 1992). The 10 species of dogs (sub-family Caninae) are spread throughout the world, excluding Antarctica, and occupy a wide variety of habitats. They are specialists in hunting mammalian prey in open habitats, although they also take a wide range of foods including fruits (e.g. coyote *Canis latrans* and jackals), invertebrates (side-stripped jackal *C. adustus*), reptiles and amphibians (golden jackal *C. aureus*) (Macdonald & Sillero-Zubiri in press). In contrast with the generalist diet of other *Canis* species, Ethiopian wolves show a very narrow and carnivorous prey-base all year round (Sillero-Zubiri & Gottelli 1995a).

The Afroalpine grasslands are rich in rodents, while densities of other mammalian prey are low. Rodents are the wolves' most important prey, being the most abundant, conveniently-sized and easiest to catch prey, whose availability was also predictable, as the abundance of rodents is closely associated with different habitat types ((Sillero-Zubiri *et al.* 1995a,b). The richness and predictability of the rodent prey explains the wolves' pack territoriality as a food-resource defence strategy (Sillero-Zubiri & Gottelli 1995b; Sillero-Zubiri & Macdonald 1998).

1.2.2 Restricted distribution

Ironically, it is precisely this refined adaptation for feeding upon the ubiquitous Afroalpine rodents that has constrained Ethiopian wolves to a scarce and fragmented habitat (Kingdon 1990). This specialisation is arguably a recent one, since Ethiopian wolves probably originated from a Eurasian grey wolf-like ancestor, which entered North East Africa through land bridges (Gottelli *et al.* 1994; Wayne & Gottelli 1997). Although specialisation to a small mammal diet may have resulted in a phenotypical convergence to foxes (Clutton-Brock *et al.* 1976), leading to the misnomer Simien fox, mitochondrial DNA analyses have shown *Canis simensis* is actually more closely related to the grey wolf (*C. lupus*) and the coyote than to any African carnivore (Gottelli *et al.* 1994). During the colder periods of the Pleistocene the Afroalpine ecosystem was geographically extensive and the ancient wolf population might have spread into then widespread rodent-rich habitats. The warming up that occurred during the late Pleistocene then restricted Afroalpine habitats to small habitat 'islands' at the top of the highest peaks.

In present times degradation of the already restricted Afroalpine ecosystem by grazing and high-altitude subsistence agriculture is further fragmenting the habitat available to the species, making populations susceptible to novel extinction hazards such as human persecution, outbreeding depression, inbreeding, disease and natural catastrophes (Gottelli & Sillero-Zubiri 1992; Sillero-Zubiri & Macdonald 1997). These threats are a direct consequence of the Ethiopian wolf's specialization to life in the Afroalpine ecosystem (Kingdon 1990; Gottelli & Sillero-Zubiri 1990, 1992; Yalden & Largen 1992; Sillero-Zubiri & Gottelli 1994). There are around 500 wolves in the world today; half of them live in the Bale Mountains and the rest are dispersed in six small, isolated populations (Sillero Zubiri & Malcom 1997; Marino 2003).

1.2.3 A solitary forager with complex sociality

Like their close Canine relatives, Ethiopian wolves live in packs that communally share and defend an exclusive territory but, contradicting the general trend in carnivores for grouping and cooperative hunting, pack members forage and feed alone on small prey, living almost exclusively on diurnal small mammals (Sillero-Zubiri & Gottelli 1995a; Malcolm 1997; Ashenafi 2001). Such specialization resulted in the evolution and maintenance of an unusual social system, which contrasts markedly with those of most carnivores.

A rich and abundant rodent community inhabits the Afroalpine 'islands' home to the Ethiopian wolf (Kingdon 1990; Sillero-Zubiri *et al.* 1995a,b,c; Yalden & Largen 1992; Ashenafi 2001). Prey availability is also predictable, insofar as their abundance varies across habitat types (Sillero-Zubiri *et al.* 1995a,b), but this food resource is also geographically restricted and at high demand. Because the wolf prey occurs in rich patches and is rapidly renewed, sociality might have been favoured by the reduced costs of tolerating conspecifics in terms of foraging success (Sillero-Zubiri & Gottelli 1995a). Philopatric groups can then be formed as a direct consequence of habitat constraints.

Lack of suitable territories limits dispersal opportunities and favours the retention of young past the age of maturity (Sillero-Zubiri 1994; Sillero-Zubiri & Gottelli 1995ab; Sillero-Zubiri *et al.* 1996a, in press a). In areas of high prey density, Ethiopian wolves live in social groups of close kin; only the dominant female reproduces but all pack members help raising the offspring of the dominant pair. A polyandrous mating system - at an extreme within canid societies- seemingly evolved as a mechanism to reduce inbreeding levels within packs while maintaining the advantages of social life and cooperative breeding (Sillero-Zubiri *et al.* 1996a, in press a).

With intense competition for rodent-rich grasslands, Ethiopian wolf groups use strength in numbers in the acquisition and retention of resources by means of territorial defence (Sillero-Zubiri & Macdonald 1998); pack group size determines the outcome of territorial boundary clashes and larger groups defend larger territories, following an expansionist strategy (*sensu* Kruuk & Macdonald 1995). An alternative explanation for tolerating conspecifics is cooperative breeding (Jennions & Macdonald 1994) but the benefits of alloparental care in Ethiopian wolves are far from evident (Sillero-Zubiri 1994; Sillero-Zubiri *et al.* in press a; see Chapter 2). Thus, the maintenance of a high quality range is arguably the greatest advantage of group-living in this species (Sillero-Zubiri & Macdonald 1998). This social organization is representative of Ethiopian wolves at high density; in contrast, in rodent-poorer areas, wolves exist at low density and organized in pairs or small groups, living in territorial home ranges much larger than those occupied by the high-density pack. Thus selective pressures and dispersal seems to affect wolves differently in relation to the aggregation of animals as allowed by the prey resource.

1.3 Scale-dependent ecological theories and specific questions

For most species, landscapes are patchy, because the species has evolved specific habitat requirements and because landscapes are complex habitat mosaics. Ecologists have long known that nature is patchy and heterogeneous, but dealing with such heterogeneity has been a major challenge in both empirical and theoretical work. In explicitly considering space in the network of organism-environment interactions, spatial ecology has been dominated since the 1960s by two theories, the dynamic theory of island biogeography and the metapopulation theory (McArthur & Wilson 1967; Hanski 1999). At a finer-grained scales, behavioural ecologists study the causes of individual movements among resource patches and the ensuing distribution of foragers (Krebs & Davis 1984; Stephens & Krebs 1986) and the influence of the spatial and temporal distribution of essential resources in a species social and spatial organization (e.g. Waser 1981; Macdonald 1983; Packer 1986; Carr & Macdonald 1986; Woodroffe & Macdonald 1993; Wrangham *et al.* 1993; Creel & Macdonald 1995).

I studied aspects of the Ethiopian wolf's biology at multiple scales of patchiness and heterogeneity in their Afroalpine environments. The underlying argument of this thesis is that process rates and spatial scales are linked (O'Neill *et al.* 1986; Urban *et al.* 1987). Generally, large-scale, slower processes tend to place constraints on finer-scale processes operating at faster frequencies. For example, long-term, large-scale climatic patterns can place constraints on finer-scale processes such as animal movements or demography. A study conducted at one hierarchical level may provide a parsimonious, mechanistic explanation for habitat selection at the next level (O'Neill *et al.* 1986), thus allowing greater understanding of how organisms assimilate information and make decisions that influence habitat choice and, ultimately, fitness. At any given scale particular environmental variables drive the ecological processes. Thus for example weather becomes important at a continental level, while at the level of regional landscape, landforms and even microclimate are an important part.

The thesis is organized following a concept of upper level constraints through a hierarchical structure of 'patches', from Afroalpine 'islands' within Ethiopia, to the aggregated distribution of rodents within wolf territories. In the following section, I describe the questions that motivated this study and the theoretical framework against which the results are contrasted, highlighting the relevance for the system under study and for the conservation of this critically endangered canid.

In **Chapter II** I provide a detailed bibliographic review of the ecology of the Afroalpine ecosystem and the Ethiopian wolf, with a detailed description of the study areas.

1.3.1 Species level – The highlands of Ethiopia

Long-term temporal processes operating at this scale, chiefly driven by post-Pleistocene climatic changes, still remain as the most intriguing aspects of the Ethiopian wolf biology: such as its proposed recent evolution from an Eurasian immigrant, its relatively quick adaptation and specialization to the Afroalpine ecosystem, and the resilience of relict populations living in an increasingly fragmented and shrinking habitat. Thus the first section of the thesis deals with the issue of past and present wolf distribution, focusing on the effect of habitat reduction and fragmentation at the broadest scale of organization: the species level.

Metapopulation theory is now a popular framework for understanding the threats faced by species in fragmented habitats. A major focus of concern in conservation biology is the effect of habitat fragmentation on the genetic structure of species (e.g. Lande & Barrowclough 1987). Empirical studies (reviewed by Harrison 1991) and theoretical extensions of the original Levins framework (Levins 1969, 1970) have shown that many conclusions of the classic metapopulation concept were robust: with or without extinction playing a central role, subdivision and dispersal are the main factors affecting population dynamics and genetic diversity. Isolation and habitat fragmentation marked the evolutionary history of Ethiopian wolves and, more recently, the fate of populations cut-off in isolated mountains under increasing human pressure. Thus dynamic processes of habitat change are bound to have a profound effect on the structure and diversity of the Ethiopian wolf genome and on the risk of local extinctions.

In assessing metapopulation processes it is necessary to have data on the distribution of populations and habitats and on the rates and patterns of regional extinctions.

Chapter III presents the results of a complete survey of Afroalpine ranges in the highlands of Ethiopia. The objectives of the study were to determine the spatial distribution of wolf populations and record recent extinctions by field observations and comparisons with historical records. Rapid assessment techniques were used to assess populations' status and the threats to their long-term persistence, and to map habitat and wolf distribution, updating previous estimates of the global population. Ultimately, this study assesses whether, and which, populations seem likely to become extinct within a short time in the absence of immigration.

In assessing the limits imposed in the distribution of wolves by the loss and fragmentation of Afroalpine habitats, it is crucial to understand the role specialization plays in determining the ecological conditions under which the Ethiopian wolves survive today.

In **Chapter IV** I present the results of dietary analysis from wolf faeces collected in all but one of the extant populations. This study aims at measuring the degree of specialization of Ethiopian wolves in human-dominated landscapes and the factors affecting dietary variations. It provides information on the food resources available to wolves and a formal test of the assumption that wolves are indeed specialist rodent-hunters all across their range.

If habitat specificity was developed early in the evolution history of Ethiopian wolves, climatic-driven changes in Afroalpine biogeography must have had a profound affect on the structure and diversity of the species' genome.

Chapter V combines information on evolutionary history from the phylogeography of mitochondrial DNA, and its overlap with the dynamic geography of Afroalpine ecosystems during the last glacial-interglacial period. Major objectives were to test the hypothesis of the out-of-Africa origin of Ethiopian wolves and the role of habitat specificity and fragmentation as crucial factors influencing the species' genomic constitution. The genetic data was used to infer the timing of genetic divergence and the most likely partition of haplotypes in groups of genetically closely related populations.

1.3.2 Population level - Afroalpine islands

Under intense human pressure many species are, or may soon be, constituted by conspecific populations virtually or completely isolated from one another, to an extent that local extinctions can lead to regional extinction, one population at a time: the 'non-equilibrium populations' of the metapopulation theory (Hanski 1999). When recolonization is sufficiently slow, the fate of a species will be decided by forces acting much faster than its metapopulation dynamics –i.e. local dynamics rather than a balance of extinction/colonization. Examining species such as the Ethiopian wolf, that naturally occur in small and highly fragmented populations, and that successfully 'solved' the problems of space constraints, can provide a model system to unravel the demographic characteristics that enable small populations to remain viable (Stacey & Taper 1992). The pattern of resource distribution within populations can additionally cause small-scale population structuring with consequences for the dynamics of populations.

Thus this section of the thesis uses long-term monitoring data from Bale to investigate the dynamics of local populations in habitats of diverse prey quality, and the affect of external and intrinsic factors in the regulation of their abundance. Wolves in Bale are aggregated in areas of high rodent biomass (up to 27kg/ha) and all suitable habitat is occupied by social groups in a mosaic of neighbouring territories. Disease epizootics in the early 1990s severely reduced wolf numbers, and after a period of apparent lack of recovery, populations grew to previous density levels by the end of the monitoring period in 2000.

This natural 'perturbation experiment' permits us to explore whether populations are regulated (i.e. if they return to the equilibrium after a perturbation) and if regulation is mediated by density dependent mechanisms. Given the simplicity of the biological system (e.g. a super-abundant food resource monopolized by a species with no natural predators), classical population models would predict populations to be regulated via a density-dependent mechanism. This is because intra-specific competition is expected among individuals that utilize a common resource that is in short supply. In turn, high rates of population growth would be expected after severe reduction, because prey availability will be high and competition for food negligible. In social cooperative species, however, the intrinsic ability to convert that extra energy into enhanced fecundity and diminished mortality, could be limited by behavioural mechanisms and Alee effects (e.g. African wild dogs *Lycaon pictus*, Courchamp *et al.* 2000). The quantification of the simultaneous levels of other factors, potentially affecting prey availability (e.g. grazing pressure) or wolf foraging efficiency (e.g. disturbance by humans), can shed light onto possible causes of decline or limited recovery.

Chapter VI presents the results of analyses of time series of wolf abundances to detect trends in three Bale wolf subpopulations, occupying areas of varying prey density. The objective of the study was two-fold: to identify potential agents of decline and assess the vulnerability of the different populations, and to study patterns of population change across a wide range of population densities. This chapter also deals with the validation of an index of wolf abundance based on transect counts.

Chapter VII uses the fall and rise of wolf numbers in Bale as a perturbation experiment to compared demographic, structural and spatial parameters - both at population and pack levels - between two stages: a period of high population density in a saturated habitat versus a subsequent period of recovery from reduced densities. The study tests for the hypothesis of intrinsic regulation mediated by territoriality and reproduction suppression, which by affecting reproduction and the access to resources can affect population growth at different levels of saturation.

1.3.3 Pack level – Territories

Some species also partition available space to defend exclusive territories that provide some economic optimum of available resources (Kruuk & Macdonald 1985), and the spatial and temporal distribution of essential resources also influence social organization. In consequence, the focus of theories has turned from behavioural (Alexander 1974) towards resource-based explanations for sociality (e.g. Waser 1981; Macdonald 1983; Packer 1986; Carr & Macdonald 1986; Woodroffe & Macdonald 1993; Wrangham *et al.* 1993; reviews in Creel & Macdonald 1995 and Johnson *et al.* 2002). While group formation and group size are undoubtedly governed by a set of cost and benefits (Krebs & Davis 1993), the benefits of group living might operate within a framework of constraints, which theory predicts will be determined largely by the dispersion and abundance of the resources available, especially food.

Chapter VIII tests the hypothesis that ecological factors, rather than direct benefits of group-living, may be the primary determinants of sociality (Resource Dispersal Hypothesis – Macdonald 1983). The availability of prey within territories was quantified and compared between packs occupying habitats of contrasting prey quality, and between packs within rodent-rich areas where the richness of the food resource appears to favour group augmentation and territorial expansion.

Chapter IX is a general discussion focussing on the predictions that the spatial pattern of the food resource at different levels - within Ethiopia, isolated mountains or territories - influences Ethiopian wolf distribution, population structure, mechanisms of population regulation, and variations in group and territory size. Results are considered in the light of the evolution of the wolves' adaptive strategies and the implications for the conservation of the remaining wolves in the mountain-islands of Ethiopia.

CHAPTER II

Afroalpine and Ethiopian wolf ecology:

A review

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2.1 The Afroalpine ecosystem

2.1.1 The Afroalpine ecosystem home to the Ethiopian wolf

Rainfall and temperature are obvious determinants of the distribution of fauna and flora, and of their adaptations. In the high mountains of East Africa the climate determines three broad altitudinal belts: an Afroalpine zone, a heath or sub-alpine belt and a montane forest or grassland belt (Kingdon 1990). Ethiopian mountains are drier than the wetter equatorial mountains further south, thus the effects of cold weather descend further down. Ethiopia has a much more extensive area of uplands and contains the largest extent of Afroalpine habitat in the African continent (Yalden 1983) (Fig. 2.1). During the Ice Ages the entire Ethiopian dome would have been less like Africa and more like the tundras of Eurasia.

The Ethiopian dome began to rise some 75 million years ago and eventually split open and fractured; the Ethiopian massifs north and south of the Great Rift Valley then acquired some interesting and significant differences in their fauna and flora (reviewed by Kingdon 1990). After periods of intense volcanism, up to 4 to 5 million years ago, the highlands were affected by the climatic fluctuations typical of the Pliocene and Pleistocene, when glaciers formed on the highest mountains. Most highland colonists have been African species that were sufficiently plastic to cope with the area's many unique traits. Tenuous links formed between northern Ethiopia and the Mediterranean region through the escarpments that flank the Red Sea, a route traveled by many animals and plants. Successful immigrants from other cold lands met habitats that closely matched their own. This was the case for two of the Ethiopian mammalian endemics with certain Palaearctic ancestors, the walia ibex *Capra walie* and the Starck's hare *Lepus starcki* (Yalden & Largen 1992). Formidable obstacles inhibited immigration of high altitude forms from most other directions (e.g. the grassy foodplains of the White Nile and the deserts of Northen Kenya).

Ethiopia's unique environment for its region, together with its isolation, was a potent stimulus for rapid speciation. The demands posed by an extreme climate and terrain influenced speciation, particularly for the smaller organisms such as rodents. Indeed, the present community of high altitude rodents include four endemic rodents that are confined to areas above 3,000m (*Tachyoryctes macrocephalus*, *Stenocephalemys albocaudata*, *Lophuromys melanonyx* and *Megadendromus nikolausi*); and six others that extend into areas higher than 3000m (*Dendromus lovati*, *Arvicanthis blicki*, *Stenocephalemys griseicauda, Praomys* *albipes, Praomys ruppi* and *Mus mahomet*); There are at least a further 16 species of non-endemic rodents, although only four of these (*Tachyoryctes splendens*, *Otomys typus*, *Lophuromys flavopunctatus* and *Arvicanthis abyssinicus*) are found above 3000 m (Yalden *et al.* 1976; Hillman 1986; Yalden 1988; Yalden & Largen 1992; Sillero-Zubiri *et al.* 1995a,b,c).

The Afroalpine areas experiences regular night frosts, diurnal temperature fluctuations that far exceed seasonal ones, and intense irradiation. Rodents can avoid extreme cold by going underground, in a way that larger mammals such as ungulates cannot, and so rodents are inherently well suited as the dominant herbivores of the Afroalpine ecosystem. Some rodents such as the grass rat *A. blicki* and the giant molerat *T. macrocephalus* can reach colossal densities in Afroalpine steppes. Birds of prey rely heavily on rodents, but their main predator is another species unique to Ethiopia, the Ethiopian wolf *Canis simensis*.

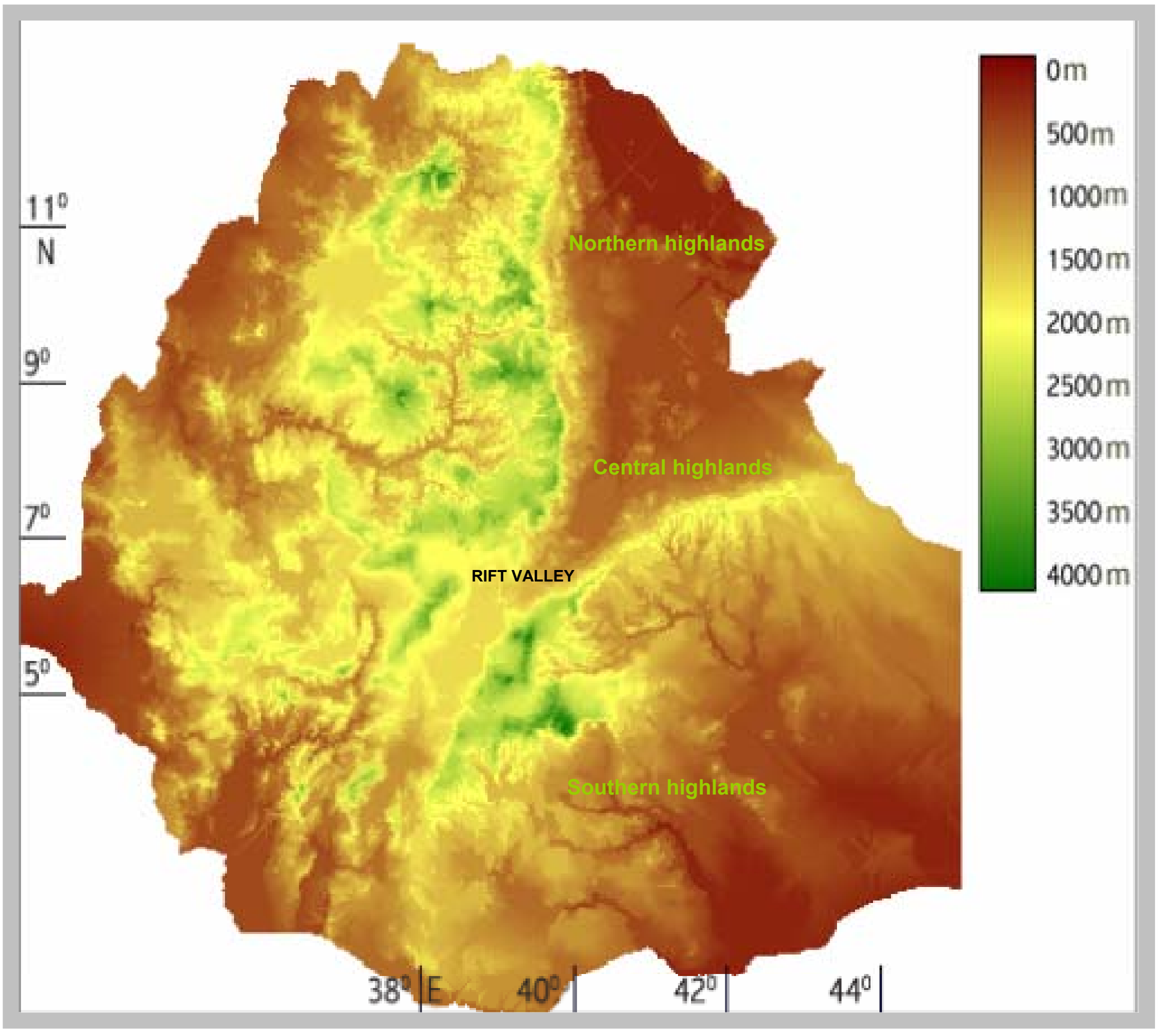

Figure 2.1. Altitudinal map of Ethiopia, showing in dark green the potential distribution of Afroalpine habitats under current climatic conditions (Derived from a Digital Elevation Model based on cartographic information, provided by the U.S. Geological Survey)

Unlike other medium- to large-sized canids, which typically are generalist predators and widely distributed (Ewer 1973; Macdonald 1992), Ethiopian wolves combine conspicuous sociability with specialised, solitary foraging for a narrow range of rodents (Sillero-Zubiri & Gottelli 1995a). They have probably persisted in these fragmented habitats because of the sheer size of the mountain massif; the most recent glaciers retreated within the last 10,000 years and as the climate warmed the Afroalpine ecosystem became restricted to the highest mountains (Fig. 2.1).

Today there are no more than 500 individuals distributed in small populations (Chapter 3), of which Bale Mountains in the Southern Highlands is the largest with around half of the world population (Fig. 2.1). That such specialized and distant vagrants should have found niches in Ethiopia is some measure of how very different these uplands were from the rest of Africa.

2.1.2 Bale Mountains and study areas

The central Sanetti Plateau in southwestern Ethiopia is one of the most distinctive of all Ethiopian habitats and represents the type of characteristic Afroalpine vegetation that would have spread over a wide area of highland during the peak of the glacials. The Sanetti Plateau is contained within the Bale Mountains National Park (BMNP) (7°S, 39°E) that protects about 2,000km^2 of one of the most intact remnants of Ethiopia's indigenous vegetation. BMNP is also home to the largest populations of two Ethiopian endemics, the mountain nyala (*Tragelaphus buxtoni*) and Ethiopian wolf, as well as the latter's varied rodent prey, of which many species are locally evolved. Wolf surveys and opportunistic observations began in BMNP in 1974 (Morris & Malcolm 1977; Hillman 1986) and detailed field studies in 1988 (Sillero-Zubiri 1994), continuing up to the present by the Ethiopian Wolf Conservation Programme (EWCP), officially established in 1995 (Sillero-Zubiri *et al.* 2000; Williams & Sillero-Zubiri in press; (http://www.wildcru.org/endangeredspecies/ethiopian wolf/intro.htm).

The Bale Mountains are high and extensive and thus sustain a wide representation of habitats across the three altitudinal belts determined by altitude and rainfall (Fig.2.2).

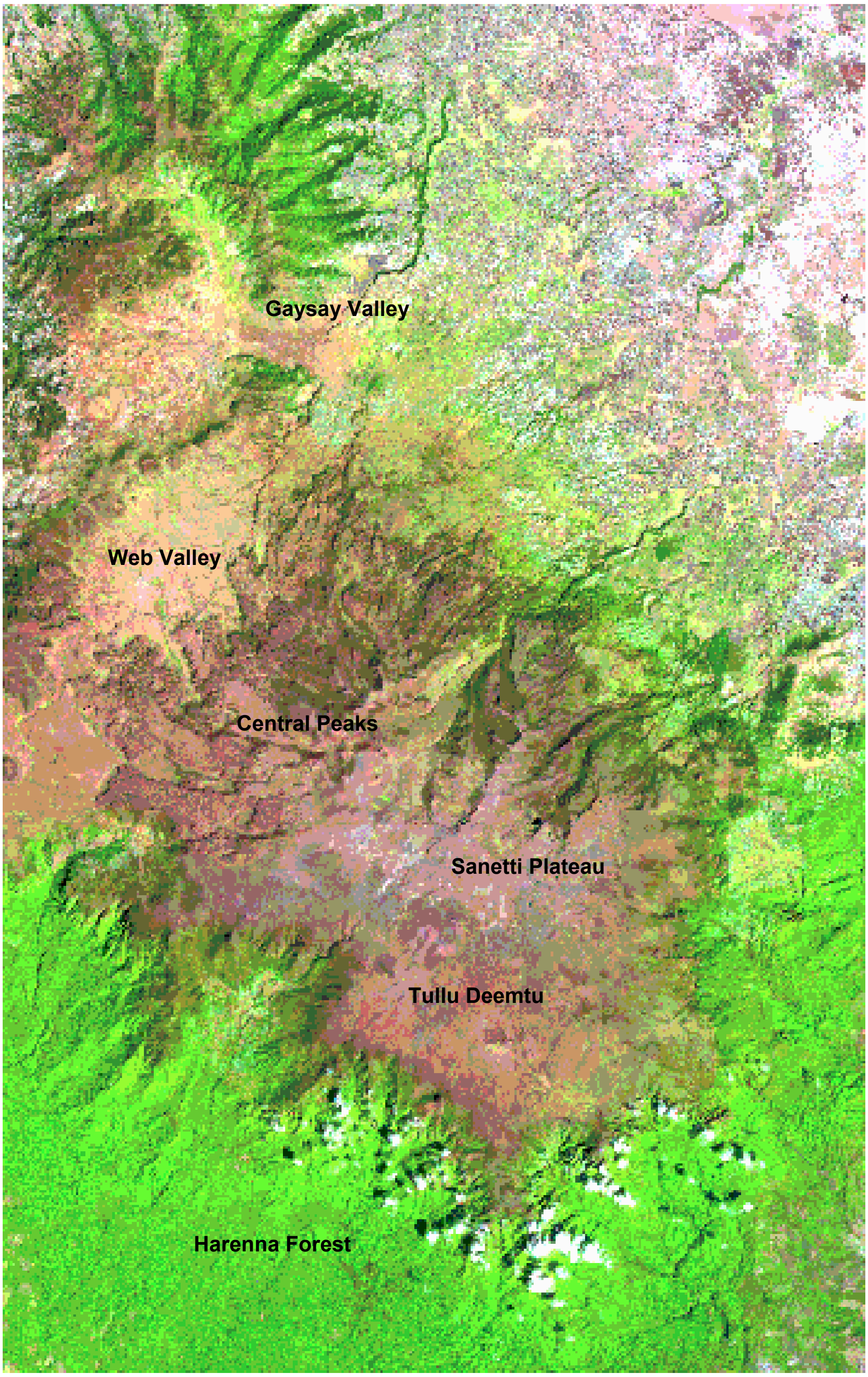

Figure 2.2 Satellite image of the Bale Mountains the study areas and major vegetation types, by combining bands 4, 5 and 6 of a Landsat Thematic Mapper Plus (U.S. Geological Survey).

The **Sanetti Plateau** (between 3,800 and 4,000m) and the broad valley bottom of the upper **Web Valley** (at 3,450–3,550 m) (Fig. 2.2) are the typical Afroalpine steppe or meadowland (PLATE 2.1), dominated by short alpine grasses and herbs, with *Artemesia* sage brush, bushes of *Helichrysum* everlasting flowers, and giant lobelias (*Lobelia rhyncopetalum*) scattered across the open uplands. On the drier southern declivity of the

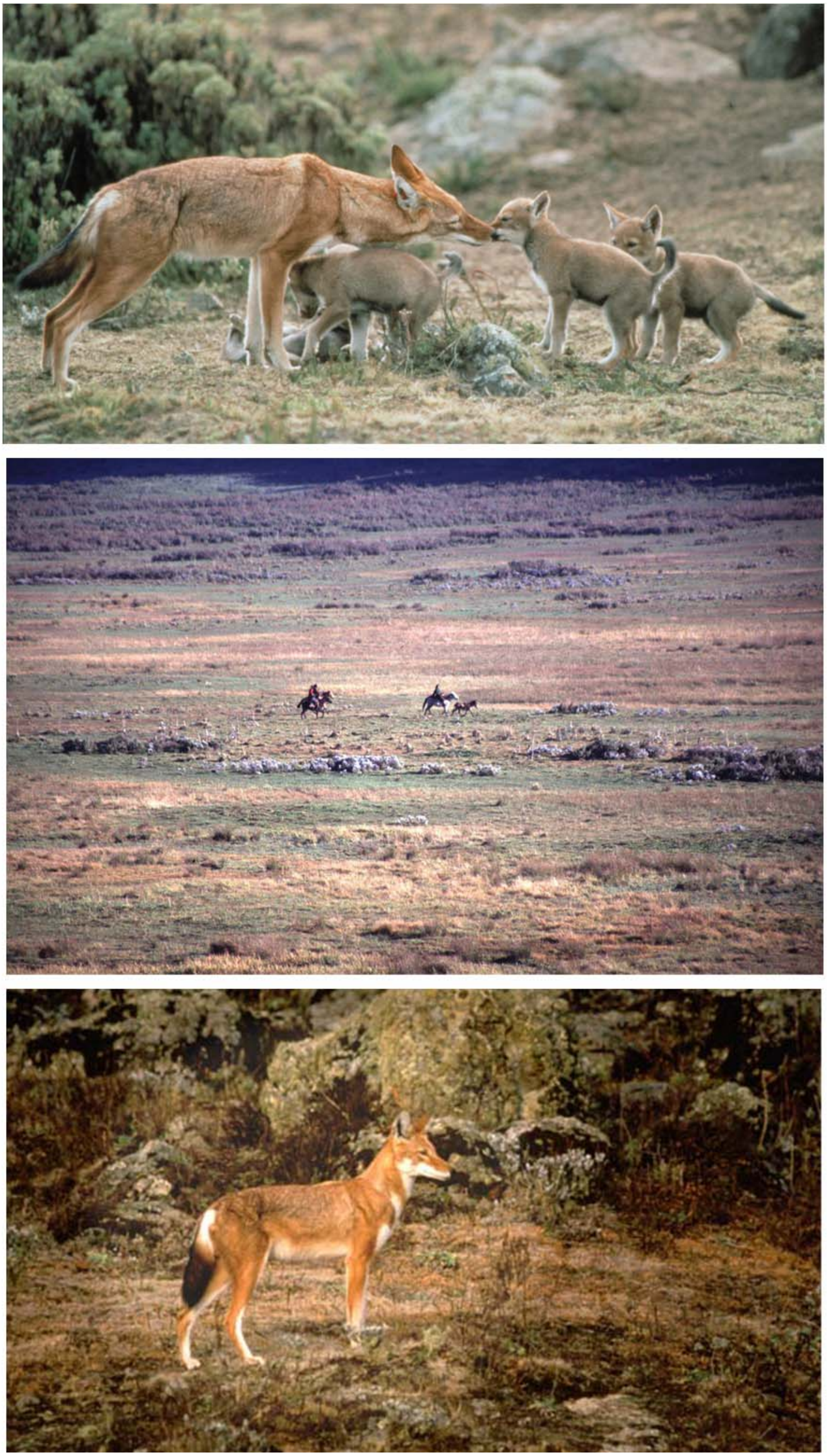

PLATE 2.1 From top to bottom: Subordinate female feeding pups - Afroalpine meadows, Web Valley- Adult male Ethiopian wolf

plateau, in the rain shadow of **Tullu Deemtu** (at 4,377m the highest mountain in southern Ethiopia), a vast and more uniform formation of *Helichrysum* heathland dominates.

In the areas just below the Afroalpine zone, and in the lava flows of the **Central Peaks** area (Fig.2.2), grow the less fertile ericaceous moorlands, dominated by *Erica trimera* shrubs (< 2m tall), kept from climax by periodic fire (Miehe & Miehe 1994a). At lower altitudes, montane grasslands are represented by the northern **Gaysay Valley** (3,000-3,100m). Lower still, along the southern slopes of the Bale massif, the **Harenna Forest** is a unique remnant of the woodlands and forests that once covered nearly half of Ethiopia.

Ethiopian wolves have been studied in detail in the three main areas within the Afrolapine belt: the Web Valley, the Sanetti Plateau, and Tullu Deemtu (Sillero-Zubiri 1994). The first two represent the typically open and short Afroalpine vegetation and sustain the highest density of wolves (*ca.* 1.2 wolf/km^2). The Sanetti Plateau is a rather uniform landscape dominated by Afroalpine grasslands and *Helichrysum* bushes and only disrupted by low rocky ridges, tall giant lobelias, marshy pans and numerous small lakes ("tarns") of glacial origin. The upper Web Valley is a broad valley bottom with pools and extensive marshes and swamps, marked by characteristics moraines and flat *mesas* that delimit small valleys with short Afroalpine vegetation. The Tullu Deemtu area represents the other common habitat type, the *Helichrysum* heaths, along the southern-western slopes of Sanetti, where wolves live at much lower densities (*ca.* 0.25 wolf/km^2).

The Afroalpine climate in Bale is influenced by desiccating north-eastern winds and orographic rains with a marked seasonality. Dampening mists and rains sweep the area daily during eight months of the rainy and intermediate seasons, followed by a four month dry season (Hillman 1986; Miehe & Miehe 1993). Annual rainfall varies from 800 to 1,150mm, increasing with altitude up until 3,850m, after which it begins to decrease again (Gamachu 1977; Hillman 1986). The mean daily maximum temperature at 3,500m is 19°C, ranging from 12.5°C to -25°C. Thus two main seasons can be recognized: a warm wet season, April to September, with 70.4% of annual rainfall; and a dry season, October to March, with extremely cold nights and warm days (Sillero-Zubiri 1994).

2.1.3 Afroalpine plant communities

The distribution of Afroalpine plants and vegetation formations in the Bale Mountains have been studied in detailed by Miehe & Miehe (1993) in whose work this revision is based. Further details of the vegetation are given in Mohr (1971), Messerli *et al.* (1977), Hillman (1986), Kingdon (1990), Sillero-Zubiri (1994), Gashaw & Fetene (1996).

Helychrisum dwarf-scrubs are the dominant plant formation in Tullu Deemtu. *H. splendidum* dominates, forming rather dense 30 to 50cm tall stands in which herbs are subordinate in magnitude. Towards the summits (4,000-4,200m), the proportion of open substratum strongly increases, largely due to the high frequency of frost-induced substrate movement. Flowering plants cover only 10-30% of the ground. Among the woody perennials, *H. splendidum* is gradually replace by the hemispheric cushions of *H. citrispinum* and flat, compact cushions of *H. gofense.*

On the Sanetti Plateau, at lower altitudes and with more humid conditions prevailing, the herbaceous constituents of the higher Afroalpine communities become more prominent than the woody plants. This herbaceous component comprises the majority of species in the Afroalpine vegetation. Short tussock grasses are mostly dominant, whereas rosette plants and cushions are conspicuous in some communities; the herbaceous stratum is not closed, and mosses may cover a large proportion of the ground.

These plants show adaptations to extreme temperatures and the soil movements induced by frost and the burrowing activity of rodents, which keep the vegetation at pioneer stages. Morphological adaptations include anchoring by means of a taproot (e.g. many rosette plants), an extensive root system (e.g. tussock grasses) or a creeping habit. The commonest rosette plants are *Agrocharis melanantha*, *Dianthoseris schimperi*, *Erigeron alpinum*, *Haplocarpha rueppellii*, *Haplosciadium abyssinicum*, *Ranunculus oreophytus*, and *Swertia spp.),* others sometimes form colonies of cushion shape (e.g. *Myosotis keniensis*, *Sagina abyssinica*, *S. afroalpina*, and *Wahlenbergia pusilla)* or have creeping habits (e.g. *Alchemilla microbetula; Cerastium octandrum; Galium hochstetteri; Geranium arabicum; Polygonum* spp.; *Satureja kilimandschari; Veronica* spp.). The group of tufted hemichryptophytes includes diverse tussock grasses (e.g. *Agrostis quinqueneseta*; *Festuca richardii*, *Helichrysum cymosum* herbaceous form; *Koeleria capensis*; *Pentaschistis pictigluma* s.l.; *Poa leptoclada*; *P. schimperiania*; *Senecio schultzii*).

In the Web Valley, situated in the lower Afroalpine belt, similar pioneer vegetation covers extensive areas. It is believed that significant livestock grazing here has compacted the soil and prevented encroachment of *Helichrysum-Artemesia* brush, considered the climax vegetation. The soil-working action of the giant molerat is particularly evident in Web. Molerats live in underground tunnels but emerge to feed on the aerial parts of plants (Yalden 1975, 1985), harvesting those herbs growing within a radius of one body length from a burrow, thus several such holes must be opened every day to satisfy the nutritional demands of one individual. Consequently, large amounts of soil are turned over within a short time. Afroalpine pioneer herbs and grasses successively colonize the soil excavated from the burrow system and deposited around the holes. In areas with high molerat densities, the vegetation is constantly kept in those stages. Molerat mounds, known as "mima" mounds (*sensu* Dalquest & Scheffer 1942), are invaded by fast growing creeping hemichryptophytes, mainly *Alchemilla abyssinica* (Rosaceae); *Polygonum plebejum* (Polygonaceae) and *Trifolium acaule* (Fabaceae) in humid habitats; and many of the rosette plants listed above. Characteristic forms are the bunchy hemichryptophytes *Anthemis tigreensis* (Asteraceae); *Poa muhaurensis* (Poaceae) and *Artemesia schimperi*. *Bryum argenteum* is the only moss pioneer. *Helichrysum citrispinum* is the most successful pioneer shrub on these mima mounds.

2.1.4 Rodent-habitat associations

The temperature extremes experienced in the high altitude areas of the Bale Mountains are a major structural force on the mammalian community. In cold conditions at high altitude, small homeotherms benefit from being larger, and indeed the community of Afroalpine rodents is characterised by a high proportion of large species (Sillero-Zubiri *et al.* 1995c). Behavioural characteristics may also protect rodents from the cold. For instance, many Afroalpine rodents show diurnal behaviour: only three were nocturnal out of the eight species recorded (Sillero-Zubiri *et al.* 1995b). Empirical studies demonstrated some separation on the basis of habitat (Table 2.1.), and presumably further trophic separation occurs, although the diets of most species are poorly known. As well as environmental constraints, interspecific competition and predation may also be important in determining the structure of the rodent community.

Within Afroalpine areas, fine-scale associations were identified between rodents and vegetation types, largely determined by drainage and soil characteristics in relation to local topography. Table 2.1 shows these habitat divisions. Stratified counts and rodent trapping demonstrated some clear habitat association between species and microhabitat conditions (Sillero-Zubiri *et al.* 1995b). This habitat classification, albeit subjective, helped to identify predictors of rodent abundance and distribution, and to interpret species' adaptations to survive the harsh Afroalpine environment (discussed below).

Giant molerats

The giant molerat is currently confined to the Bale Mountains (Yalden & Largen 1992; Sillero-Zubiri, pers. comm.), where it shows clearcut habitat selection between vegetation types, and between sub-habitats (Table 2.1). It has been proposed that giant molerats are constrained by thermoregulatory requirements: they need to be able to dig to a depth where soil temperature remains constant, particularly during the dry season when daily temperature variation is extreme (Yalden 1975, 1985; Sillero-Zubiri *et al.* 1995b). Fresh giant molerat signs were indeed most abundant in habitats with soils deeper than 50cm, and at this depth soil temperature remained constant throughout a 24-hour period (Sillero-Zubiri *et al.* 1995b). Molerats may be able to regulate their burrow temperature by plugging foraging holes after use, and regulate their body temperature by early morning and late evening basking in the dry season (Yalden 1975). Micro-habitat suitability for giant molerats was also associated with soil moisture content: highest densities were found along waterlogged swamp shores and seasonally flooded valley bottoms (Table 2.1).

In the Web Valley giant molerats are most abundant in *swamp shore* areas. The *valley floors* of Web Valley and the *herbaceous communities* of Sanetti Plateau also sustain high molerat abundance. These two habitats have more than twice as many fresh molerat signs (i.e. holes and earth mounds) as any other of the remaining habitat except swamp shore. The absolute giant molerat biomass has been estimated at 18.0 kg/ha in *herbaceous communities* and 16.8 kg/ha in *valley floors*, with densities between 17 and 24 individuals per hectare, up to a local maximum of 52 per hectare.

In all other Afroalpine grassy habitats molerat abundance is low. There were more fresh signs of giant molerats on *ridges* and *mesas* in Web and Sanetti than on Tullu Deemtu and the ericaceous belt, even though soil depth was approximately the same in these habitats, indicating that other factors are also important in determining giant molerat abundance. Giant molerats feed mainly on grasses with some dicotyledons,

Habitat category		Vegetation and microhabitat conditions	
***Alchemilla* pasture (WB)**	**Bogs**	Shallow seasonally waterlogged valley bottoms with underlying rock. Partially occupied by giant molerats during	Mostly short herbaceous community, covering the valleys between marshes and ridges. Dominated by *Alchemilla* (mainly *A. abyssinica*) and dotted with *Helichrysum* shrubs and *Artemesia afra*. Plant composition and soil depth vary along the valley floor gradient.
	Swamp shores	Mima mounds dominated by *Alchemilla*-molerat successions. Plant cover <50%. Preferred molerat habitat. Partially flooded during the rainy season.	
	Valley floors	Dominated by *Alchemilla*. Plant cover >50%. Fewer mima mounds. Preferred by colonies of Murinae rats	
	Low ridges	Rocky, superficial soils. Grassy pasture with *Helichrysum* shrubs. Lower rodent density. Similar to *Helichrysum* heath.	
***Mesa* tops (WB)**		Flat, with thin soil (<10cm) and a low thick mat of grass; few mima mounds. Relatively low rodent density.	
Banks and slopes (WB)		*Mesas*, cliffs and steep slopes covered with *Helichrysum/Artemesia afra* and *Lobelia rhynchopetalum*. The valley walls are covered by Ericaceous moorlands. Relatively low rodent density.	
Herbaceous communities (SN)		Afroalpine herbaceous communities dominated by *Alchemilla*-molerat successions. Spongy soils, short herbs and grasses. High density of rodents.	
Rocky grasslands (SN)		Short grasslands in rocky slopes, hilltops and low ridges, or seasonally waterlogged depressions with underlying rock that support little vegetation. Often with sparse *Helichrysum* shrubs. Relatively high rodent density.	
Swamps (SN-WB)		Valley floors that are permanently wet or become flooded during the rainy season. The swampy areas are dominated by the sedge *Carex monostachya*. Lowest rodent density.	
Helichrysum heaths (TD)		*Helichrysum* dwarf-scrub is the main plant formation, dominated by *H. splendidum* and *H. citrispinum* shrubs, 30 to 50cm tall. Herbs and tussock grasses (Agrostis quinqueseta and Festuca richardii) occurr in the herbaceous layer and open areas. Rodent biomass less than one third of that in Web and Sanetti, concentrated in *Alchemilla* spp. stands along drainage lines.	

Table 2.1. Description of Afroalpine habitat subdivisions as defined by vegetation and microclimatic conditions, and for which rodent abundance and preferences have been determined (extracted from Sillero-Zubiri *et al*. 1995a,b). WB= Web Valley; SN=Sanetti Plateau; TD=Tullu Deemtu

but apparently do not favour *Helichrysum* (Yalden 1975). Lack of suitable food may therefore limit their abundance on Tullu Deemtu, and possibly also in the ericaceous belt, where major plant types are the rather woody *Philippia* and *Erica* species.

The burrowing habits of giant molerats have a modifying effect on the landscape and the composition of vegetation communities (Yalden 1975; Bayene 1986; Miehe & Miehe 1994a). Mima mounds are probably the result of soil slowly accumulating from burrowing. A correlation between the presence of mima mounds and the abundance of molerat signs supports the hypothesis that fossorial rodents produce mima type micro-relief (Dalquest & Scheffer 1942). Soil depth at mima mounds is considerably deeper than around them (Sillero-Zubiri *et al.* 1995b). The existence of these patches of deep soil could be vital to the survival of giant molerats during extremely cold periods, and nearly every tunnel system contains at least one such mound, inter-mound frequency could conceivably determine population densities. In *Helichrysum* dwarf-scrubs, a shallow-soil habitat devoid of large mima mounds, all molerat signs were associated with mounds. During the wet season, their activity is restricted to mound tops when inter-mound valleys are flooded. Molerats migrate slowly down to swampy areas and bogs at the onset of the dry season, using new tunnels or reconstructing old ones, presumably to feed on greener, undepleted vegetation.

Murinae rats

Lophuromys melanonyx, *Stenocephalemys albocaudata* and *Arvicanthis blicki* are characteristic of the Afroalpine belt (Sillero-Zubiri *et al.* 1995a). Yalden (1988) suggested that *Otomys typus* might be an Afroalpine moorland specialist, but although the species was well represented in wolf diet on Sanetti and Tullu Deemtu it was never trapped in these zones (Sillero-Zubiri *et al.* 1995a). *L. flavopunctatus* and *S. griseicauda* were characteristic of the montane grasslands of the Gaysay Valley and, along with *O. typus*, decreased in abundance in trap returns as altitude increased through the ericaceous and Afroalpine belts (Sillero-Zubiri *et al.* 1995b). None of these three species were found on the Sanetti Plateau, although *S. griseicauda* was occasionally found at Tullu Deemtu, suggesting that it was limited by factors other than altitude.

Trap success in the Web Valley was lowest in sedge swamp areas, where only *A. blicki* and *S. albocaudata* were occasionally trapped. In the Web Valley *A. blicki* and *L. melanonyx* were commonest on valley floors and low ridges. *S. albocaudata*, in contrast, was most abundant on mesa tops, although also favoured mesa slopes, ridges and valley floor. *L. flavopunctatus*, *S. griseicauda* and *O. typus* were all most commonly trapped on mesa slopes, and were rarely - or never, in the case of *O. typus* - found in other Web Valley sub-habitats (Table 2.2).

Habitat	**Trap effort day / night**	**% Total area**	**Trap success (%):**					
			AB	**LM**	**LF**	**SA**	**SG**	**OT**
Alchemilla pasture:								
Valley floor	2011 / 1951	45	16.7	22.4	0.2	14.9	0.05	0
Low ridges	360 / 360	15	15.6	17.5	0	13.3	0	0
Swamp shore	420 / 420	6	4.8	12.4	1.4	6.2	0.24	0
Mesas:								
Slope	620 / 620	2	5.7	13.4	8.4	15.0	8.1	1
Top	519 / 519	20	1.4	1.5	0.8	18.1	0.8	0
Sedge swamp:	340 / 340	12	0.9	0	0	2.4	0	0

Table 2.2 Percentage trap success for rodents within Web Valley sub-habitats. From Sillero-Zubiri *et al.* (1995b). Percent total area refers to the percentage of the total area covered by a sub-habitat within Web Valley. Percentage trap success for SA and SG was calculated using night-time trapping effort; percentage trap success for the remaining species was calculated using day-time trapping effort. AB = *Arvicanthis blicki*; LM = *Lophuromys melanonyx*; LF = *L. flavopunctatus*; SA = *Stenocephalemys albocaudata*; SG = *S. griseicauda*; OT = *Otomys typus*.

Habitat	**Trap effort day / night**	**% Total area**	**Trap success (%):**		
			AB	**LM**	**SA**
Herbaceous community:					
Valley floor	790 / 740	65.0	12.4	21.6	17.9
Swamp shore	260 / 260	2.5	3.1	7.7	8.1
Rocky grassland:					
>20% vegetated	731 / 731	15.0	9.3	12.1	18.9
<20% vegetated	440 / 440	12.5	2.7	1.6	8.2
Sedge swamp:	80 / 80	4.0	0	0	1.3

Table 2.3 Percentage trap success for rodents within Sanetti Plateau sub-habitats. From Sillero-Zubiri *et al.* (1995b). Percent total area refers to the percentage of the total area covered by a sub-habitat within Web Valley. Percentage trap success for SA and SG was calculated using night-time trapping effort; percentage trap success for the remaining species was calculated using day-time trapping effort. AB = *Arvicanthis blicki*; LM = *Lophuromys melanonyx*; LF = *L. flavopunctatus*; SA = *Stenocephalemys albocaudata*; SG = *S. griseicauda*; OT = *Otomys typus*.

Only *A. blicki*, *L. melanonyx* and *S. albocaudata* were trapped on Sanetti. Overall trap success was greatest in herbaceous communities on valley floors, which were the preferred habitat for *A. blicki* and *L. melanonyx*. *S. albocaudata* was the commonest species in rocky grassland (its most preferred habitat) and sedge swamp. As in Web Valley, trap success was lowest in sedge swamp, where only *S. albocaudata* was found (Table 2.3).

The preference for protective habitats by some Murinae rats might also play a part in thermoregulation. For example, *L. flavopunctatus*, a small, partly nocturnal species, and the nocturnal *S. griseicauda*, were found in the Web Valley mostly on mesa slopes. These areas are dominated by tall (up to 50cm) *Artemesia* and *Helichrysum* shrubs and rocky boulders, which may protect the rodents from the more extreme temperatures of the open valleys. *S. albocaudata* was the dominant species in Tullu Deemtu, mesas and rocky grassland; all with a mean soil depth of less than 40cm. It was also a dominant species in swamp habitats, although neither *S. albocaudata* nor *A. blicki*, the only species found in swamp, actually dug their burrows there. *S. albocaudata* might be particularly adapted to environments with shallow soils, or may avoid the danger of flooding its burrow, while it improves thermoregulation via its large size (and presumably metabolic rate).

2.2 The Ethiopian wolf

2.2.1 A specialized relative of grey wolves

At ca. 20kg, the Ethiopian wolf differs from such typical, medium-sized canids as the coyote (*C. latrans*) in its unusually long legs and a long muzzle (Sillero-Zubiri & Gottelli 1994; Sillero-Zubiri & Marino in press). Endemic to the Afroalpine ecosystem of the Ethiopian highlands, its diurnal habits and distinctive coat render this species conspicuous. A bright tawny rufous fur, with a characteristic pattern of white marks, a thick black and white bushy tail and broad, pointed ears result in a rather 'foxy' appearance (PLATE 2.1). This, and its reliance upon small prey, misled early European naturalists to name this species the Simien fox. Uncertainty over its taxonomy led to an array of alternative vernacular names, including the Simien jackal, Abyssinian wolf and *ky kebero* (which translates from Amharic to red jackal). Phylogenetic analyses based on mitochondrial DNA however, have shown that Ethiopian wolves are indeed more closely related to grey wolves (*C. lupus*) and coyotes than to any African canid (Gottelli *et al.* 1994). This is supported by their many similarities with wolves in biology and behaviour, and by the relative ease at which they hybridise with domestic dogs (Gottelli *et al.* 1994, Wayne & Gottelli 1997).

The species may have originated from a grey wolf/coyote-like ancestor that invaded Ethiopia during the Pleistocene. During this period, Europe and Africa were connected by land bridges and alpine habitats formed a continuum that extended through Eastern Europe, the Middle East and Northeast Africa (Kingdon 1990). During the last glacial period (70,000-10,000 years before present (BP) the African tropics were generally cooler and drier than at present (Bonnefille *et al.* 1990) and the hypothetical ancestor may have been pre-adapted to the cold-temperate Ethiopian highlands. There, the incoming canid specialised on the small mammals, particularly molerats (Rhyzomyinae) and grass rats (Murinae) that filled the niche of the large grazing ungulates characteristic of the African plains.

The end of the Pleistocene brought a change in the climate, and the extensive Ethiopian Afroalpine steppes shrunk to their present state, reducing the habitat available to Ethiopian wolves by an order of magnitude (Gottelli & Sillero-Zubiri 1992). Analyses of microsatellite and mitochondrial DNA have suggested that small population sizes may have characterised the evolution of Ethiopian wolves. Indeed, the Ethiopian wolf appears to have the most limited genetic variability at the population level of any extant canid (Wayne & Gottelli 1997; Chapter 5). Ironically, the specialisation on Afroalpine rodents that was once the basis of the species' success is now the force that constrains Ethiopian wolves to a fragmented habitat (Kingdon 1990; Yalden & Largen 1992), and heightens the risk of local extinctions in the face of stochasticity and anthropogenic factors (Sillero-Zubiri & Macdonald 1997).

2.2.2 Top predator of the Afroalpine rodent community

The diet of Ethiopian wolves was studied by scat analysis (689 droppings) and 946 hours of watching focal animals that yielded 811 attempts to kill prey, of which 361 corresponded to successful kills/feeds (Sillero-Zubiri and Gottelli 1995a). Rodents accounted for 96% of all prey occurrences in droppings and 97% by volume of undigested faecal material. Wolf prey included six rodent species, Starck's hare (*Lepus starcki*), cattle, birds, insects and undigested sedge leaves, *Carex monostachya.* Giant molerat *(Tachyoryctes macrocephalus* – mean weight 618g) was the main component in the overall diet (36% of total prey occurrences) and was present in 69% of all faecal samples, whereas diurnal rats *Arvicanthis blicki*, *Lophuromys melanonyx* and *Otomys typus* (respective mean weight 126g, 94g and 100g) together accounted for 59% of occurrences and appeared in 78% of the samples. These four species together accounted for 86% of prey occurrences and no significant differences were found for these main four prey items between months or between dry and wet seasons.

Direct observations indicated a higher incidence of large prey (hare, rock hyrax *Procavia capensis capillosa*, birds, lambs, and antelopes) than suggested by scat analysis. Of all feeding instances observed, 69% were grass rats while giant molerat kills accounted for 22% of all successful attempts. Giant molerats formed the bulk of the prey by weight (40%), while diurnal rats were second (23%), although taken more often. Carrion, hares, hyraxes, and birds contributed the remaining 36.5% of the total prey weight, of which 12% was scavenged from livestock carcasses.

The diet was broadly similar at the three sites, with giant molerat as the single most important food item. In areas where this species is absent or rare it is often replaced by the common molerat (*Tachyoryctes splendens*). For instance in Bale's northern montane grasslands, common molerats constituted 32% of all animals eaten (Malcolm 1997), and in Menz, central Ethiopia, 31% of occurrences - 17% by volume - in the wolf diet (Ashenafi 2001).

During 946 hours of focal observation away from dens, wolves spent 43% of their time foraging. They foraged solitarily throughout the day, travelling widely at a walk or trot, covering large areas of their home range. Peaks of foraging activity were synchronised with the activity of diurnal rodents above the ground. The wolves used various hunting strategies: molerats were commonly stalked, while zigzag and hole-checks were aimed at grass rats. Although foraging wolves were mostly observed alone, their daily hunting ranges overlapped considerably. Of 35 occasions in which more than one wolf was present during kills involving rats, only 23% were within 10m. In the remaining observations, wolves shared the same foraging area, but did not appear to interfere with each others' foraging attempts or prey captures. Occasionally small packs hunted hares, antelope calves, and sheep. In 12 of 20 attempts to catch hares, 2 to 4 wolves hunted simultaneously. In the northern grasslands wolves have been observed in packs of 3 to 4 animals hunting reedbuck *Redunca redunca* (*n*=3) and a mountain nyala calf *Tragelaphus buxtoni* (Sillero-Zubiri pers. obs.).

2.2.3 Rodents as predictors of Ethiopian wolf distribution

The role of the Afroalpine rodent community in limiting the distribution of Ethiopian wolves was studied in Bale by looking at the relationship between wolf abundance and the species composition, relative abundance and activity pattern of the rodent community in various habitats (Sillero-Zubiri *et al.* 1995a,b). Combined biomass of all diurnal rodents and hares in the Afroalpine grassland habitats was estimated at 24kg/ha in Sanetti and 26kg/ha in Web: giant molerats contributing about half of this biomass (assuming an average molerat weight of 618g; *n*=11), with a biomass of around 10-25kg/ha, and patches of up to 55kg/ha; hares averaged 2,250g (*n*=4), giving a projected biomass of 0.4-0.7kg/ha. Although hares were more conspicuous on the ground than were rodents they accounted for only a small fraction of the total potential prey biomass.

Indices of giant molerat biomass for *Helichrysum* dwarf-scrub and ericaceous belt were only 1/5 and 1/150 respectively of those in Afroalpine grasslands. Positive correlations between wolf density and molerat abundance in four areas (Tullu Deemtu, Sanetti, Web and the ericaceous belt) suggested that molerats were a vital determinant of wolf presence (Sillero-Zubiri *et al.* 1995b). Because they are roughly six times the weight of any other rodent, hunting *T. macrocephalus* is likely to be considerably more efficient than hunting a smaller species. Nonetheless, the positive correlation between wolf abundance and an index of biomass of smaller rodents showed that the giant molerat was not the only determinant of wolf distribution.

The biomass index for grass rats (in kilograms per 100 transect snap-trap nights) was highest on Sanetti Plateau, followed, in order, by Web Valley, montane grasslands, the ericaceous belt and Tullu Deemtu (Table 2.4). *A. blicki* and *L. melanonyx* were the most numerous species in Afroalpine grasslands. Ethiopian wolf density, measured both from observation and road counts, correlated positively with the total biomass index and the biomass index for diurnal species, but not for nocturnal species. Also a positive correlation was detected between rodent burrows and wolf sign (droppings or diggings) along habitat assessment transects. A similar correlation was found between wolf signs and the average index of fresh giant molerat signs (Sillero-Zubiri *et al.* 1995a,b).

	Web Valley	Sanetti Plateau	Montane Grassland	Tullu Deemtu	Ericaceous Belt
Biomass index:					
diurnal rats	2.7	2.9	1.6	0.4	0.4
nocturnal rats	1.8	2.1	1.2	1.4	1.7
TOTAL	4.4	5.0	2.8	1.8	2.1
Ethiopian wolf density:					
road counts	1.0	1.2	0.1	0.2	0.1
observation	1.2	1.2	0.3	0.2	0.1
Pack home ranges:	6.5 ± 2.1	5.5 ± 1.3	7.4	13.4 ± 2.0	-
Group sizes:	6.7 ± 0.7	4.9 ± 0.3	4.5 ± 0.3	2.6 ± 0.4	-

Table 2.4 Ethiopian wolf density (individuals/km²) and biomass index, weighted for sub-habitat area, for diurnal and nocturnal snap-trapped rodent prey (from Sillero-Zubiri 1994). The biomass index represents the biomass (kg) contributed per 100 trap nights using data from all months. Mean weights used as follows: *Arvicanthis blicki*: 126g; *Lophuromys melanonyx*: 94g; *L. flavopunctatus*: 49g; *Stenocephalemys griseicauda*: 101.5g; *S. albocaudata*: 129.5g; *Otomys typus*: 100g. Home ranges (km2 ± SD) were estimated as average 100% minimum convex polygons of wolf packs in Bale between 1988-1991. Group size is the average number of adult and subadults (mean ± SE) in a pack.

Large mammal densities in the Afroalpine grasslands are low and, anyway, they might be largely unavailable to the wolves. Rodents were the most abundant, conveniently-sized prey, and easiest to catch. Their availability was more predictable, insofar as their abundance was closely associated to different habitat types. The predictability of the rodent prey may be one selective pressure favouring pack territoriality in Ethiopian wolves (Sillero-Zubiri 1994).

2.2.4 Wolf packs carve out the precious suitable habitat available

While the Afroalpine rodent fauna constitutes a very rich and predictable source of food, the availability of Afroalpine habitats is limited by its geographical distribution. In Bale, all areas supporting a substantial rodent biomass were occupied by resident wolf packs.

Wolves were organised into discrete groups, and their composition was spatially and temporally stable. Groups were composed of 2 to 13 adults and subadults (> 1 year old). Average group size for all 14 known packs in Web and Sanetti between 1988-92 was 5.9 ± 0.5 (*mean* ± SE), with Web packs significantly larger than Sanetti's (Table

2.4). Tullu Deemtu packs were notably smaller and averaged 2.6 ± 0.4 (Sillero-Zubiri and Gottelli 1995b). Home ranges of resident wolves overlapped almost completely with other pack members and entirely contained the home ranges of pups and juveniles (81 to 87 percentage intragroup annual home range overlap between adult-adult and adult-subadult dyads, *n*=4 packs).

Home ranges of individual residents ranged between 2.0 - 15.0km² (*n*=92) and most of this variability was attributed to habitat type (Table 2.4). For instance, combined home ranges (i.e. pack home ranges estimated as minimum convex polygons) in Afroalpine grasslands averaged 6.5km² ± 2.1 and 5.5km² ± 1.3 (Web and Sanetti respectively, *n*=7 packs), while in *Helichrysum* dwarf-scrub home ranges where twice as large, and explained by the different density of prey species (Table 2.4). On the other hand, the home ranges of three non-resident *floater* females (*sensu* Sillero-Zubiri *et al.* 1996a) in Web overlapped widely with other packs and ranged from 8.5-8.7km², their mean range being significantly larger than those of resident dominant females.

Small ranges, particularly those recorded in the grasslands and herbaceous communities of Web and Sanetti, are a reflection of the great density of the food resources available in some Afroalpine habitats. The ranges observed are among the smallest, and density among the highest reported for all eight *Canis* species (reviewed by Macdonald & Sillero-Zubiri in press). Established relationships between metabolic rate, body weight and size of home range in mammals (McNab 1963; Harestad & Bunnell 1979) would predict home ranges of 42km², nearly eight times the mean values observed in Web and Sanetti.

Home range size was correlated with group size in the Afroalpine grasslands of Bale, and territories were enlarged whenever a reduction in group size in a neighbouring pack allowed it, which is indicative of an expansionist strategy (Kruuk & Macdonald 1985; Macdonald *et al.* in press). Under intense competition for rodent-rich grasslands, pack group size may determine the outcome of territorial boundary clashes and the maintenance of a high quality range may be the greatest advantage of group-living (Sillero-Zubiri & Macdonald 1998).

2.2.5 Marking and territoriality

Studies of scent-marking behaviour and inter-pack aggression in Ethiopian wolf packs provided detailed evidence of territoriality (Sillero-Zubiri & Macdonald 1998). Movements and activity at the periphery of ranges was characterised by 'border patrols' during which groups of pack members of both sexes trot and walk along the territory boundary. In 167km of border patrols totalling 68 hours, 1,208 scent marks were deposited at an overall rate of 7.2/km. Raised-leg urinations were the most frequently deposited scent mark (4.7/km), followed by ground scratching (2.3/km). Defecations and squat urinations during border patrols were rare (0.23/km and 0.04/km respectively). Scent-marking rates were highest along or near territory boundaries (mean number of scent-marks deposited per kilometre significantly greater ($F_{(1,313)}$=6.40, P=0.012) during patrols than at other times) where wolves vigorously over-marked neighbours' scent-marks. Most direct encounters between neighbouring wolves at territory borders were aggressive and involved repeated chases (102 out of 119 encounters) and the larger group was most likely to win (the larger group won in 77% of cases, whereas victorious and defeated groups were the same size in 15% of encounters).

In Bale, Ethiopian wolf packs occur at saturation density, in a system of highly stable tessellated territories (Sillero-Zubiri and Gottelli 1995b). Frequent scent-marking, inter-pack encounters and aversion to strangers' marks probably constrain each pack to its territory, while positive feedback keeps each territory boundary adequately marked. A further function of scent-marking may be to indicate sexual and social status. Wolves in Bale are seasonal breeders and in any given year, mating was synchronised to a period of one to three weeks in the latter part of the rainy season (August-October), suggesting that a social mechanism triggered mating (Sillero-Zubiri *et al.* 1998). Scent-marking might allow females to monitor their reproductive condition reciprocally, and synchronise their oestrus. On the other hand, neighbouring packs' males may gather information on the receptivity of females. While border encounters occurred throughout the year, peak intrusion pressure coincided with the mating season. Fifty out of 169 observed encounters between wolves of neighbouring packs, consisted of territorial intrusions by small groups of neighbouring males, attracted by a receptive resident female. Highly seasonal mating may be connected to the occurrence of a philandering mating system in Ethiopian wolves (Sillero-Zubiri 1994; Sillero-Zubiri *et al.* 1996a).

2.2.6 Philopatry and the risk of inbreeding

Lack of suitable habitat places a tight constraint on dispersal in Ethiopian wolves. In Bale immigration was rare, births and deaths predominated over transfers between packs, and all pack members were potentially close kin. With kin of opposite sex residing in the same group, natal philopatry provided the potential for inbreeding, in a situation of severely limited dispersal opportunities (Sillero-Zubiri 1994).

Although dispersal was rare, that which occurred was sex biased. In Web and Sanetti, 63% of females dispersed at, or shortly before, sexual maturity at two years, some becoming '*floaters*' Sillero-Zubiri *et al.* 1996a). Males did not disperse and were recruited into multi-male philopatric packs. The population sex-ratio of adults was biased toward males at 1.9:1 ± 0.07 (SE), with the mean pack sex-ratio of adults at 2.6:1 ± 0.2.

Adaptive explanations of single-sex dispersal include avoidance of reproductive competition - for breeding status or resources - (Dobson 1982) or of inbreeding (Harvey & Ralls 1986; Wolff 1992). In Ethiopian wolves, observations of same-sex aggression prior to female dispersal support the competition-for-breeding-status hypothesis. In Bale, only the dominant female in each pack bred, indicating a high level of reproductive competition. Each breeding female was clearly dominant over her daughters. During the study period 1988-1992, in all packs with more than one subordinate female the lowest ranking female left the group at 18-28 months-old. Fourteen subordinate females emigrated or disappeared from focal packs, whereas only four entered a different pack and two returned to their natal group, suggesting that approximately 57% of dispersing females either died or failed to find residence in the study population. Of the 14 females known prior to dispersal, 10 settled as floaters next to their natal territory.

No new packs were formed during the 4-year study. An apparent attempt by a subordinate female to split a pack - suggesting that fission could be a mechanism for pack formation - ended when the subordinate's litter succumbed, probably killed by the dominant female. During this period, female ascendancy to breeding status, either by immigration or inheritance, only occurred after the death of a dominant and so the chances of a female ever securing a breeding position were low. Five out of 10 dominant females retained their breeding position throughout four years of observation, whereas the remainder maintained that role til they died. Breeding openings occurred at an average of 0.12 ± 0.09 opportunities for a subordinate female per year per pack. During contests for a breeding position, resident females appeared to have an advantage over floaters (three breeding females were replaced by their daughters after their deaths).

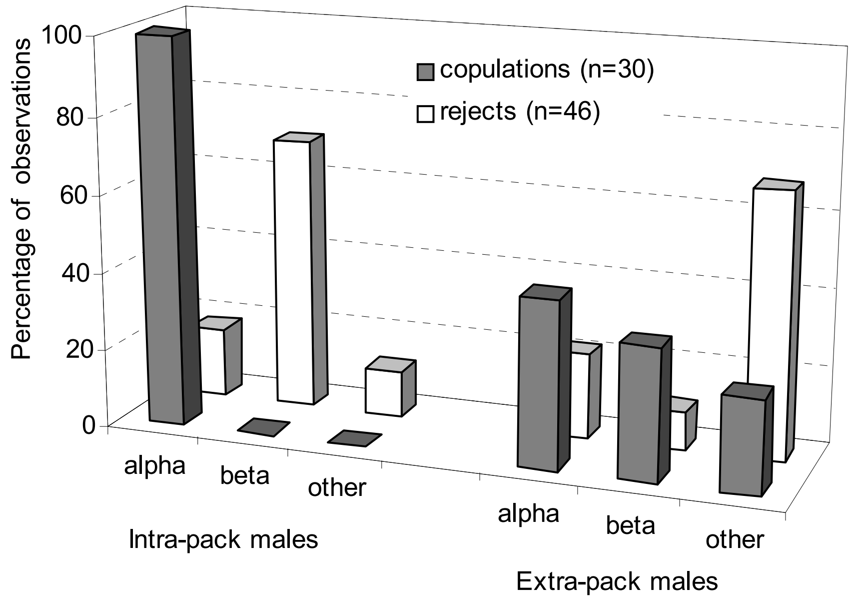

Figure 2.3 Frequency with which Ethiopian wolf females were observed in sexual encounters with males from their packs or neighbouring packs.

During the short mating season, the dominant female exercised choice in accepting when and with which male she mated. Of 30 observed instances of mating that involved copulation, only nine (30%) took place with males from the female's pack, whereas the other 21 (70%) involved males from other packs (Fig. 2.3). Within packs, females copulated only with the dominant male, and rejected all mating attempts by lower ranking males. In contrast, mate choice with regard to male status was not apparent when a female courted and mated with outside males. Microsatellite DNA analysis confirmed the occurrence of multiple-paternity in two litters (Gottelli *et al.* 1994). Multiple paternity and male excursions into neighbouring territories during the mating season suggest that this is an important tactic for male wolves. Cuckoldry and multiple-paternity may rival male philopatry and female-biased dispersal in importance as an out-breeding mechanism in a situation where habitat constraints impede dispersal. An alternative, but non-exclusive, explanation may be the prevention of infanticide from neighbours who, in this competitive milieu, could benefit by killing the offspring of neighbouring packs (Wolff & Macdonald in press).

2.2.7 Cooperative breeding

All wolves that stayed in the natal pack helped to rear the litter of the dominant female, guarding the den, chasing potential predators, and regurgitating or carrying rodent prey to feed the pups (Sillero-Zubiri 1994). Given the high degree of relatedness among group members, subordinate wolves may increase the indirect component of their inclusive fitness by acting as helpers (Creel & Waser 1991) or, if competition within the group is intense, subordinates may be induced to help as a '*payment*' for remaining in the territory. Ethiopian wolf males helped throughout their lives and never dispersed; the dominant male at least shared paternity, whereas subordinate males appeared generally to have no probability of fathering the pups, nevertheless they still helped. Subordinate females helped more intensely than did males for one or two years before dispersing or inheriting the breeding position. The balance of costs and benefits to all participants in a cooperative breeding system has been widely debated (e.g. Macdonald & Carr 1989; Emlen 1991; Solomon and French 1997). One aspect of the debate is whether groups containing many helpers deliver more food and care to the young than do smaller groups.

The development of the young was divisible into three broad stages (Sillero-Zubiri 1994). First, early denning (birth to four weeks), when the pups are confined to the den and are entirely dependent on milk. Second, mixed nutritional dependency (week five to week 11), when milk is supplemented by solid foods such as rodents provisioned by all pack members until pups are completely weaned. And third, post-weaning dependency (week 12 to six months), when the pups subsist almost entirely on solid foods supplied by breeders and non-breeding helpers. Juveniles were considered independent after six months, when they ceased receiving appreciable quantities of food from adults. A juvenile became subadult and was 'recruited' at one year of age.

Although the mother and putative father spent more time at the den on average than did other wolves, some non-breeders spent more time at the den than did the breeders themselves. The proportion of time pups were left unattended declined significantly as the number of helpers in the pack increased. Pack size may thus influence anti-predator behaviour, because baby-sitters were active in deterring and chasing potential predators. Unattended young might be taken by spotted hyaenas (*Crocuta crocuta*), domestic dogs, honey badgers (*Melivora capensis*) and eagles (*Aquilla verreauxi*, *A. rapax*). However, there was no evidence that increases in pack size resulted in measurable increases in numbers of pups at any age.

Observations were made of nine Ethiopian wolf packs during the breeding season to quantify the amount of solid food provisioned to pups. Non-maternal food provisioning for 17 litters constituted 478 of 713 feedings (67%) observed other than nursing. Independent of the number of donors, there were significant differences in the rate of food provisioning (contributions per hour) by individuals of different breeding status, sex or age ($F_{(5,119)}$=9.08, P <0.0001; Table 2.5). Breeders contributed significantly more food than did non-breeders, and females more than males. The contributions by breeding females were greater than those by any other wolves (up to 0.3 contributions per hour). Dominant males made the second largest contribution, and non-breeding males contributed on average the least food. When the net contribution rate was considered (i.e. food items contributed minus items eaten by the individual helper), breeding females were still the most generous individuals, followed by subadult females, which contributed more than any other non-breeder. Subadult males on the other hand, did not always provision the packs' offspring.

	Breeders		**Non-breeders**	
behaviour/age	**male** *mean ± SD*	**female** *mean ± SD*	**males** *mean ± SD*	**females** *mean ± SD*
Baby-sitting				
Visits per hour:				
adults	1.9 ± 0.6	2.6 ± 0.7	1.1 ± 0.7	1.3 ± 1.2
subadults			1.3 0.7	1.6 ± 1.1
Percentage of time:				
adults	17.3 ± 8.6	23.6 ± 11.4	11.4 ± 9.5	11.4 ± 9.5
subadults			8.6 ± 8.4	11.1 ± 8.8
Grooming rate:				
adults	0.04 ± 0.05	0.06 ± 0.06	0.02 ± 0.03	0.04 ± 0.08
subadults			0.03 ± 0.04	0.03 ± 0.05
Food provisioning				
Hourly total food contribution:				
adults	0.06 ± 0.05	0.12 ± 0.09	0.03 ± 0.03	0.04 ± 0.06
subadults			0.03 ± 0.03	0.06 ± 0.07
Hourly net food **contribution**				
adults	0.05 ± 0.04	0.10 ± 0.08	0.02 ± 0.03	0.04 ±0.04
subadults			0.02 ± 0.04	0.06 ± 0.04

Table 2.5 Individual contributions of Ethiopian wolves to cooperative pup-care in relation to reproductive status, sex, and age during 2,115h of den observations. From Sillero-Zubiri 1994. Values are mean ± SD. Sample size was 17 breeding males, 18 breeding females, 49 non-breeding adult males, 11 non-breeding adult females, 16 subadult males and 12 subadult females. Baby-sitting measured as the percentage of observation time in which individuals of a given category were present within 200m of the den. Feeding measured in number of solid food items (i.e. whole rodents or regurgitations) contributed per hour.

The prediction of a positive correlation between the total amount of food delivered to the pups and the number of non-breeding helpers present was not supported, since the presence of helpers did not increase feeding frequency at the den (r_s=0.18, *n*=7, *P*

>0.05). However, while the total food-provisioning rate did not increase significantly with the number of contributors to the den, the share contributed by non-breeding helpers did do so. Food contributions by non-breeders were accompanied by reduced parental input in pup rearing - reducing food contributions by the dominant male (r_s=-0.63, *n*=7, *P* > 0.05) and female (r_s=-0.85, *n*=7, *P* <0.05) -, and hence a reduction in energy expenditure by the breeding pair (Fig. 2.4). The hypothesis that the number of non-breeding helpers enhances the reproductive output of the group was also not supported, The survival of pups at emergence was not correlated with the number of non-breeding helpers (r_s=-0.26, *n*=20, *P* >0.05), nor was survival at whelping (r_s=-0.28, *n*=20, *P* >0.05). Similarly, there was no significant correlation with survival at six months, one or two years and the number of non-breeding helpers. The litters observed therefore provide little evidence that helpers' feeding contributions *per se* influence the indirect fitness of helpers.

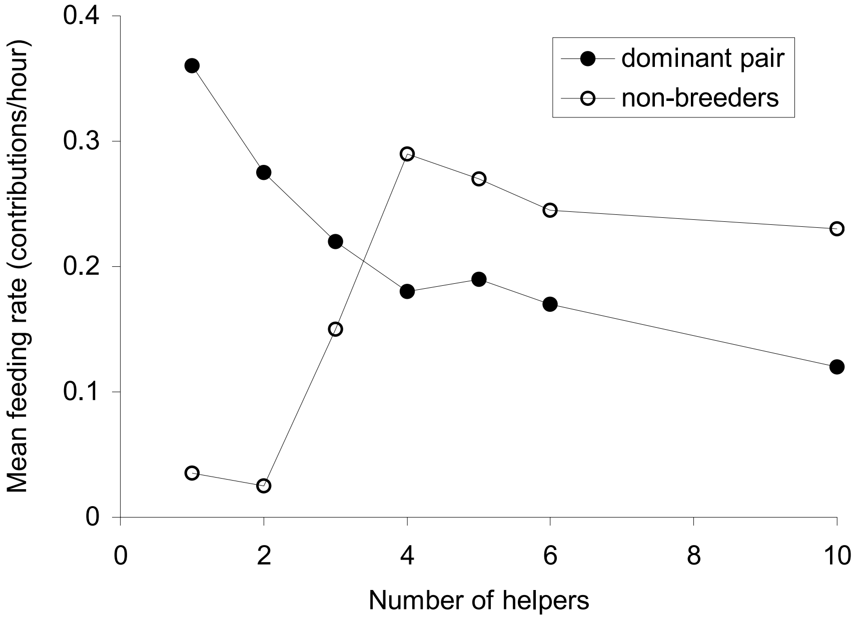

Figure 2.4 Rate of feeding pups (contribution of solid foods per hour) by the dominant pair in relation to the number of non-breeder helpers.

The most extreme manifestation of cooperative care by Ethiopian wolves involved nursing the offspring of the dominant female, or *allo-suckling* (Sillero-Zubiri 1994). Of the 20 successful breeding attempts observed, eight dens had a subordinate female acting as allo-suckler. Allo-sucklers were two year-old or older, and often were closely related to the breeder (daughter or younger sibling). At least two allo-sucklers showed signs of pregnancy (or pseudo-pregnancy) but both either lost or deserted their own offspring before suckling the dominant female's. In at least two cases where an allo-suckler was present, two females were seemingly pregnant. One might therefore have expected double the average litter size of pups from single females (5.1 ± 1.2 SD, *n*=12, range=2 – 6) to emerge. In contrast, significantly fewer pups than expected emerged (*t* =4.88; *df* =16; *P* =0.0002), indeed, barely half the litter expected of a single female (2.6 ± 1.1 SD, *n*=8, range=1 – 4). Our evidence was that these few pups were invariably the offspring of the dominant female. The presence of an allo-suckler was associated with distinct social unease in the pack and evident tension between the dominant and subordinate females. Female aggression inside the den may have an influence on pup mortality prior to emergence. In one case where litter size at parturition was known *a posteriori* from placental scars as five, only two pups had emerged from the den (Sillero-Zubiri 1994).

Allo-suckling obviously has the potential to confer benefits to infants, and reduce the mother's energetic costs (Oftedal & Gittleman 1989). Mean suckling bout rate between weeks 4-13 was 0.26 ± 0.03 (SE) bouts per hour at dens with a single nursing female (*n*=9). Assisted mothers suckled at a similar frequency (*n*=7), but pups with access to two lactating females were suckled significantly more often, at 0.43 ± 0.05 bouts per hour (*t*=2.78, *df*=60, *P*=0.007). Suckling was undertaken by only one female at a time. The suckling bouts of unassisted females were not only longer, but also involved more pups per event. Pups that nursed from two females may receive relatively more milk than those in larger litters with a single female, insofar as the share of female nursing time is a measure of milk flow. Dominant females apparently benefited from allo-suckling by sharing the costs of lactation, and thus lowering their *per capita* suckling frequency, without effecting a reduction in the pups' overall milk intake.

For those dens in which pups were produced, reproductive success at whelping (12 weeks) was variable but typically high. Mean whelping success at four months was 3.55 ± 0.47 (SE) pups for 20 litters, but dropped to 2.8 ± 0.45 (SE) at independence (6 months), and 2.0 ± 0.37 at one year of age (*n*=14). Of 10 litters whose survival was monitored for at least two years, seven produced an adult, at an average of 1.0 ± 0.25 per litter. Most den mortality and pre-whelping mortality was due to the mother's death (*n*=5). Pre-independence mortality was mostly due to disease and starvation (Sillero-Zubiri 1994), while there was no evidence of losses to predation. Considering all packs that bred successfully (*n*=20), the number of pups emerging from the den was not significantly correlated with the number of adults and subadults at the den ($\underline{r}_s$=-0.26). Subsequent to emergence, pups whose mother was assisted by an allo-suckler received a higher energetic input *per capita* until weaning (weeks 4 to 18) and enjoyed better survival than did those nursed by their mother alone.

The foregoing results raise several interesting puzzles to be resolved by continuing research. First, to the extent that the allo-sucklers do indeed make a long-term contribution to pup survival, this is initially disguised by the counter-intuitive earlier effect of litter reduction. Although the helpers in general, and allo-sucklers in particular, appeared to work assiduously for the well-being of the pups, and notwithstanding the rather large size of the data set, demonstrating any survival benefit was at best difficult. Perhaps such benefits are conditional upon circumstances. One intriguing speculation is that males nursed by two females do well: one such male grew up to acquire the dominant male position in his pack, another became dominant male in a pack with six adult males, and three survived a rabies epizootic in which nearly all other pack members perished[8]. Additionally, the benefit of the presence of an allo-suckler in a pack of Ethiopian wolves might be contingent on the availability of prey. In a good year, unassisted females may not need help, but allo-suckler assistance might be important in harsh years. In a scenario where the chances of successful dispersal are very low, concentrating resources in fewer, fitter, individuals might raise their prospects of securing a dominant position, and eventually breeding status.

2.3 The cost of specialisation, a conservation challenge

The apparently sterile Afroalpine steppes of Ethiopia support a rodent biomass which is spatially and temporally predictable, and higher than all other figures quoted for Africa, which may explain why the Ethiopian wolf is the only canid to specialize so completely on rodents (Sillero-Zubiri and Gottelli 1995a). Moreover, the rodents' distribution and diurnal activity coincide with Ethiopian wolves' diurnal and solitary foraging habits, and their confinement to Afroalpine habitats over 3,000m.

Global warming during the last 10,000 years progressively confined the Afroalpine ecosystem to the highest mountains, and 60% of all Ethiopian land above 3,000m has been converted to farmland. Ethiopian wolf populations face threats that arise from their isolation, small size, and the increasing contact with humans and their domestic dogs. Wolf killings seem to have decreased recently (Marino 2003), whereas transmission of rabies remains the main threat with serious consequences for small populations (Sillero-Zubiri *et al.* 1996b; Heydon *et al.* 2002). [A new rabies epizootic has been reported in Bale in October 2003, whose impact on the wolf population remains unknown (S. Williams pers. comm.).]

Protective measures require the consolidation of the management of protected areas and active efforts to monitor and protect all remaining populations, backed up by the establishment of a population management program (Sillero-Zubiri & Macdonald 1997). On the face of it, their small, fragmented populations are poor omens for Ethiopian wolves, but their concentration in a few clearly defined sites, their charisma and, we hope, a fair understanding of their biology, lend hope that with unwavering commitment to a well-founded management plan, they may survive.

CHAPTER III

Ethiopian wolves persist in small Afroalpine enclaves*

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Abstract

The Ethiopian wolf *Canis simensis* is an Afroalpine specialist endemic to the highlands of Ethiopia. Half of the world population, estimated at around 500 individuals, lives in the Bale Mountains of southern Ethiopia. Little is known, however, about the presence of wolves and suitable habitat in other Afroalpine ranges. Assessing the distribution, abundance and threats to all extant populations is a conservation priority for this Critically Endangered canid. With this objective in mind, expeditions to little known and unexplored regions of Arsi, Wollo, Gondar and Shoa were conducted between 1997 and 2000. Suitable habitat and resident wolves were found in all the regions. Outside Bale, six other extant isolated populations, including two previously undescribed, were confirmed. All were small, estimated at no more than 50 individuals, and some less than 25. Two population extinctions were documented and habitat loss to agriculture largely explained local extinctions in small habitat patches. While Bale remains crucial for the long-term persistence of the species, the finding of several small and threatened populations highlights the need for *in situ* conservation actions to be expanded to other regions in the Ethiopian highlands.

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3.1 Introduction

Ethiopian wolves *Canis simensis* evolved in the geographical isolation of the Ethiopian massif and are currently restricted to a few pockets of high altitude ecosystem (Gottelli & Sillero-Zubiri 1992; Yalden & Largen 1992). Unlike other canids, renowned for their adaptability, they prey almost exclusively on the abundant Afroalpine rodent fauna. It is mainly because of this feeding specialisation that they are now on the brink of extinction. Categorized as Critically Endangered on the 2002 IUCN red list (IUCN 2002), the Ethiopian wolf is the rarest canid in Africa (Sillero-Zubiri & Macdonald 1997).

The world population of the Ethiopian wolf has been estimated at *ca.* 500, of which about half live in the Bale Mountains of southern Ethiopia (Sillero-Zubiri & Macdonald 1997; Sillero-Zubiri *et al.* 2000). Studies in Bale have shown that the abundance and distribution of wolves closely follow that of their main prey (Gottelli & Sillero-Zubiri 1992; Sillero-Zubiri & Macdonald 1997). Further evidence of their dependence on Afroalpine rodents has been provided by data on historical sightings in Ethiopia (Gottelli & Sillero-Zubiri 1992) and recent studies of wolves in the central highlands (Ashefani 2001).

Little is known, however, about the presence of wolves and the actual extent of suitable habitat in other regions. Previous estimates of the species' total populations were on the basis of the predicted extent of Afroalpine habitats from topographic maps (Gottelli & Sillero-Zubiri 1992; Malcolm & Sillero-Zubiri 1992). Populations in the highlands of Wollo were assumed to be extinct, and threats to population persistence outside Bale remained speculative. More recently, a population of around 30 wolves was studied in the Shoa region (Ashefani 2001), but the political situation in the 1980s and early 1990s prevented field surveys into the northern highlands.

The Ethiopian wolf action plan (Sillero-Zubiri & Macdonald 1997) stress the urgent need for a complete survey of all areas of potential habitat, as a priority for the development of a global strategy to protect the species from extinction. In the face of current trends in habitat destruction and the risks of persecution, disease transmission and hybridization with domestic dogs, the implementation of conservation measures for every major wolf population is crucial for the survival of the species (Sillero-Zubiri *et al.* 2000).

Between 1997 and 2000 surveys were organized by the Ethiopian Wolf Conservation Programme (EWCP) to all potential wolf ranges in Ethiopia. Surveys extended to the areas occupied by the species in the past and to all other high altitude ranges in Ethiopia. Standard techniques for rapid assessment were applied to meet the following objectives: a) to determine wolf presence/absence and relative abundance, b) to record any local extinctions and, where possible, their circumstances, c) to map habitat distribution and d) to assess threats to the persistence of populations. In this chapter I present the results of these surveys, provide an updated summary of the distribution and status of *C. simensis*, discuss the threats that the species faces across its range, and provide preliminary guidelines for *in situ* conservation of Ethiopian wolves outside Bale.

3.2 Study area

The Ethiopian massif is characterized by marked altitudinal variations that produces a range of climates affecting plant and animal distribution and the concentration of people (Yalden & Largen 1992). Most people live in the fertile highlands of the *Woina Dega* (warm temperate) and *Dega* (temperate) zones. The *Wurch* zone (alpine, >3,000m) is colder and less favorable for agriculture and broadly corresponds with the distribution of habitats suitable for the Ethiopian wolf (Fig. 3.1). Within the *Wurch*, ericaceous heathlands dominated by *Phillipia* and *Erica* spp. (Miehe & Miehe 1993) are replaced at higher elevations by the Afroalpine grasslands, scrubs and meadows above about 3,200m.

Field surveys were carried out in the Simien Mountains, Mount Guna, Mount Choke, the highlands of North and South Wollo, Gosh Meda and the Arsi Mountains (PLATE 3.1). Study sites were selected from historical records, previous surveys and the identification of high altitude ground from topographic maps. The name and location of study sites within Afroalpine ranges are indicated in Fig. 3.1. Detailed descriptions of itineraries can be found elsewhere (Marino *et al.* 1999; Ash 2000).

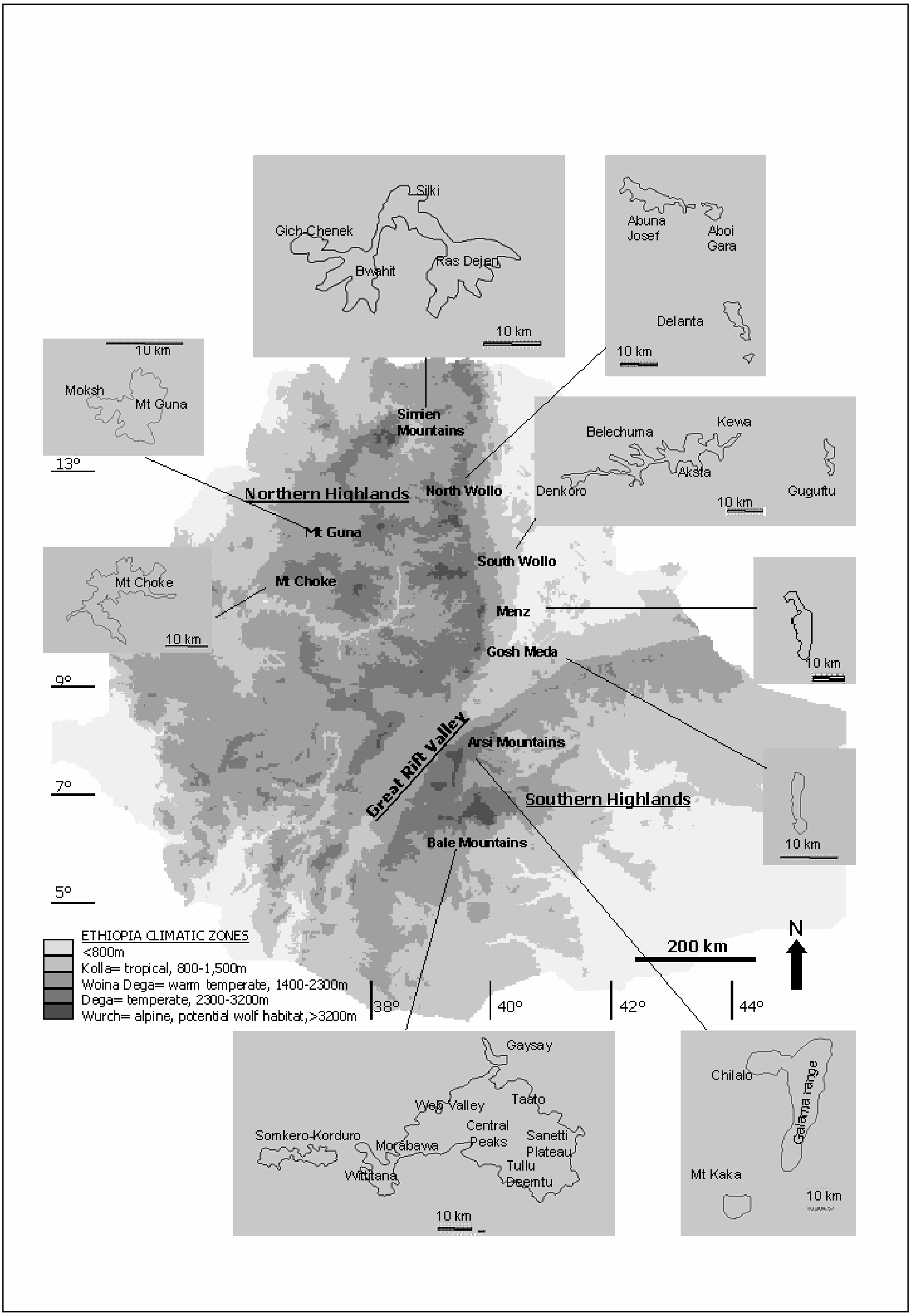

Fig. 3.1 Afroalpine ranges and remaining wolf habitats in Ethiopia. Climatic zones are illustrated in a gradient of grey; the darkest correspond to the Afroalpine ecosystem, above 3,200m (derived from a Digital Elevation Model by the U.S. Geological Survey). The more detailed maps (a to j) show the remaining suitable wolf habitat, above the current limit of agriculture.

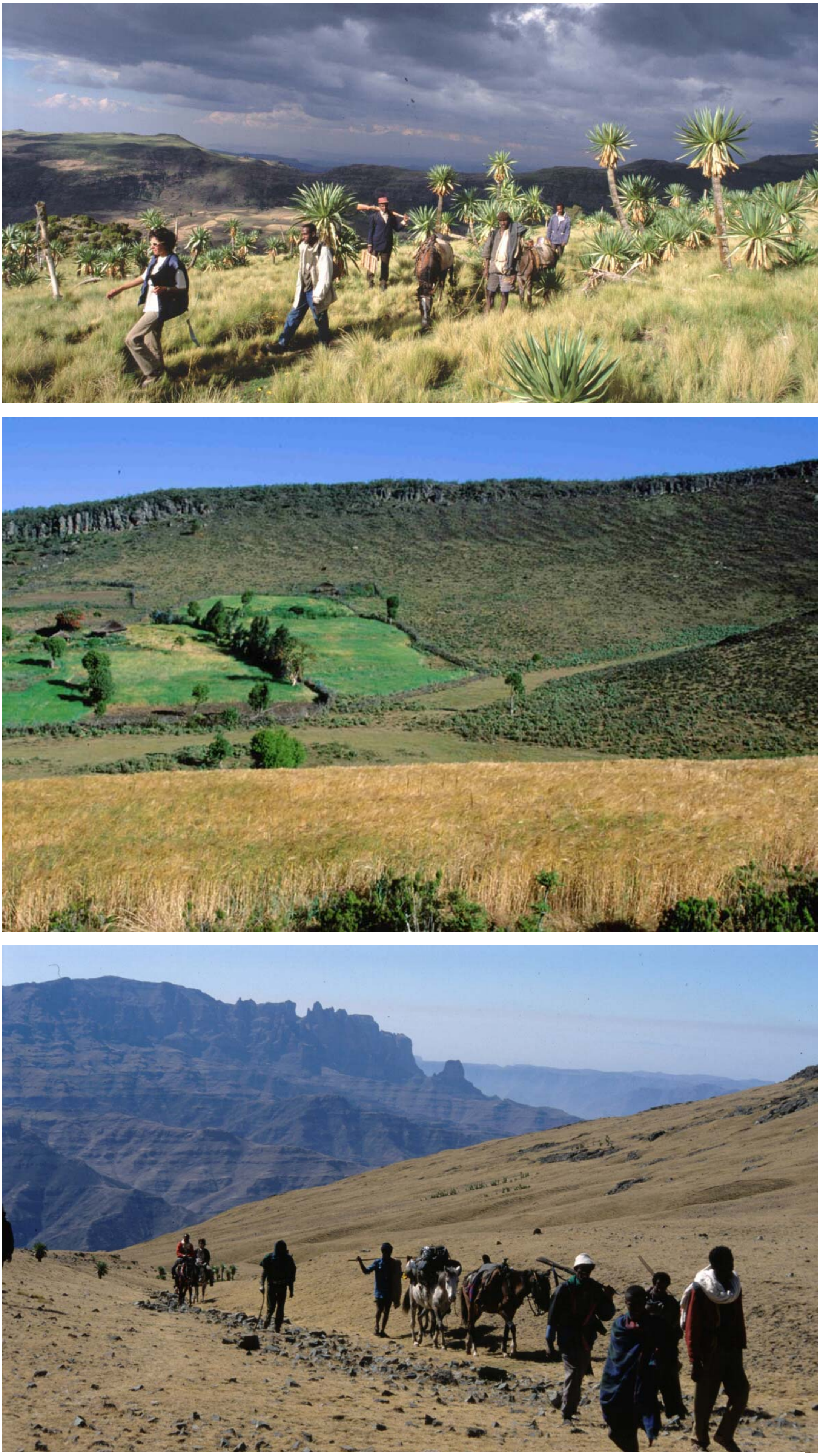

PLATE 3.1 From top to bottom: Field surveys in Denkoro, South Wollo - Encroaching agriculture, northern Bale Mountains National Park - EWCP expedition to the Simien Mountains

3.3 Methods

Surveys consisted of short visits to each study site and the use of techniques for rapid assessment (Sillero-Zubiri & Macdonald 1997). Surveys were carried out on foot or horseback, and were designed to cover all suitable habitat in each site. Survey teams comprised 2 to 3 trained EWCP members, a wildlife expert from the relevant Zone's Agricultural Department, and 1-4 guides from the local Peasant Associations. Surveys in each Afroalpine range lasted between 2-6 days depending on its area.

3.3.1 Census transects

Census transects consisted of sections of continuous trekking or horse riding along survey routes, lasting a whole morning or afternoon. Sightings and signs of wolf activity in the form of 'dig-outs' (made by wolves while searching for rodents) were recorded. Sequential positions were taken along transects using a Global Positioning System. Transect length varied between four and 25km and the number of transects varied between two and 10, depending on the size of the study site. For each census transect, encounter rates were calculated as the number of sightings (independent of the size of the group observed) and dig-outs observed per km. For each Afroalpine unit (defined in the habitat analysis section below) an average encounter rate was calculated.

3.3.2 Interviews

Following a standard questionnaire (Appendix III in Sillero-Zubiri & Macdonald 1997), local people were asked about the presence of wolves in the area, causes of wolf mortality, perceived population trends, incidence of disease, cases of wolf predation on livestock and attitudes towards wolves. Interviews were aimed at people who frequently visited the Afroalpine area, either to herd their livestock, collect grass and firewood, or en route to local markets. A total of 103 interviews were carried out, varying between 10 and 32 in the various areas. Interviews were analysed separately for region. Results, where possible, were calculated as the percentage of respondents giving a positive answer or a specific answer from a set of choices.

3.3.3 Mapping and habitat analysis

Suitable wolf habitat was mapped along surveys routes and from vantage points. Habitat was hand-mapped over 1:50,000 topographic maps (1:100,000 for Simien and 1:125,000 for parts of North Wollo). Habitat mapping was GPS-assisted in order to achieve the fine level of detail provided by the topographic maps. Notes were taken on the nature of the lower limit of wolf ranges, whether corresponding with natural features, such as escarpments, or with agricultural fields.

Additionally, habitat quality was mapped on the basis of vegetation types, as described by Gottelli & Sillero-Zubiri (1992) who showed that the density of Ethiopian wolves in Bale was negatively correlated with vegetation height and positively correlated with the density of rodent prey . On this basis, habitats in the areas surveyed were classified either as ‘marginal’ or ‘good’, the latter encompassing both the ‘good’ and ‘optimal’ categories of Gottelli & Sillero-Zubiri (1992) to reduce subjectivity. In Bale, optimal habitat is characterized by Afroalpine meadows with short grass and herbs and a rodent biomass of 3,500-4,000kg km^{-2}, good habitat is characterized by *Helichrysum* scrub and montane grassland with a rodent biomass of one third of optimal habitat. Marginal habitats include dense ericaceous and *charanfe* (*Euryops pinifolius*) heathlands; steep slopes and escarpments, rocky barren peaks and overgrazed grasslands near settlements. In Bale, ericaceous heaths sustain a rodent biomass one fifth to one tenth of optimal habitat (Gotelli & Sillero-Zubiri 1992).

To calculate the area of each habitat type, field maps were digitized with IDRISI Geographical Information System software (Clark Labs, Clark University, Worcester, USA). Extant wolf habitat was grouped into geographical entities or ‘Afroalpine units’ (AU). By definition, distances between AUs were larger than the potential dispersal of individual wolves, known to be up to 20km from previous records (Sillero-Zubiri & Gottelli 1992b; Z.T. Ashefani pers. comm.; Z. Kibrit pers. comm.). It is reasonable to assume that wolf dispersal between AUs was not occurring at a substantial rate, if at all. Each AU was therefore assumed to contain an isolated population or isolated group of populations connected by dispersal (cf. the ‘habitat isolates’ concept of Morrison *et al.* 1998).

3.3.4 Population estimates

An attempt to improve previous population estimates was undertaken using information on the actual size of remaining habitat patches collected during field surveys. Known densities of wolves in Bale (Gottelli & Sillero-Zubiri 1992) were used to estimate the number of wolves in each AU, extrapolating densities to the extent of ‘marginal’ and ‘good’ habitats. To minimize overestimates, the lowest densities recorded in Bale’s good (0.2 - 0.3 wolves per km^2) and marginal (0.1 wolves per km^2) habitats were used. A range of population sizes were derived as upper value = (km^2 of good habitat x 0.3 wolves km^{-2}) + (km^2 of marginal habitat x 0.1 wolves km^{-2}), and lower size value = (km^2 of good habitat x 0.2 wolves km^{-2}) + (km^2 of marginal habitat x 0.1 wolves km^{-2}).

3.4 Results

3.4.1 Simien Mountains

The area of available habitat for wolves in Simien was the largest North of the Rift Valley (Table 3.1) and the third most important in Ethiopia. Steep escarpments limited suitable habitat along north-facing slopes. Elsewhere the upper limit of agriculture and encroachment restricted wolf ranges to areas above 3,700- 3,900m in four main areas and connecting corridors (Fig.3.1a). Gich-Chenek, the only area contained within the Simien Mountains National Park, was affected by the construction of a road and newly ploughed fields along its southern border. Bwahit, east of the park, contained the least disturbed habitats. Short grasslands, seemingly overgrazed, characterized the habitat in Silki and Ras Dejen. Wolves and wolf signs were recorded in all areas and were most abundant in Bwahit, but average encounter rates for Simien were the lowest of all AUs in which wolves were recorded (Fig. 3.2). Although most interviewees had seen wolves in the area, many believed the population was declining because of overgrazing and agricultural expansion (Table 3.2). A positive or indifferent attitude towards wolves was dominant; people from around the park thought wolves could be beneficial because they attract tourists. Cases of livestock losses to wolves were reported, but golden jackals *Canis aureus* were indicated as the main predator.

3.4.2 Mount Guna

Mt Guna was the smallest AU that sustained a resident population (Table 3.1). This isolated patch was limited to the east by steep escarpments and on its western slopes by newly cultivated fields, human encroachment and degraded pastures at around 3,650m (Fig. 3.1b).

	Suitable wolf habitat				
Afroalpine Unit	Potential (km^2)	Available (km^2)	Percentage remaining	Protected areas	Spatial structure
North of Rift Valley					
Simien Mountains	960	273	28%	26km^2(SMNP)	patches and corridors
Mt Guna	210	51	24%		isolated patch
Mt Choke	500	134	27%		isolated patch
North Wollo	1,150	140	12%		patches and corridors
South Wollo	1,220	243	20%	*ca.* 20km^2 (DSF)	Patches
Menz*	124	112	90%	82km^2 (GCM)	isolated patch
Gosh Meda	90	20	22%		isolated patch
South of Rift Valley					
Arsi Mountains	1,000	870	87%	*ca.* 50km^2 (BLHB)	mainland-island
Bale Mountains*	1,990	1,141	57%	1,100km^2 (BMNP)	mainland-island
TOTAL	7,220	2,984	41%	*ca.* 1,278km^2	

Table 3.1 Distribution and extent of suitable wolf habitat in Ethiopia. The potential area is the land above 3,200m, and the area of remaining habitat was calculated from the field survey maps (see text for details). * Habitats areas from recently updated maps of Bale and Menz (from Sillero-Zubiri *et al*. 2000). SMNP=Simien Mountains National Park; DSF=Denkoro State Forest; GCM=Guassa community Management; BLHB=Bora Luku Hunting Block; BMNP=Bale Mountains National Park.

The presence of wolves was confirmed by sightings and dig-outs (Fig. 3.2), concentrated on the central and northern parts of the range. Encounter rate of dig-outs was the highest recorded (Fig. 3.2). Everybody interviewed had seen wolves in the area and most perceived that wolves were breeding well and their numbers increasing or stable. Although some alleged that human encroachment was negatively affecting the population, attitudes towards wolves were in general positive, and wolf predation on livestock was not perceived as a problem (Table 3.2).

	Simien Mountains	Mount Guna	North Wollo	South Wollo	Arsi Mountains
Number of interviews	32	10	20	26	15
Wolf presence and abundance					
Wolf sightings (% interviewees)	81	100	100	77	100
Largest group seen	5	9	15	6	9
Perceived population trend (% interviewees)	60% decreasing 20% increasing	80% increasing or stable 20% decreasing	80% increasing or stable	80% decreasing	60% increasing 20% decreasing
Mortality and disease					
No. dead wolves (year if known)	1	1 (1973)	3 (1987 and 1997)	3	2 (1998 and 1999)
Cause of death	rabies	killed by people	killed by people	traps and starvation	unknown
Rabies awareness (% interviewees)	59%	80%	60%	70%	78%
Years of reported rabies cases	1995, 1997	1998, 1999	1996, many in 1997	every year, 1991-1997	1995, 1996, 1998, 1999; frequency increasing.
Reports of dog-wolf interactions	5	1	1	2	0
Perception and conflicts					
Attitude towards wolves (% interviewees)	80% positive or indifferent	70% positive	90% negative	70 % indifferent 15 %negative	71 % indifferent 28 % positive
Wolf predation on livestock (% int.)	59	10	100	31	0
Wolf predation from own herd (% int.)	(no data)	0	80%	20%	0
Main predator in the area	GJ	GJ	EW	SH	GJ & SH
Other predators	SC	SH	LP	GJ & LP	SH

Table 3.2 Results of interviews with local people, showing their knowledge of wolf presence and abundance, mortality and disease, and their perceptions of wolves and of conflicts with wolves. GJ golden jackal *Canis aureus*, SH spotted hyaena *Crocuta crocuta*, EW Ethiopian wolf *Canis simensis*, LP leopard *Panthera pardus,* SC serval cat *Felis serval*.

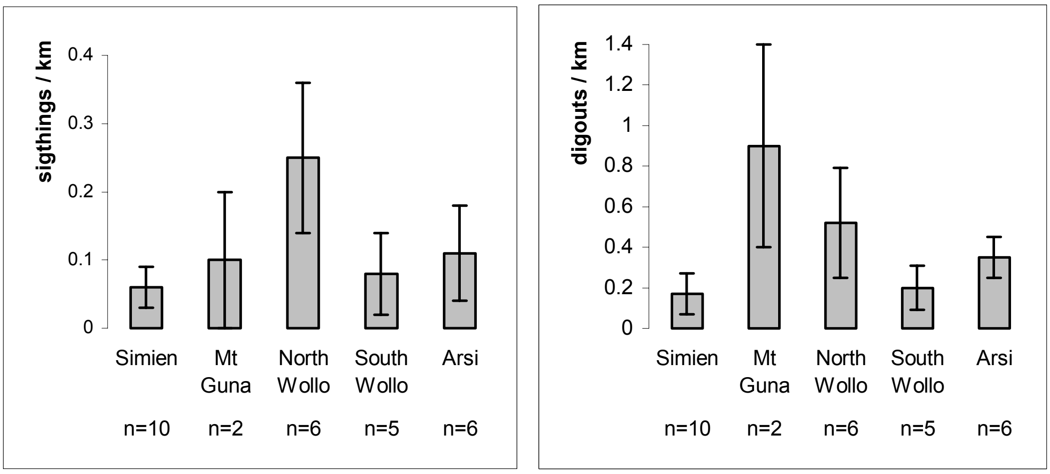

Fig. 3.2 Average encounter rate of wolves and wolf 'dig-outs' along census transects in those Afroalpine units where wolves were detected. Error bars are standard errors, *n*= number of transects.

3.4.3 North Wollo highlands

The available wolf habitat in North Wollo (Table 3.1) was discontinuous (Fig. 3.1c). The Abuna Josef massif was the largest area, loosely connected by narrow ridges with the small Aboi Gara range to the east, in turn separated by approximately 20km from the Delanta range in the south. Steep escarpments to the North of Abuna Joseph and east of Delanta limited wolf ranges. Elsewhere, overgrazed meadows and cultivated fields restricted suitable habitat to areas above 3,700-3,800m, or 3,450-3,500m in Delanta.

Sightings and signs of wolves were recorded in all areas, but they were most abundant in Delanta, where the largest group with 6 individuals, was observed (Fig. 3.2). Wolf sightings were the highest recorded across AUs. All people interviewed had seen wolves in their area and many believed the wolves were recovering from past persecution (Table 3.3). A large proportion of people reported a negative attitude towards wolves, and invoked wolf predation on livestock as the reason. Many reported having lost animals and perceiving wolves as the main predators of livestock.

3.4.4 South Wollo highlands

Over 240km^2 of suitable wolf habitat were found in South Wollo (Table 3.1). Agriculture and human settlements extended up to 3,700-3,800m, except for Denkoro State Forest, created to protect the last remnant of ericaceous forest in northern Ethiopia, where grasslands extended down to 3,200m. Wolf habitat was distributed along a main massif with narrower ridges heading off to the North and South (Fig. 3.1d). Vast areas of short grasslands and narrow corridors appeared degraded by overgrazing. In a small patch of suitable habitat in Guguftu, east of the main massif, a commercial sheep farm had been established and the area was ploughed for the cultivation of pasture. With the exception of Guguftu, wolf sightings and signs were recorded in all sites (Fig. 3.2). Most of the people interviewed had seen wolves, but only a third of them within the last year (Table 3.2), and most believed wolves were declining as a result of the pastures being overgrazed. Reported sightings in Guguftu were 5 -10 years old, and past persecution was considered the main cause of this local extinction. People were mostly indifferent to wolves. Some reported negative attitudes because of livestock predation, but only a third reported livestock losses to wolves; spotted hyaenas *Crocuta crocuta* were considered the main predators in all areas.

3.4.5 Mt. Choke

Available wolf habitat in Mt. Choke was in a single patch limited by escarpments and agricultural fields at 3,700m (Fig. 3.1e). No sign of wolves or their activity were recorded. Interviews with local people indicated that extinction might have occurred several decades ago, because even the oldest respondents did not remember having ever seen wolves. Golden jackals were frequently observed.

3.4.6 Gosh Meda

With only 20km^2 of suitable wolf habitat remaining, this was the smallest AU (Table 3.1), limited to the east by the escarpments of the Rift Valley, but otherwise surrounded by recently ploughed fields and human settlements up to 3,700m. No sign of wolves or their activity were recorded. Interviewees indicated wolves were common as recently as 10 years ago, but were no longer resident in the area. There were reports of sporadic sightings of single wolves in 1992, 1996 and January 1999. Reasons for the decline were not known. Local people believed that wolves bring good luck and forecast years of good crops, killings were reportedly infrequent in the past, and wolf predation on livestock was not perceived as a serious conflict. Common jackals were encountered and were reported to have extended into the area, where they are considered the main predator of livestock.

3.4.7 Arsi Mountains

The Arsi highlands comprised 870km^2 of suitable wolf habitat, the largest AU after Bale (Table 3.1). Around 50km^2 formed part of the Bora Luku Hunting Block. Lower boundaries to wolf habitat were cultivated fields at 3,200-3,400 m (3,700m in Mt. Kaka) or in parts the natural lower limit of ericaceous heathlands. The remaining habitat was distributed across the extensive Galama range, Mount Chilalo, a lower saddle, called Chelelaka, connecting both, and an additional patch to the south in Mt. Kaka (Fig. 3.1h). A broad band of extensively burnt ericaceous heathlands surrounded better quality patches for wolves at higher altitudes.

Wolves and wolf signs were sighted in all areas, but more frequently in Galama. The average sightings per km were second only to that recorded in North Wollo (Fig. 3.2). All interviewees had seen wolves; the majority believed that they were breeding well and recovering from past persecution, but a few perceived that numbers were declining because of recent agricultural expansion (Table 3.2). Indifference and lack of conflicts was alleged to be due to the fact that people and livestock in Arsi used the high altitude pastures only seasonally. The main predators of livestock were golden jackals and spotted hyaenas.

3.4.8 Comparative analysis of habitats and populations

The habitat currently available for wolves occupied less than half of the regions' land above 3,200m (Table 3.1). Of the approximately 3,000km^2 left, 40% was under a certain degree of protection, but only *ca.* 200km^2 in areas other than the Bale Mountains National Park. Including Menz and Bale (Figs. 3.1f and 3.1i), suitable wolf habitat exists in nine AUs, of which Mount Choke and Gosh Meda were unoccupied by wolves.

AUs differed in their size, spatial structure and proportion of habitat lost (Table 3.1). All AUs North of the Rift Valley, with the exception of Menz, contained less than a third of their potential wolf habitat. The current lower boundary of wolf habitats tended to occur at consistently higher altitude towards the North (Fig. 3.3), following a human density cline from South to North (Statistical Authority 1998). Similarly, the altitudinal upper limit of cultivated fields increased lineally with decreasing latitude of AUs (R^2= 0.75; F=18.12, df=6, P=0.005). Particularly in the north, the areas below 3,700m -the approximate limit of sustainable agriculture in Ethiopia- are highly vulnerable to further loss of habitat to agriculture (Aboi Gara and Delanta; Denkoro and Menz are under some form of protection). The two recent local extinctions recorded, in Guguftu and Gosh Meda, were in relatively low-lying ranges.

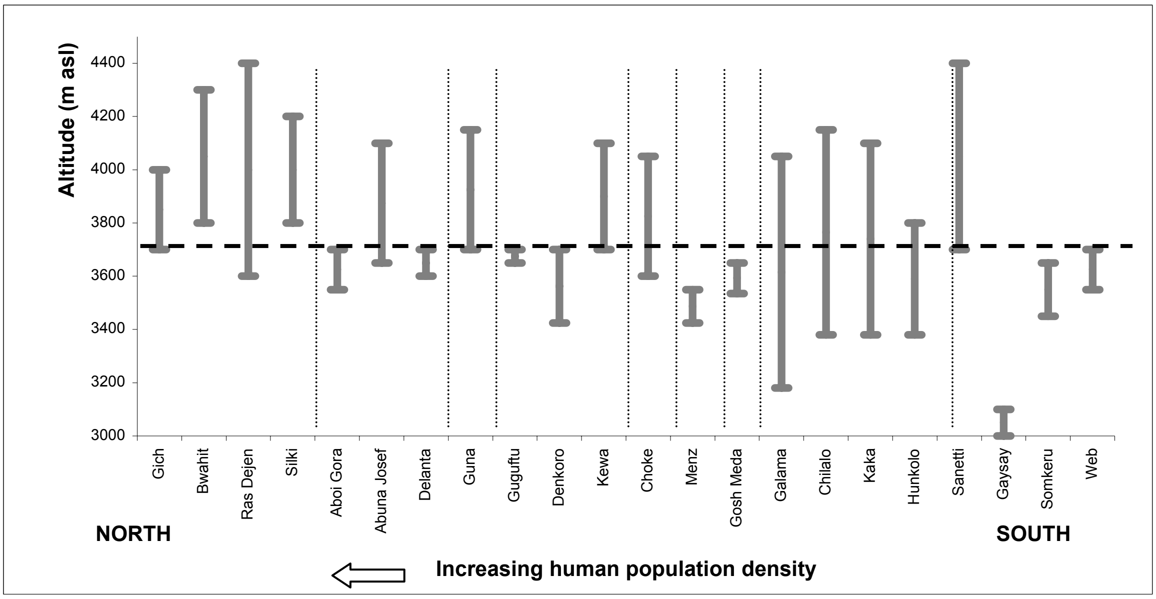

Figure 3.3 Current altitudinal distributions of Ethiopian wolf habitats. The bars represent the altitudinal range of remaining wolf habitats in each study site and in the Bale Mountains. The dashed line at 3,700m indicates the approximate limit of sustainable agriculture in Ethiopia.

Wolf population estimates were based on the extent of habitat available. Thus estimates tended to be larger in larger AU's, but a high proportion of 'good' to 'marginal' habitat in Menz gave a relatively high population estimate for such a small AU (Table 3.3). With the exception of Arsi and Simien, all other populations were estimated at fewer than 25 individuals. These conservative estimates appeared more appropriate for Simien and South Wollo, where wolf abundance was relatively low, but wolf numbers in North Wollo, Mt. Guna and possibly Arsi may have been underestimated. In the case of Arsi, however, it was unclear whether resident wolves used all marginal habitat along the vast ericaceous heathlands.

3.5 Discussion

Field surveys confirmed the existence of seven isolated Ethiopian wolf populations, and described two new populations, in South Wollo, and North Wollo, the latter previously thought to be extinct, and with only a historical record from 1862 (in

Gottelli & Sillero-Zubiri 1992). The study also confirmed the persistence of populations, such as Mt Guna, provided the first comprehensive survey of the Simien massif, and demonstrated that the Arsi population was more secure than previously thought (Malcolm & Sillero-Zubiri 1997). The study recorded the extinctions of the population on Mount Choke and Gosh Meda; the last sightings on Mount Choke were in 1932 (Yalden *et al.* 1980), and Gosh Meda had last been visited in 1989, when wolves were still present despite a dense human population (Gottelli & Sillero-Zubiri 1990).

	Habitat types (km^2)		
Afroalpine Unit	**'good'**	**'marginal'**	**Population estimate**
North of Rift Valley			
Simien Mountains	132	142	40 - 54
Mt Guna	22	29	7 - 10
Mt Choke	46	88	extinct
North Wollo	46	94	19 - 23
South Wollo	21	122	16 - 19
Menz*	59	53	17 - 23
Gosh Meda	8	13	extinct
South of Rift Valley			
Arsi Mountains	144	646	93 - 108
Bale Mountains **	-	-	250
TOTAL			**442-487**

Table 3.3 Populations estimates in Afroalpine units North and South of the Rift Valley, derived from extrapolations of wolf densities in the Bale Mountains to the areal extent of each habitat category. *Habitat areas from recently updated maps **Most recent estimate of Bale's population from Sillero-Zubiri *et al.*, 2000).

The finding of resident wolves in most of the remaining suitable habitat, and their persistence in small Afroalpine pockets, suggests that the species has some resilience to fragmentation and the effects of small population sizes. But with the exception of Bale and possibly Arsi, all populations are small, estimated to contain fewer than 50 individuals, and some fewer than 25. Although these estimates are based on habitat availability they clearly indicate the small size of some of the populations, which makes them susceptible to extinction from deterministic and stochastic factors (Soulé 1987). Local extinctions in habitat patches of less than 20km^2 may indicate a minimum size for sustainable populations.

The Ethiopian wolf is a rare species under considerable pressure. The key to its survival resides in the security of its habitat and the isolation of populations from adverse impacts of people, livestock and domestic dogs. Habitat protection to prevent or reduce further habitat loss would reduce the risk of extinction in particular of those populations in small areas and at lower altitudes (e.g. Menz; Aboi Gara and Delanta, Fig. 3.3). Conservation initiatives at regional and local community level, such as ones currently in place in Denkoro and Menz, are an alternative option to the traditional approach of habitat protection in national parks.

Rabies appears to be a threat in all surveyed areas, with cases reported in domestic dogs, livestock and wildlife, including one Ethiopian wolf (Table 3.2), a finding corroborated by more extensive disease questionnaire data in several areas (K. Laurenson, unpubl. data). Diseases transmitted from domestic dogs have had devastating effects on wolves in Bale, and rabies is considered the main short-term threat to the persistence of all populations (Sillero-Zubiri *et al.* 1996b; Laurenson *et al.* 1997; Haydon *et al.* 2002). A large-scale vaccination programme of domestic dogs is ongoing in Bale (Sillero-Zubiri *et al.* 2000) and was recently extended to other populations in northern Ethiopia (S. Williams, pers. comm.).

Conservation actions to minimize threats such as persecution, loss of habitat due to road construction and commercial sheep farming, would require a close monitoring of those populations most vulnerable to these specific threats. In general, contacts and conflicts between wolves and humans are bound to increase with increasing human density and habitat fragmentation. In the heavily populated northern highlands, for example, livestock graze on high altitude pastures all year round. There livestock predation by wolves has resulted in negative attitudes amongst the local people, and sporadic killings, at least in South Wollo. Still persecution appeared to have been more common in the past, when indiscriminate wildlife killings occurred during a period of civil war during the 1980s and early 1990s; a phenomenon also documented in Bale and Menz in the early 1990s (Sillero-Zubiri *et al.* 1996b; Ashenafi 2001). Hybridization between dogs and wolves seems to be restricted to a single population in Bale (Gottelli *et al.* 1994), because no other cases of hybridization either in the past or recently have been reported or were discovered during the surveys.

This study provides an evaluation of the status and distribution of Ethiopian wolves that is crucial for the planning of future conservation activities. It confirms the importance of Bale for the long-term persistence of the species, but also highlights the need for conservation actions to be extended to other extant populations. The population in South Wollo is a good candidate for a priority area for conservation because it sustains wolves at relatively high density yet it is threatened in many diverse ways. Following the outcome of these surveys and a workshop in Bale (Sillero-Zubiri *et al.* 2000), the Ethiopian Wolf Conservation Programme expanded to other populations in the North, widening the use of the Ethiopian wolf as a flagship species for the conservation of the Ethiopia's unique Afroalpine ecosystem.

CHAPTER IV

Geographical variation in the diet of Ethiopian wolves: climatic-linked specializations

Abstract

Ethiopian wolves are unusual among canids and other carnivores in their restricted distribution and degree of feeding specialization. In the Bale Mountains and Menz, where the biomass of Afroalpine rodents is very high, wolves depend almost entirely on the rodent fauna all year round. Little is known however of the food available to wolves elsewhere, their diets or degree of specialization. Analysis of prey remains in 161 wolf scats, representing five other populations, confirmed that wolves are specialized hunters of diurnal rodents across their distribution, but the composition of the diets differed among populations. Diurnal Murinae rodents were represented in 60% to 83% of all the prey occurrences in scats. Of these, *Otomys typus* - a rare prey item in Bale and Menz - was consistently the commonest prey (40% to 50% of occurrences), followed by the grass rat *Arvicanthis abyssinicus* (17% to 33 % of occurrences). The remaining portion of the diet (21% to 45% of the prey occurrences) was the most variable. Changes in the consumption of common molerats *Tachyoryctes splendens*, *Lophuromys spp.*, and nocturnal rats were consistent with geographical patterns in climate and productivity. With the inclusion of Bale and Menz in the comparison, the broader pattern of dietary variation was also consistent with the expectation of climatic-induced changes in prey productivity and composition: giant molerats (*Tachyoryctes macrocephalus)* were common prey in the Bale Mountains; common molerats (*T. splendens*) were relatively important in the more productive Southern and Central Highlands; and diurnal and nocturnal rats dominated the diet in the drier Northern Highlands. This study sheds light on the food resources available to wolves across populations and enhances our capacity to predict priority areas for habitat conservation.

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4.1 Introduction

Canids are renowned for their adaptability and extensive geographic distributions (Macdonald & Sillero-Zubiri in press). In contrast, the Ethiopian wolf *Canis simensis* is only found in Afroalpine 'islands' in the high altitude ecosystem of Ethiopia (Chapter 3). Like other high altitude endemics, the species evolved in the geographical isolation of the Ethiopian massif, where it became highly adapted to prey on the abundant Afroalpine rodent fauna.

The wolves' feeding specialization is associated with a rich and predictable rodent resource. The small rodents on which wolves depend are the dominant herbivores in the Afroalpine ecosystem. In the highlands of Bale rodents attain a biomass of 24-26kg/ha (Sillero-Zubiri *et al.* 1995a,b; Chapter 2), an estimate higher than all other figures for rodent biomass quoted for Africa by Delany (1972) and comparable to the biomass of medium and large mammals in African grasslands (e.g. Nairobi National Park - Foster & Coe 1968). Arguably it is this dietary specialisation that led to the wolves' confinement to a scarce and fragmented habitat (Yalden & Largen 1992).

Wolves in Bale have a year-round specialized diet mostly composed of diurnal rodents (Sillero-Zubiri & Gottelli 1995a) and wolf abundance and distribution closely follows that of theirs rodent prey (Gottelli & Sillero-Zubiri 1992; Sillero-Zubiri *et al.* 1995a,b; Sillero-Zubiri & Macdonald 1997). The giant molerat (*Tachyoryctes macrocephalus*) is the single most important food item (accounting for 47% of the volume and 36% of the prey occurrences in scats), followed by two diurnal species of Murinae rats, the grass rat *Arvicanthis blicki* and the harsh-furred rat *Lophuromys melanonyx* (28% and 21% of prey occurrences in scats respectively). Giant molerats however are believed now to be absent throughout the rest of Ethiopia (Yalden & Largen 1992; C. Sillero-Zubiri pers. comm.) and Sillero-Zubiri & Gottelli (1995a) hypothesized that the common molerat *T. splendens* might be an important prey at lower altitudes or where giant molerats are rare or absent. Subsequent studies in Gaysay, in Bale (Malcolm 1997) and Menz, in the Central Highlands (Ashenafi 2001) confirmed that where giant molerats were absent the common molerat replaced it in the diet, or at least partially in Menz (47% and 17% of the prey occurrences in scats in Gaysay and Menz respectively). The commonest prey in Web was *A. abyssinicus* and *L. flavopunctuatus*, close relatives of the Bale endemics *A. blicki* and *L. melanonyx*. Wolves rarely predated upon nocturnal rats in Bale and Menz, and although they retained the capacity to hunt larger prey in small groups, only occasionally killed hares, young antilopes or unguarded lamb (Ashenafi 2001; Sillero-Zubiri & Gottelli 1995a). Livestock losses in these areas were attributed to spotted hyaenas (*Crocuta crocuta*) and golden jackals (*Canis aureus*); wolves readily consumed carrion or fed on a carcass when available but in Bale carcasses were rapidly monopolized by hyaenas or domestics dogs (Sillero-Zubiri & Gottelli 1995a).

The rodent biomass in Bale and Menz is similarly high, and giant molerats and molerats contributes respectively about a half or a quarter of total prey biomass. Such optimal conditions for rodents in general and molerats in particular do not seem to be representative of Afroalpine areas elsewhere (Marino *et al.* 1999; Marino 2003). Circumstantial evidence also suggests that overgrazing in the densely populated highlands of the North may have negatively impacted upon the highland rodent fauna (e.g. Nievergelt *et al.* 1998), and that wolves may predate more frequently on livestock (Marino 2003), or become crepuscular or nocturnal when human interference is severe (Yalden & Largen 1992). The scarcity of information raises the question of what degree of wolf dietary specialization prevails where the rodent resource is poorer, and in habitats more profoundly modified by humans. This study attempts a simple way forward to obtain relevant ecological information by analyzing and comparing the composition of diets from 161 wolf scats, representing five populations distributed across the Ethiopian highlands.

A predator's niche width is broadly determined by the abundance and diversity of potential prey (Schoener 1971) and predators occupying a broad geographical range should experience variations of their food-niche breadth. Because of their habitat specificity Ethiopian wolves are believed to be specialized rodent hunters all across their distributional range (e.g. Sillero-Zubiri 1994). This, however, has not been formally demonstrated. It is also reasonable to expect certain degree of dietary variation along climatic gradients, following changes in the productivity and composition of the rodent community. Marked altitudinal variations characterize the climate, fauna and flora of the Ethiopian highlands (Yalden & Largen 1992; Chapter 2); temperature decreases with altitude and rainfall begins to fall above 3,850 m (Hillman 1986; Sillero-Zubiri 1994) determining an altitudinal component in the diversity of Afroalpine plants and rodents (reviewed in Chapter 2). A broader-scale variation in humidity and precipitation superimposes a latitudinal pattern, by which mountains along the North-South highlands axe (between 6° and 14° North) experience drier or wetter climates (Gamachu 1991). The drier Northern Highlands are located in the 'moist subhumid' region and the Southern and Central Highlands in the 'humid' region (Gamachu 1977). Therefore, within the high-altitude environment, primary productivity will tend to increase with decreasing altitude and southwards with increasing humidity. Being predominantly herbivores, the biomass of Afroalpine rodents should be higher in the more productive Southern and Central Highlands than in the poorer environments of the North, and in lower than higher-lying land. A northwards pattern of increasing human densities (Statistics Authority 1998) may strengthen this effect, because agriculture extends further up towards the north (Chapter 3), and Afroalpine pastures are more intensively grazed (in contrast with their seasonal use in the Central and Southern Highlands; Malcolm & Ashenafi 1997; Ashenafi 2001). Dietary variations consistent with geographical patterns would support predictions of climatic-induced changes in prey availability. Improved knowledge of the diets of Ethiopian wolves will help to assess the food resources available and to make more confident predictions of the potential for an area to support wolves.

4.2 Study Areas

Ethiopian wolf populations occur in three main mountain blocks: the Northern and Central Highlands, separated by the dividing Great Rift Valley from Southern Highlands (see Fig. 3.1). Wolves inhabit the Afroalpine ecosystem occurring above the treeline -at around 3,200m. Recognized as *Wurch* in the traditional Ethiopian classification, these areas are dominated by grasslands, meadows and low-lying shrubs. The *Wurch* is used by livestock but climatic conditions are unfavourable for permanent human settlement or cultivation. In the Northern Highlands, however, increasing human densities have brought about an expansion of subsistence agriculture well within the *Wurch*, further reducing and fragmenting the habitat suitable for wolves.

Faecal samples come from five Afroalpine units, or 'regions', each defined as to contain one isolated population of Ethiopian wolves (Chapter 3, Fig. 3.1; Table 4.1). Study sites within regions were areas naturally divided by landscape features or cultivated land. Study sites represent the extent of the wolf range in each region with the exception of South Wollo where surveys were restricted to the Kewa range on the eastern side of the massif. Somkeru-Korduro is a little explored wolf population west of the main Bale massif. For each study site an elevational range was defined by an upper altitudinal limit (i.e. the highest ground in the study site) and a lower limit, which in most cases was imposed by the limit of agriculture, rarely by escarpments or the natural limit of forests (in Arsi and Somkero-Korduro). The latitudinal location is the geographical centre of the study site.

Region	Sudy sites	Scats	Latitude (UTM)	Altitudinal range (m ASL)	
Northern Highlands					
Simien		*40*			
	Geech plateau	11	8110000	3,700-4,000	high
	Bwahit	12	8060000	3,700-4,300	high
	Ras Dejen	9	8060000	3,800-4,400	high
	Silki	8	8180000	3,800-4,200	high
North Wollo		*51*			
	Aboi Gara	8	7110000	3,550-3,700	low and narrow
	Abuna Josef	11	7160000	3,650-4,100	high
	Delanta	32	6900000	3,600-3,750	low and narrow
South Wollo		*13*			
	Kewa	13	6250000	3,700-4,100	high
Southern Highlands					
Arsi		*39*			
	Galama	29	3560000	3,300-4,100	broad
	Chilalo	9	3700000	3,400-4,150	broad
Bale		*18*			
	Somkeru-Korduro	18	2860000	3,450-3,650	low and narrow

Table 4.1 Study areas and scat sample sizes.

4.3 Methods

4.3.1 Scat collection

Scats were collected in visits to Afroalpine ranges during surveys organized by the Ethiopian Wolf Conservation Programme between February 1998 and February 1999 (Chapter 3). Scats were found along survey routes; each route covered all suitable wolf range in a given study site and was searched only once (diminishing the likelihood that any two samples emanated from the same individual). Areas close to human habitation were avoided to reduce the risk of confusion with domestic dog scats. Genetic analysis using DNA remains in scats confirmed the wolf provenance of the scats (Chapter 5).

4.3.2 Identification of prey remains

Skeletal remains, mainly teeth and jaws, and hair from prey species were identified from macro and microscopic examination to the level of species, with the exception of *Lophuromys* and *Arvicanthis* species. These however were safely assumed to be *L.*

flavopunctuatus and *A. abyssinicus*, as the other known highland species in each genus are restricted to Bale (namely *L. melanonyx* and *A. blicki*). Prey items designated as 'medium size mammals' were identified from large bones inadequate for species identification. Prey remains in the scats were compared to a reference collection of hair, bones, and teeth from species of potential prey including livestock (horse, cattle or sheep/goat categories). The techniques and parameters used for identifications, with an assessment of methods, are presented in Appendix I (pp 76-82).

4.3.3 Diet composition

Diet composition was analyzed in terms of prey species and of ecological categories, defined by weight or activity as:

- **'molerats'**: Rhizomyinae subfamily; common molerats, average weight 200g and giant molerats, 600g.
- **'rats'**: Murinae subfamily; less than 130g; subdivided between:
  'diurnal' rats (absolute or predominantly): *Avicanthis* spp, *Lophuromys* spp, *O. typus,* and,
  'nocturnal' rats: the remaining Murinae rats.

The contribution of each prey item or category was measured as its relative frequency of occurrence in each region or study site. This was calculated as the total number of occurrences of a particular prey item divided by all the occurrences, expressed as percentages (Lockie 1959; Reynolds & Aebischer 1991). Being a robust, and frequently used, method (Jacobsen & Hansen 1996), the relative frequency of occurrences (RFO) was considered an appropriate measure whereby to quantify dietary changes (it was common to find more than one type of prey per scat). The standardized Levin's niche breath (applied to frequency of occurrences) was used to quantify trophic diversity (Krebs 1999) and the Kruskal-Wallis test was used to evaluate differences in the median number of prey items per scat.

4.3.4 Dietary patterns and geographical analysis

Between-regions differences in the relative contribution of prey items were tested using contingency tables and Chi-square tests (MINITAB release 13.31). Tables were constructed with the number of occurrences of all prey items, and with the occurrence of a single prey item against all other occurrences grouped together when overall significant differences were observed. The test could not be applied to some comparisons involving prey items at relatively low frequencies (the test requires no more than 20% of the cells with expected frequencies less than five (Zar 1984).

Spearman rank correlations were calculated between geographical parameters (latitude and altitude) and the contribution of each prey type per study site. Study sites rather than regions were used to explore correlations to account for local variations in prey frequencies and because study sites differed markedly in their altitudinal range within some regions (Table 4.1).

Using all scats, a Principal Component Analysis (PCA) from presence/absence data of each prey species was performed to explore whether the ordination-derived gradients co-varied with changes in altitude or latitude (by calculating their correlation with the PCA loading factors). A Mantel test (Liedloff 1999 Mantel Non-Parametric Test Calculator version 2 1999) checked for associations between sites with respect to dietary differences (i.e. Euclidean distances, Krebs 1998) and their physical proximity (latitudinal distances). Finally, broader-scale dietary patterns were explored on a second PCA with occurrence data by prey category that included all regions in this study as well as Bale and Menz. This analysis is only indicative because at least 20 samples for each site would be required for robust results (Tabachnick & Fidell 1989).

4.4 Results

4.4.1 Diet composition

Rodents of the sub-family Murinae (Family Muridae) dominated the diet of Ethiopian wolves in all five study areas. Together they accounted for 96% of all prey occurrences in the scats, and diurnal species were the commonest (‘totals’ per species in Table 4.2). Overall, *Otomys typus* contributed the largest proportion of the occurrences, followed by *Arvicanthis abyssinicus* and, at lower frequencies, by common molerats and *Lophuromys flavopunctatus*. The nocturnal species each contributed relatively small proportions, including narrow-headed rats *Stenocephalemys albocaudata* and *S. griseicauda*, the rat *Praomys albipes,* and the mouse *Dendromus lovati*. Other prey types were rare. Remains of medium-size mammals, most probably from Starck's hares (*Lepus starcki*) or rock hyraxes (*Procavia capensis capillosa*), were found in four scats from the Southern Highlands (Arsi and Somkero-Korduro); and a mongoose skull (*Herpestes sp.*) was found in one scat from

Simien. Livestock remains were only found in four scats from the Northern Highlands (two were hooves of an infant sheep or goat, and two others were sheep wool). Tufts of reddish unidentified hairs found in two wolf scats from the Geech Plateau in Simien may be from gelada baboons *Theropithecus gelada*, which are common in the area (reported previously in wolf scats for Menz, Ashefani 2001). Insect remains were found in one scat.

a) Diet composition by region

Prey items	Totals	S-Korduro			Arsi			South Wollo			North Wollo			Simien		
	RFO	N	RFO	*r*	N	RFO	*r*	N	RFO	*r*	N	RFO	*r*	N	RFO	*r*
T.splendens	**9%**	6	**16%**	*2*	10	**15%**	*3*				4	**4%**	*6*	8	**9%**	*3.5*
O. typus	**45%**	17	**45%**	*1*	30	**46%**	*1*	11	**46%**	*1*	44	**50%**	*1*	36	**40%**	*1*
Arvicanthis spp	**18%**	4	**11%**	*4*	11	**17%**	*2*	8	**33%**	*2*	15	**17%**	*2*	17	**19%**	*2*
Lophuromys spp	**6%**	5	**13%**	*3*	4	**6%**	*4*	1	**4%**	*5*	8	**9%**	*3.5*	1	**1%**	*9*
S.albocaudata	**5%**	1	**3%**	*6.5*	2	**3%**	*7*	2	**8%**	*3*	7	**8%**	*5*	2	**2%**	*7.5*
S. griseicauda	**4%**	2	**5%**	*5.5*	3	**5%**	*5*							7	**8%**	*5.5*
D.lovati	**3%**				2	**3%**	*7*	1	**4%**	*5*				7	**8%**	*5.5*
P. albipes	**5%**										8	**9%**	*3.5*	8	**9%**	*3.5*
medium-size mammals	**2%**	2	**5%**	*5.5*	2	**3%**	*7*							1	**1%**	*9*
livestock	**1%**							1	**4%**	*5*				1	**1%**	*9*
others	**1%**	1	**3%**	*6.5*	1	**1%**	*9*				2	**2%**	*7.5*	2	**2%**	*7*
all occurrences	303	38			65			24			88			90		
ratio molerats/rats			0.21			0.19			0			0.05			0.10	
number of prey types			8			9			6			7			11	
Levin's niche breadth			0.28			0.26			0.20			0.23			0.34	

b) Diet composition by study site within regions

Prey items	Arsi		North Wollo			Simien			
	Galama	Chilalo	Aboi Gara	A.Josef	Delanta	Geech	Bwahit	R.Dejen	Silki
T. splendens	15%	17%			8%	4%	21%	5%	
O. typus	44%	53%	40%	36%	59%	36%	37%	42%	47%
Arvicanthis spp	19%	12%	27%	23%	12%	11%	20%	21%	27%
Lophuromys spp	4%	12%		14%	10%		3%		
S.albocaudata	2%	6%	27%	14%		4%	3%		
S. griseicauda	6%					11%	7%	11%	
D.lovati	4%					18%		11%	
P. albipes			7%	9%	10%	11%		11%	20%
medium-size mammals	4%						3%		
livestock				5%	2%				7%
others	2%					7%			
all occurrences	48	17	15	22	51	15	28	19	28
ratio molerats/rats	0.18	0.21	0	0	0.09	0.04	0.31	0.06	0
number of prey types	9	5	4	6	6	8	7	6	4
Levin's niche breadth	0.29	0.19	0.23	0.33	0.16	0.40	0.34	0.29	0.20

Table 4.2 Composition and diversity of the diet of wolves in five populations (a) and in subpopulations for the regions with more than one study area (b). N = number of prey occurrences in scats; RFO = relative frequency of occurrence; r = rank by RFO.

Figure 4.1 illustrates the composition of wolf diets by region (RFO values in Table 4.2). With a contribution of between 55% and 79% of the occurrences per region, *O. typus* and *A. abyssinicus* combined dominated the diet in all populations. *O. typus* always ranked first with between 40% and 50% RFO. With the exception of Somkero-Korduro, *A. abyssinicus* was the second commonest prey with a contribution ranging between 17% and 33 % RFO. When the contribution of the other diurnal rodents was added (*L. flavopunctuatus* and *T. splendens)*, diurnal rodents together reached 70% to 85% RFO.

While *O. typus* and *A. abyssinicus* showed consistent contributions (Chi-square 1.875, df 4, P=0.745 and Chi-square 5.369, df 4, P=0.258 respectively), common molerats and *Lophuromys spp.* varied significantly between regions (Chi-square 9.694, df 4, P=0.046 and Chi-square 8.541, df 4, P=0.080 respectively). The common molerat was the second commonest prey in Somkero-Korduro (16% RFO), third in Arsi and Simien, but rare or absent in the Wollo populations. *L. flavopunctuatus* ranked highest in Somkeru-Korduro and South Wollo. The remaining prey included nocturnal rats, medium-sized mammals and livestock, presenting variable contributions totalling 15% to 30% of the prey occurrences across regions (Fig. 4.1).

Species of nocturnal rats were each present at frequencies lower than 10% but combined reached a maximum of 27% in the diet of wolves in Simien. *S. albocaudata* was the only nocturnal rat that occurred in all diets regions, and *P. albipes* the most restricted (only found in scats from North Wollo and Simien). Medium-sized mammals (in samples from the Southern highlands) and livestock (in samples from the Northern highlands) combined accounted for only 2% to 8% of the prey occurrences.

The degree of dietary variation among study sites was explored for the regions of Arsi, North and South Wollo (Table 4.2b). The contribution of the two main prey items (*O. typus* and *A. abyssinicus*) was not significantly different among study sites within regions, but there were differences in the contribution of molerats (Table 2b). Molerat remains were frequent in scats from Bwahit but rare or absent elsewhere in Simien; and in North Wollo molerat appeared only in scats from Delanta.

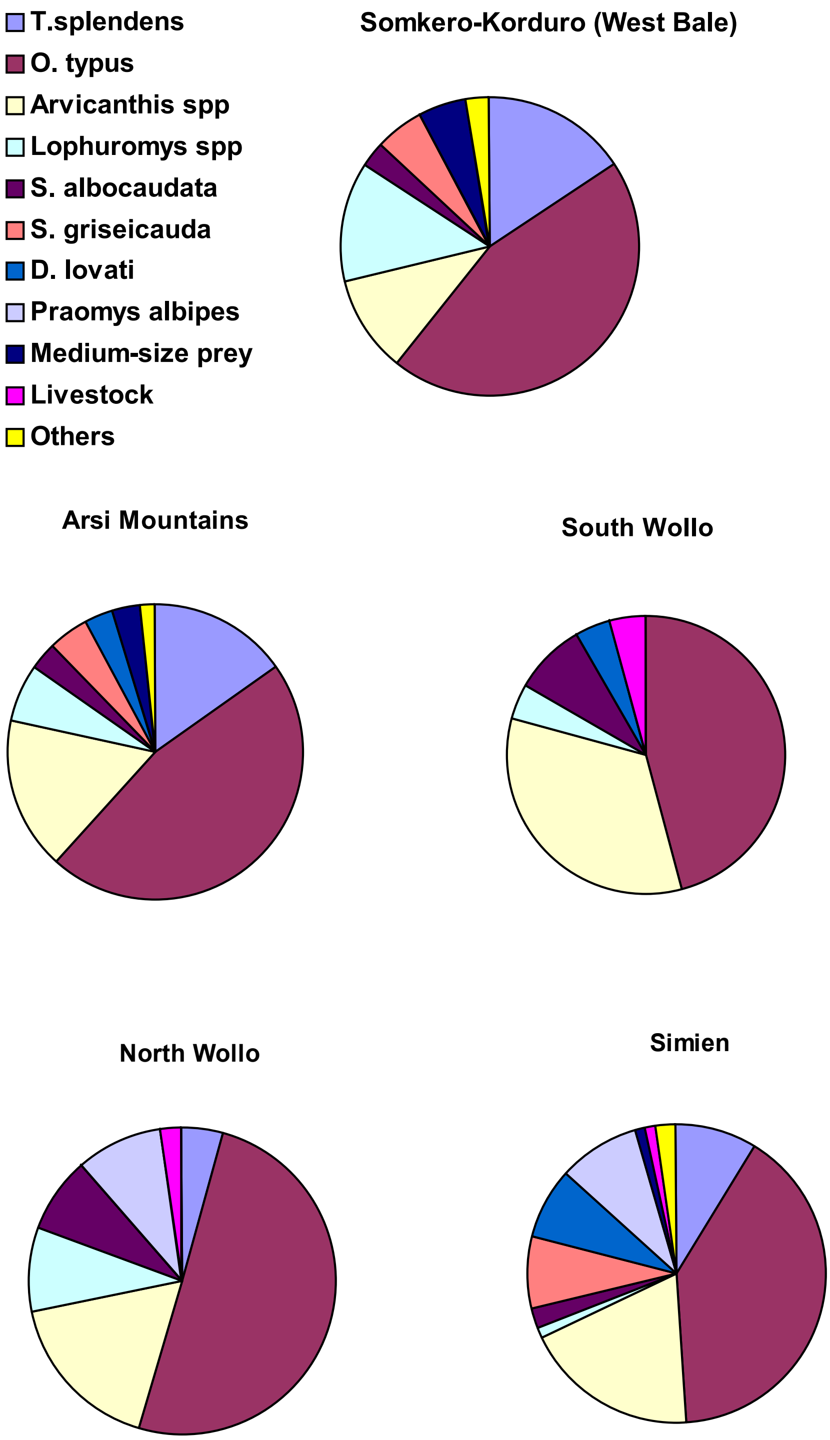

Figure 4.1 Pie charts of prey's relative frequency of occurrence (RPO) per region.

4.4.2 Patterns of dietary change

An ordination of all samples explained 33% of the observed variation in prey presence/absence data. The first and second axis correlated positively with *O.typus* and negatively with *A. abyssinicus,* and because the two axes changed in opposite directions with regards to altitude and latitude, their contributions to the diets did not appear associated to geographical patterns. Differences in the consumption of common molerats and *Lophuromys* spp were inversely proportional to predation on species of nocturnal rats (Table 4.3). Correlations with the PCA loading factors indicated increasing consumption of common molerats and decreasing predation upon nocturnal species from North to South, and across populations with decreasing lower and higher altitudinal limits (i.e. with more habitat at low altitude). Opposite geographical trends reflected decreasing consumption of *Lophuromys* spp. and increasing consumption of *S. griseicauda*.

	PCA 1	PCA 2
T.splendens	0.28	-0.26
O. typus	0.44	0.29
A.abyssinicus	-0.52	-0.33
L.flavopunctuatus	0.09	-0.68
S. albocaudata	-0.30	-0.06
S.griseicauda	-0.21	0.50
D. lovati	-0.42	0.15
P.albipes	-0.37	0.03
Eigenvalues	1.484	1.161
Variance explained	18.6%	14.5%
Lower altitudinal limit	-0.19**	0.14*
Higher altitudinal limit	-0.15*	0.13*
Latitude	-0.22*	0.15*

Table 4.3 Correlations between prey items and the PCA loading factors, and between the loading factors and geographical variables (altitude and latitude). In two shades of grey are highlighted the strongest positive and negative correlations.

The null hypothesis of no association between an index of diet similarity and the physical proximity (latitudinal distance) between study sites could not be rejected (Mantel test: r= -0.06, g=-0.3118 < critical value for P<0.05). Study-site level correlations showed that the contribution of the diurnal *Lophuromys spp.* was negatively associated with latitude (r=-0.60, P=0.052); the frequency of the nocturnal *P. albipes* was positively correlated with latitude and with the lower altitudinal limit of the study sites (r=0.67, P=0.023 and r=0.64 P=0.033 respectively); and the combined contribution of nocturnal rats increased northwards (r= 0.61, P= 0.045). The contribution of molerats increased southwards and across sites with lower altitudinal limits, but correlations were only significant at P<0.1 (r=-0.53, P=0.093; r=-0.53, P=0.090 respectively).

Across populations and prey categories, instead of species, (Table 4.4), significant differences emerged when the relative contributions of molerats, nocturnal and diurnal rats were contrasted (Chi-square 8.541, df 8, P=0.006). Differences in the relative contribution of molerats and rats fell just short of significance (Chi-square 8.882, df 4, P=0.064) but the ratio of molerat to rat frequencies in the southern populations (e.g. Arsi and Somkeru-Korduro) was double that in Simien (Table 4.2). Singly the relative contribution of nocturnal rats differed between regions (Chi-square 12.8, df 4, P=0.012), but not that of diurnal rats (Chi-square 8.127, df 4, P=0.087).

	Southern Highlands				**Central H.**	**Northern Highlands**		
	S-K	Bale	*Gaysay*	Arsi	Menz	S.Wollo	N.Wollo	Simien
Molerats	**16%**	**36%**	***47%***	**15%**	**17%**	**0**	**5%**	**9%**
Rat-size rodents	**76%**	**59%**	***53%***	**76%**	**72%**	**96%**	**93%**	**87%**
Diurnal	68%	59%	*47%*	69%	70%	83%	76%	60%
Nocturnal	8%	1%	*5%*	11%	2%	13%	17%	27%
Large	63%	59%	*47%*	71%	48%	88%	75%	69%
Small	13%		*5%*	9%	23%	8%	18%	18%
Others	**8%**	**4%**	***pres.***	**5%**	**12%**	**4%**	**2%**	**4%**
All occurrences	38	689	*(19)*	65	637	24	88	90

Table 4.4 Composition of wolf diets by prey ecological group in all but one extant population, arranged from south to north. In grey the results from previous studies (Sillero-Zubiri & Gottelli 1995a, Malcolm 1997; Ashenafi 2001). Values are relative frequencies of occurrence. *The results from Gaysay are not directly comparable (i.e. they represent a pool of scats collected near a den; medium size prey not considered in frequency calculations).

4.4.3 Broad-scale pattern

Major dietary patterns are summarized in the PCA of prey ecological categories, using RFO data (Fig. 4.2). This comparison included the five regions in this study plus Bale and Menz. Regions were arranged along a gradient from diets with relative high proportions of molerats to others with high predation on rats, both diurnal and nocturnal (Table 4.4). PCA 1 clearly separated Bale from all other regions reflecting the dominance of giant molerats in the diet (Fig. 4.4; Table 4.5). The other populations in the Southern Highlands and Menz in the Central Highlands were grouped in an intermediate position, with common molerats as a relatively important component of the diet. The diets of the northern populations were dominated by rats, in turn organized along a second axis of dietary change showing varying contributions of diurnal and nocturnal rats (the latter highest in the northernmost population of Simien).

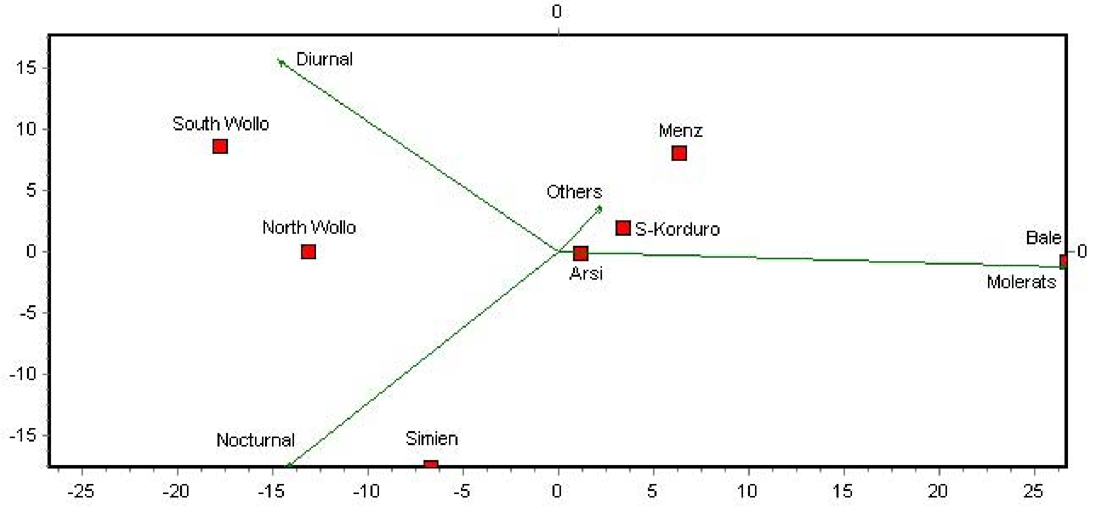

Figure 4.2 PCA bi-plot showing the location of seven wolf populations in relation to prey species' eigenvectors and PC1 and PC2 axes.

Prey items	PCA 1	PCA 2
Molerats	0.79	-0.05
Diurnal rats	-0.43	0.65
Nocturnal rats	-0.42	-0.74
Others	0.07	0.15
Eigenvalue	1300	453
Explained variance	71.5%	24.9%

Table 4.5 Correlations between prey categories and PCA loading factors, including all Afroalpine regions in this and previous studies (n=7). For each axis, the strongest correlations with opposite signs are highlighted in two shades of grey.

4.4 Discussion

This study confirmed that Ethiopian wolves are specialist predators of diurnal Muridae rodents across their range of distribution. Remains of diurnal rodents accounted for between 60% and 83% of the prey occurrences in scats across five newly studied populations. Giant molerats, the main prey of wolves in Bale (Sillero-Zubiri & Gottelli 1995a), were not detected in the sample, confirming that this species is confined to the main Bale massif in the Southern Highlands. Although it has been proposed that common molerats would replace its larger relative elsewhere, wolves in the study populations preyed mainly upon rat-sized Murinae species. The swamp rat O. *typus* was the most frequent prey, followed by the grass rat *A. abyssinicus*, and common molerats

T. splendens or *L. flavopunctatus* at lower frequencies. The finding of *O. typus* as the main alternative prey outside Bale and Menz is unexpected, because this species contributed little to the diet of wolves in these populations. The substantial contribution of nocturnal rats in the Simien Mountains (26% of the prey occurrences) also contrasted with the rarity of predation upon nocturnal species in Bale and Menz (0.8% to 1.7% of prey occurrences in scats respectively). *Praomys albipes*, which accounted for 20% of the prey occurrences in Silki, Simien, had not been recorded as a wolf prey item before, and the mouse *Drendomus lovati* (Dendromurinae) was found only once in a scat from Gaysay, Bale (Malcolm 1997).

Remains of larger prey, including livestock, were rarely found in the samples. The prediction of higher livestock consumption in mountains with high human and livestock densities, and where rodent biomass is presumably low, was therefore not supported. Negative feelings of local people towards the wolves for taking livestock (Chapter 3) may therefore be unjustified in most areas, but where people did recognize Ethiopian wolves as a predator of livestock (North Wollo) this was supported by findings of livestock remains in scats. It should be noted that direct observations of wolves foraging in Bale indicated a higher incidence of large sized prey than that shown by scats (Sillero-Zubiri 1994). In Bale carrion, hares, hyraxes, and birds contributed 36% of the total prey weight, of which 12% was scavenged. Still livestock remains in droppings from the study areas were sufficiently rare to suggest they were taken very infrequently.

While highly specialized, Ethiopian wolves preyed differentially upon a range of potential preys in the different populations. A large-scale pattern of change in the consumption of molerats (Rhizomyinae) versus rats (mostly Murinae) was detected, particularly after including Bale in the comparison. Bale in the Southern Highlands was unique in that the giant molerat is a main component of the diet; the common molerat was relatively important in the other Southern populations and in the Central Highlands; and diets dominated by rats were characteristic of the Northern Highlands, including nocturnal species in the northernmost population of Simien. This pattern of dietary change fitted the model of latitudinal variations, with molerats as an important prey in the more productive Southern and Central Highlands, and Murinae rats in the less productive Northern Highlands.

Among the five newly studied populations, dietary variations were subtler. *O. typus* and *A. abyssinicus* dominated the diets with consistent contributions. In accordance with its constant representation, the grass rat *A. abyssinicus* is widespread, can be abundant in drier localities and short grasslands, and is tolerant of grazing (Ashenafi 2001). On the other hand, little is known about the ecology of *O. typus*. The species was well represented in the diet of wolves in Bale and Menz but it was trapped at low frequencies there; this study would indicate a widespread distribution. The remaining portion of the diet was the more variable. Increasing predation upon common molerats and *Lophuromys spp*., and decreasing predation upon nocturnal rodents, occurred southwards and across areas at lower altitude. In the North, consumption of molerats was overall low but molerats appeared to be abundant in some localities (i.e. Bwahit in Simien, and Delanta in North Wollo). The predominance of molerats in the more productive areas coincides with their preference for tall grasslands in humid localities at relatively low altitudes (e.g. Menz and Gaysay in Bale) (Sillero-Zubiri & Gottelli 1995a; Malcolm 1997; Ashenafi 2001). Field surveys also indicated that common molerats in the Northern Highlands are overall rare, although favourable conditions occurred in localized areas (Marino *et al.*1999). Lower consumption of *L. flavopunctatus* towards the North can be explained by their lower abundances, because the species is negatively affected by grazing and predominates in the low lying ericaceous moorlands (Sillero-Zubiri & Gottelli 1995a; Ashenafi 2001). Lack of ecological information makes it difficult to interpret the pattern of predation upon nocturnal species. Not all species are particularly common in high-altitude habitats, and the increasing consumption of *P. albipes* at higher altitudes would contradict findings of the species being common in or near forested areas (although there records of the species above 3,700m in Simien - Yalden & Largen 1992) .

In summary, the wolf diet appears to reflect prey availability, but wolves may also be selective in what they eat. An ‘optimal’ diet will reflect preference for the highest-ranking prey in terms of profitability, and exclusion or partial preference for lower-ranking prey (Krebs & McCleery 1984), while shifts towards alternative prey will most likely imply declines in the availability of the preferred prey (Stephens & Krebs 1986). In Bale and Menz the representation of molerats in the diet is higher than expected from their density when compared with that of the Murinae rats, and Sillero-Zubiri (1994) found that wolves preferred giant molerats above other rodents offered in a cafeteria experiment; *Arvicanthis spp*. above *Lophuromys* spp.; and actively rejected the nocturnal S*tenocephalemys* species. Despite our lack of knowledge on prey availability in the study areas, the composition of the diet approached expectations based on an optimal diet: where giant molerats were absent, common molerats were an important food item, unless they were uncommon, and then wolves preyed more heavily upon less preferred Murinae species, including nocturnal species. Consideration of the distribution and availability of food resources is crucial for the conservation of wolf populations, particularly those in the poorer Northern highlands. Conserving the prey resources in pockets of high prey productivity, such as Delanta and Bwahit, may ensure the survival of more wolves and improve the chances of the long-term persistence of populations.

APPENDIX I

Assessment of methods of scat analysis for the study of Ethiopian wolf diet

Remains of prey items found in carnivore faeces can be identified from macro- and microscopic examination to the level of Family or better (Day 1966); such methods are generally accepted to accurately represent the components of the animal's diet (Putman 1984). Prey remains in 161 scats of Ethiopian wolves, collected from five populations scattered across the range of wolf distribution (including Somkero-Korduro, Arsi, North and South Wollo, and Simien) were analysed. In order to evaluate the reliability of different approaches to diet analysis, findings based on identifications from hard skeletal remains (bones and teeth) only, hairs only, or both were compared.

Droppings were oven dried and hair and bone were removed from the fecal matrix. Samples were kept in store in sealed labelled plastic bags until analysis took place. All samples were autoclaved to ensure there were no health risks involved and the identification of prey items was conducted using a fume hood, gloves and facemask.

Prey remains were compared with a reference collection from the Dinsho Museum in the Bale Mountains National Park (Table A.1). All samples were analysed by one person to avoid inconsistencies between observers; an experienced mammalogist verified correct identification on a subset of samples. Identifications were conducted twice, independently, using prey remains and hairs respectively.

Prey species	Reference material
Tachyoryctes macrocephalus	Hair
T. splendens	Hair & skull
Otomys typus	Hair & skull
Arvicanthis blicki	Hair & skull
Lophuromys flavopunctatus	Hair & skull
L. melanonyx	Hair & skull
Stenocephalemys albocaudata	Hair & skull
S. griseicauda	Hair & skull
Dendromus lovati	Hair & skull
Crocidura fumosa	Hair & skull
C. baileyi	Hair
Praomys albipes	Skull
Lepus stacrki	Hair
Horse, sheep, goat & cattle	Hair

Table A.1 Reference material available for the analysis of prey remains.

The examination of hairs, teeth and bones was successful in identifying prey items to the level of species, with the exception of species in the genus *Lophuromys* and *Arvicanthis*. Hard remains were examined by eye and under a binocular microscope and compared with teeth and jawbones from the skull reference collection. Useful hard parts for rodent identifications were large incisors, teeth and parts of the upper and lower jaws of rodents. Large bones, teeth and hooves were useful to identify larger prey.

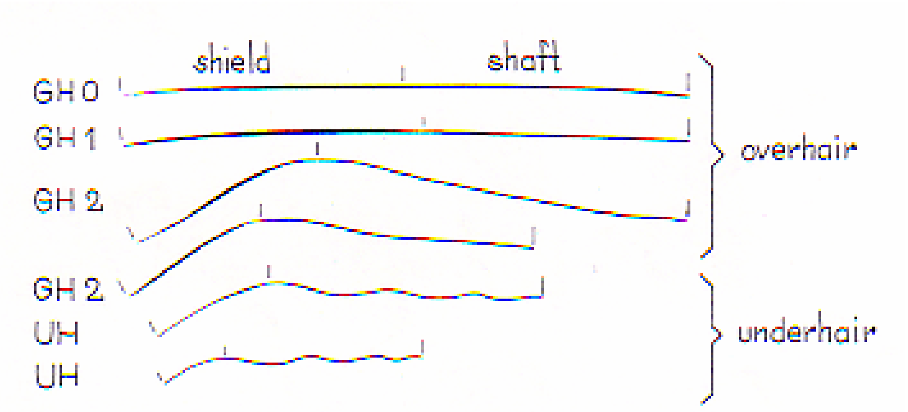

Figure A.1 Types of hair and shield and shaft portions (the tip of the hair points to the left).

Hairs differed in macroscopic characteristics such as size, shape and pigmentation, but microscopic examination of the cuticule of over hairs was necessary for a definite identification (Fig. A.1). Standard procedures were applied to identify cuticular patterns from gelatine casts (Day 1966; Teerink 1991; Sillero-Zubiri & Gottelli 1995a). A solution of gelatine was made up using 1 teaspoon of gelatine crystals to 20ml of hot water. A small amount of the solution was poured on to a microscope slide and spread around to create a thin layer of gelatine. Guard hairs (as described by Teerink 1991) were selected and laid in the same orientation on to the slide. When a film of solid gelatine formed, as the water evaporated, the hairs were carefully lifted leaving casts on the gelatine film. A reference set of casts was prepared using the reference collection. One or two slides were created for each scat, using between 10 and 20 hairs per slide. Those include at least three hairs from "tuft' or group of hairs, to ensure adequate print and the inclusion of all prey items in the sample. The casts were examined under 10x and 40x objectives of a compound microscope.

The most useful parameters for species identification were scale patterns in the shaft region of the hair (Fig. A 2 - following Teerink 1991), although in some cases the description of the shield assisted with identifications. An identification key (Table A2) was created on the bases of diagnostic parameters easy to observe (unless otherwise stated, the characters used refer to scale patterns in the shaft region). This key can be of much utility for future trophic studies in Ethiopia's Afroalpine ecosystems.

1 a)	Longitudinal petal pattern	**2**
b)	Intermediate petal pattern	**4**
2 a)	Very elongate petals with streaked regular wave in the shield	*Lepus stacrki*
b)	Narrow diamond petal pattern	**3**
3 a)	Two or more scales wide	*Otomys typus*
b)	One scale wide	*Crocidura fumosa*
4 a)	Broad diamond petal pattern	**5**
b)	Mosaic pattern	**8**
5 a)	Two or more scales wide	**6**
b)	One scale wide with an irregular, rippled wave in the shield	*Dendromus lovati*
6 a)	Clear diamond petals intermediate in length with a smooth regular wave in the shield	*Arvicanthis spp.*
b)	Elongate diamond petals with a less regular arrangement and a rippled irregular wave in the shield	**7**
7 a)	Regular arrangement, rippled wave in the shield	*Stenocephalemys albocaudata*
b)	Very irregular arrangement, smooth wave in the shield	*Stenocephalemys griseicauda*
8 a)	Two or more scales wide with a smooth regular wave in the shield	*Lophuromys spp.*
b)	One scale wide with irregular, rippled wave in the shield	*Tachyoryctes splendens*

Table A.2 Identification key from hair remains.

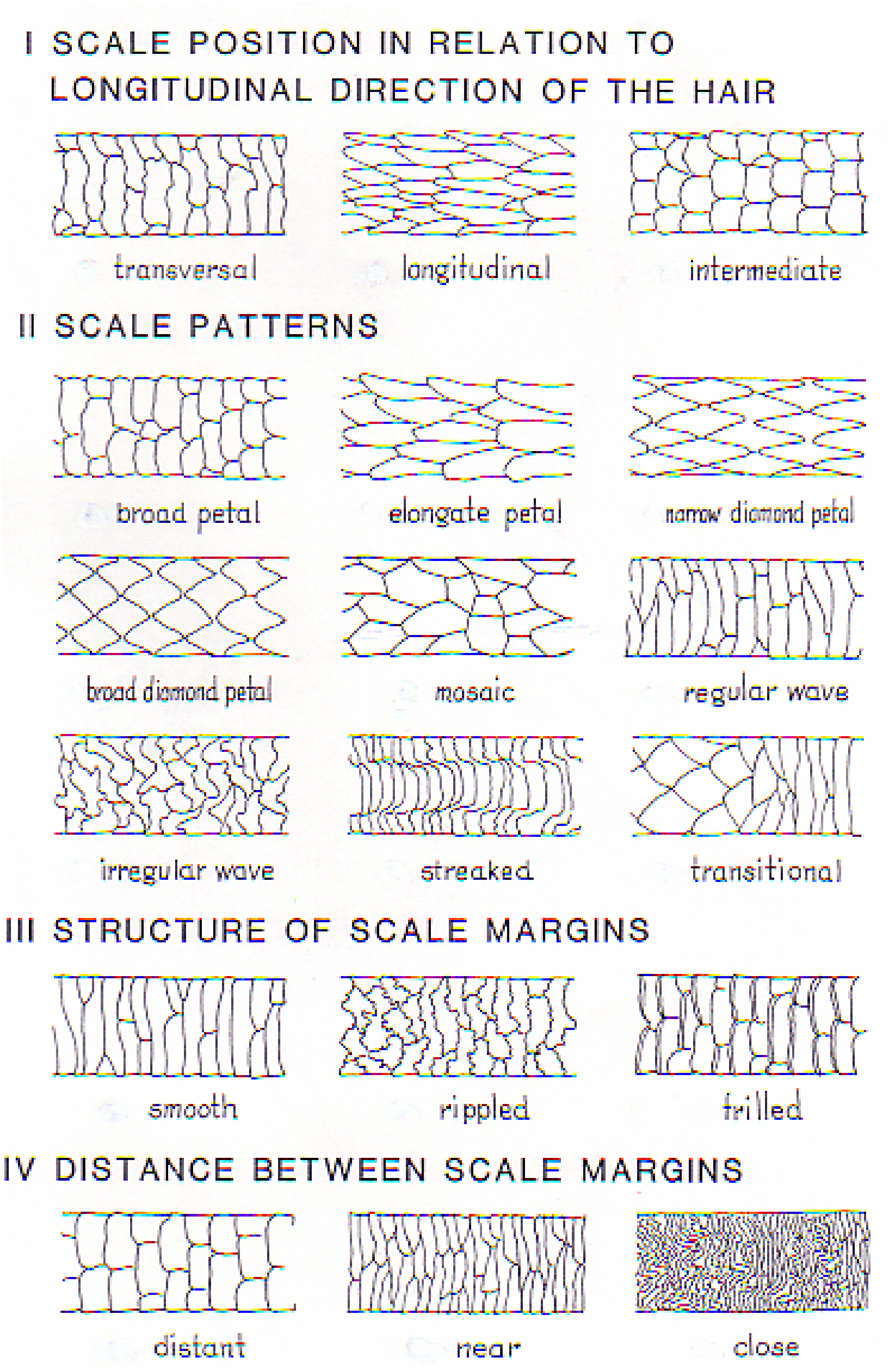

Figure A.2 Cuticular patterns used for hair identification (the tip of the hair points to the left) (from Teerink 1991).

Table A.3 shows occurrences of each species discriminating between those in which the prey was identified from hard remains only (mainly teeth), hairs only, or both. The

Mcnemar change test (Seigel & Castellan 1988) can be used to compare the effectiveness of the two methods by comparing the instances in which a species was identified by one method and not the other, with each sample as its own control. To yield accurate results the test requires at least 10 cases changing categories across the two variables. This requirement was only nearly fulfilled for the two commonest species *O. typus* and *Arvicanthis* spp. For these, the null hypothesis of no difference in the likelihood of a prey item being detected by hairs or hard remains was rejected (Chi-square 50.95, df 1, P=0.000 and Chi-square 81.478, df 1, P=0.000).

	Teeth only	Hair only	Both	All occurrences
T.splendens	8	4	15	27
O. typus	4	23	111	138
Arvicanthis spp	7	12	36	55
Lophuromys spp	6	7	6	19
S. albocaudata	6	7	2	15
S. griseicauda	4	6	2	12
D. lovati	1	3	6	10

Table A.3. Number of samples with one type or both types of prey remains.

Total occurrences for any given species therefore differed when one or both methods were used to identify remains. If each method detects a proportional number of occurrences, however, the resulting frequencies of occurrence may be similar. Fig. A.3 shows the results of diet composition analysis expressed as relative frequency of occurrence of each prey item (i.e. number of occurrences of a given prey divided by all occurrences) from identification using hairs only, teeth only or both. No significant differences were found between the three (Chi-square 4.469, df 12, P=0.973). This result showed that in spite of the different likelihood of identifying a prey in scats from skeletal remains or hairs, the relative contribution of prey species to the diet was consistent between methods.

For practical reasons, using hard remains or hairs for faecal analysis of the Ethiopian wolf diet will be equally effective, and examining bones is less time consuming. By using both, however, statistical analysis will be facilitated by larger samples sizes, as the total number of occurrences is higher when teeth and hairs are analysed (n=276) in comparison with hairs only (n=240) or teeth only (n=214). This may become a problem for the comparative analysis of differences in diet composition among the regions where scats were collected.

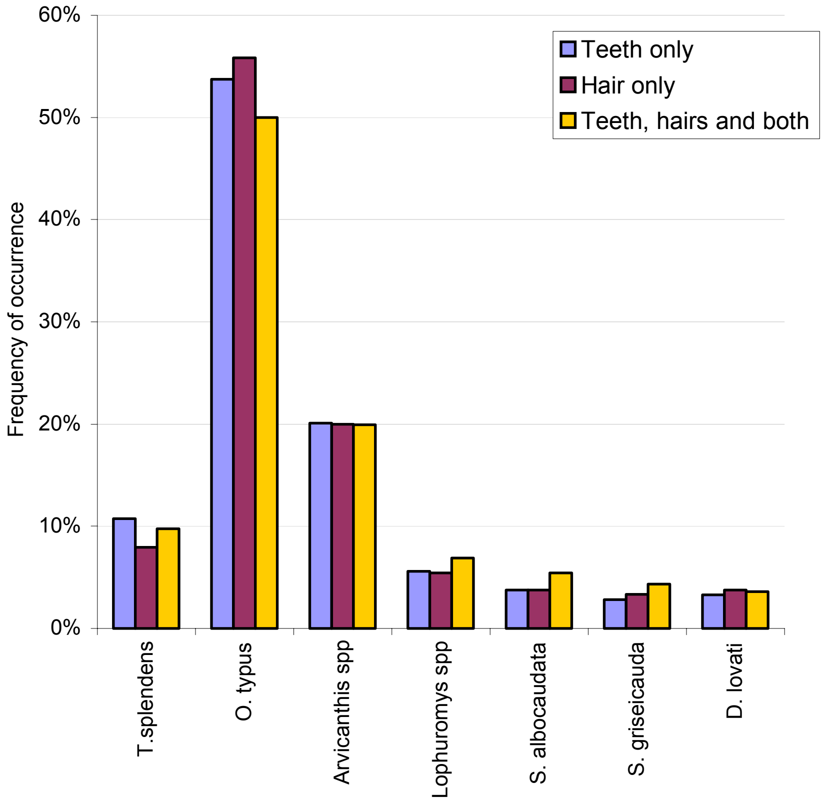

Figure A.3 Diet composition from frequency of occurrence of each rodent prey using three methods of identification: hairs only, hard prey remains only (mainly teeth), or both.

Limitations to faecal analysis have been pointed out by several authors (Lockie 1959; Reynolds & Aebischer 1991). In the case of the Ethiopian wolf, the merits of the method have been supported by previous studies that combined faecal analysis, behavioural observations and estimates of prey availability and seasonal variations (Sillero-Zubiri & Gottelli 1995a; Ashenafi 2001). A consideration to take into account, however, is that the consumption of larger prey is under-represented in wolf scats when compared with hunting rates and carrion feeding from direct observations.

CHAPTER V

Afroalpine biogeography underlies the evolution and genetic structure of Ethiopian wolves*

*This chapter is the result of a collaboration with Dada Gottelli and Stephan Funk at the Institute of Zoology, Zoological Society of London.

Abstract

During the last glacial age Afroalpine habitats were widespread across the highlands of Ethiopia. A wolf-like ancestor is thought to have colonized the expanding habitat and gave rise to a new species well adapted to life in high altitude environments: the Ethiopian wolf *Canis simensis*. Based on the phylogeography of the mitochondrial DNA sequence, this study aims to test this theory, addressing the timing of genetic divergence, and exploring genetic history and structure as affected by the climatic changes of the last glacial-interglacial period. Very low levels of genetic variation were detected, but the variability observed today still appeared to be a relict of an ancient larger population. Nested Clade Analysis suggests an initial population expansion probably immediately after coalescence, at around 100,000 years ago, when vast Afroalpine areas provided opportunity for dispersion. The partition of haplotypes that followed was most likely the result of habitat reduction and fragmentation at the onset of the deglaciation approximately 15,000 years ago. The distribution of haplotypes indicates random fixation in isolated populations. There is a degree of clustering of haplotypes from either side of the Rift Valley, but the lack of reciprocal monophyly does not support the taxonomic classification of two subspecies. Phylogenetic and geographic associations tested by AMOVA shows that the most likely genetic partitioning corresponds to three mountain groups, Arsi/Bale, Wollo/Shoa, and Simien/Mt.Guna. This study stresses the importance of northern populations for the maintenance of genetic variability and its implications for conservation.

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5.1 Introduction

Major ice ages dominated the last 700,000 years of global history, with 100,000 year old cycles interrupted by relatively warm interglacials. Much is known about the last glacial cycle spanning ~135,000 years and particularly the progression from full ice conditions 20,000 years before present (BP) to the present warm period (Hewitt 1996). These severe climatic oscillations of the late Pleistocene are believed to have shaped the distribution patterns of many species (Hewitt 2000) and climatic cycles have been identified as an important mechanism for speciation (Roy 1997). It is believed that during the last glaciation (70,000-10,000 years BP) tropical mountain blocks supported environments with greater continuity through climatic shifts, which would provide more opportunity for newly formed species to persist (Fjeldsa & Lovett 1997). Indeed, these mountain areas, including the highlands of East Africa, show a dominance of recently radiated or new species (Roy 1997).

The moorlands and Afroalpine zones of East Africa were geographically much more extensive during the last glacial interval (10,000-70,000 years ago), when the African tropics were generally cooler and drier than today (Yalden 1983; Bonnefille *et al.* 1990; Kingdon 1990). In these newly extended mountain habitats, highland-adapted vertebrate species increased their ranges following the expansion of suitable habitat into lower altitudes (Hewitt 2000). Ethiopia in particular is notable for the extent of its high ground, encompassing nearly 80% of all land above 3,000m in the Afrotropical region (Yalden 1983). Until as recently as 10,000 years ago, the highlands of Ethiopia were widely covered with Afroalpine heathland and grassland (Messerli *et al.* 1977); high-altitude adapted species flourished in this vast mountain massif with high levels of endemism (Kingdon 1990).

These habitats generally lack the herds of large ungulates characteristic of the African plains, but smaller mammals are present in great abundance, particularly mole rats (Rhizomyinae) and grass rats (Murinae), most of them Ethiopian endemics (Yalden & Largen 1992). It has been suggested that under this scenario a wolf-like canid colonized the Afroalpine ecosystem (Gottelli *et al.* 1994) via land bridges connecting alpine habitats through a continuum from Eastern Europe, the Middle East and Northeast Africa (Kingdon 1990). The existence of at least two other Ethiopian mammalian endemics with certain Palaearctic ancestors (walia ibex *Capra walie* and

Starck's hare *Lepus starcki*), would suggest that these taxa have not been isolated in Ethiopia for as long as most other endemics, and may have arrived from the North during the Pleistocene (Yalden & Largen 1992). A molecular phylogenetic study provided further support for the recent-immigration-to-Africa hypothesis for Ethiopian wolves, showing a recent speciation from an ancestor closely related to coyotes (*Canis latrans*), grey wolves (*C. lupus*) and domestic dogs (Gottelli *et al.* 1994; Wayne & Gottelli 1997).

Unlike other medium- to large-sized canids, which typically are generalist predators and widely distributed (Ewer 1973; Macdonald 1992), Ethiopian wolves developed an extreme feeding specialization on high altitude rodents, with a narrow ecological range and habitat specificity (Sillero-Zubiri & Gottelli 1995a). Today the wolves are limited to small populations occupying Afroalpine pockets in the highest of Ethiopia's mountains (Chapter 3; Marino 2003). The morphology of their skull indicates adaptations for catching rodents such as a very elongated skull, long jaws and widely spaced teeth (specially the premolars) (Clutton-Brock *et al.* 1976; Sillero-Zubiri & Gottelli 1994; Dalton 2001). A close relationship between wolf density and rodent prey biomass has further strengthened the thesis that the present distribution of Ethiopian wolves is limited by the distribution and availability of Afroalpine rodents (Sillero-Zubiri 1994; Sillero-Zubiri *et al.* 1995a,b).

Wolves probably responded to climatic changes during the late Pleistocene by tracking the distribution of their potential prey. With the onset of the present interglacial, an increase of temperatures brought about a dramatic reduction in suitable habitats and the ancestral wolf population may have contracted and fragmented into the populations currently inhabiting scattered and isolated mountain refugia. Indeed, the Ethiopian wolf's low values of heterozygocity in the larger population of Bale - 46% of the heterozygocity and 38% of the allelic diversity of an average population of wolf-like canids - are consistent with an equilibrium effective population size of only a few hundred individuals (Wayne and Gottelli 1997), suggesting that small population sizes may have characterized the recent evolution of the Ethiopian wolf (Gottelli *et al.* 1994).

The Great Rift Valley dividing Ethiopia's massif into the north-western and south-eastern highlands is a major zoogeographical barrier (Yalden & Largen 1992; Freitag & Robinson 1993; Arctander *et al.* 1999) and may have created further opportunities for evolutionary diversification of *Canis simensis*. The existence of two subspecies has been suggested on the basis of wolf skull morphology and coat coloration, namely *C.s. simensis* North of the Rift valley, and *C. s. citernii* in the South (De Beaux 1922; Yalden *et al.* 1980). The recognition of subspecies or other forms of genetic structuring is a major conservation issue that needs to be resolved with a large sample representative of the potential population variation, and with the rigour of molecular studies. A better understanding of the history and genetic structure of this Critically Endangered canid would assist in the development of efficient management for the preservation of genetic diversity, the prioritization of conservation areas, and re-establishing gene flow when and where appropriate (Sillero-Zubiri & Macdonald 1997).

This chapter investigates genetic variation in the mitochondrial genome of Ethiopian wolves to characterize the extent and differentiation of genetic diversity among individuals from seven isolated populations. Rather than considering a static approach to geographical variation, the changing biogeographical range of the species is recreated on the bases of habitat associations of modern wolves, and the distribution of Afroalpine habitat reconstructed through the last glacial-interglacial cycle. This cycle is regarded as representative of the climatic changes spanning the evolutionary history of Ethiopian wolves since their putative origin. It is logical to expect that habitat specificity and the fragmentation of populations may have been crucial factors influencing the species' genetic diversity. If no geographical isolation was likely, and gene flow between populations could be maintained until modern times, then distinct populations could not have evolved. To test this hypothesis a multi-pronged approach that combined Afroalpine biogeography, information on genetic variability, phylogenetic relationships, changes of population size and inferred past population processes was used. The results have direct implications for the conservation of genetic diversity in the Ethiopian wolf and for the definition of the spatial scale at which populations should be monitored and managed.

5.2 Study area and methods

5.2.1 Genetic samples and DNA extraction

Blood, tissue, faecal and historic skin samples were collected from 66 Ethiopian wolves covering six out of seven extant populations, and one extinct population in Gojjam (Table 5.1 and Fig. 5.1). For one population, Arsi, both recent and historic samples were available. The extinct population from Mt. Choke was represented with three historic skins. Samples from historic skins were provided by the British Museum of Natural History, London, UK (BMNH, n=4), the Powell-Cotton Museum in Kent, UK (n =4) and the Chicago Field Museum, USA (n=4). DNA was extracted from tissue and blood samples by proteinase K digestion followed by DNA isolation with phenol/chloroform/isoamyl alcohol (Sambrook *et al.* 1989). DNA from faecal and historic skin samples was independently extracted two or three times using the QIAGEN stool or QIAGEN tissue extraction kits according to the manufacturer's protocols.

				Samples		
Region	**Locations**	**Suitable wolf habitat**	**Population estimate**	**skins (1900s-1920)**	**faecal (1998-1999)**	**blood/tissue (1990s-2000)**
North-West of the Rift Valley						
Gondar	*Simien Mountains*	273 km^2	54	1	6	2
	Mt Guna	51 km^2	10	-	-	2
Gojjam	*Mt Choke*	134 km^2	extinct	3	-	-
Wollo	*North Wollo (Kewa)*	140 km^2	23	-	5	-
Shoa	*Northeast Shoa*	112 km^2	23	-	-	10
South-East of the Rift Valley						
Arsi	*Arsi Mountains*	870 km^2	108	8	6	-
Bale	*Bale Mountains*	1,141 km^2	250	-	-	23

Table 5.1 Study populations and samples, and estimates of present habitat available and population size (Marino 2003; Chapter 3).

5.2.2 Control region sequencing

The polymerase chain reaction (PCR) was used to amplify approximately 231bp of the control region I (Saiki *et al.* 1988). Two primer pairs specific for the Ethiopian wolf mitochondrial control region were designed using the MACVECTOR computer program (IBI-Kodak) based on the consensus of eight complete control region sequences derived from cloning (Funk & Gottelli in prep.). Primer pair EW3 (L, 5'-AAGACTCAAGGAAGAAGCTCTT–3'; H, 5'- AGATGCCAGGTATAGTTTCATG -3') was used for PCR. Primer pair EW4 (L, 5'- TTCCCTGACACCCCCTCA–3'; H, 5' - GCAAGGATTGATGGTTTCTCG-3'), which nests within the amplification product from EW3L/H, was used for PCR and sequencing. PCR amplification was carried out in a total volume of 50 µL containing approx. 10 ng of genomic DNA in a reaction buffer of 50 mM KCl, 2.0 mM MgCl 2 , 10 mm Tris HCl (pH = 8.8), 1 mM dNTP mix, 2.5 –12.5 units of Taq DNA polymerase, and 25 pmoles of each primer. PCR products were purified using the QIAGEN PCR purification kit and subsequently sequenced using the ABI BigDye® chemistry and ABI 377 Sequencer.

5.2.3 mtDNA control region analysis

Forward and reverse sequences for each individual and the consensus sequences for all individuals were aligned using the SEQUENCHER program. The model of DNA substitution that best fitted the data was identified by a hierarchical likelihood ratio test approach using the programs MODELTEST 1.03 (Posada & Crandall 1998, version SMF) and PAUP* 4.01b (Swofford 1998). Nucleotide diversity, π (Nei 1987), was estimated for populations using the program DnaSP 3.53 (Rozas & Rozas 1997). The population parameter $\theta=2\,N_{ef}\,\mu$, where N_{ef} is the female effective population size and μ is the mutation rate per site per generation, was derived from the nucleotide diversity π of current populations ($E(\theta)=\pi$) (Tajima 1983) and or from genealogical data with the historic population as the population of inference (Kuhner *et al.* 1998). The maximum likelihood estimates of the present-day value of θ and the growth parameter g were jointly made using the program FLUCTUATE 1.3 (Kuhner *et al.* 1998). Monte Carlo simulations were used to ensure stability of the parameter estimation, conducting 10 short Monte Carlo chains of 4000 steps each and five long chains of length 20,000, with a sampling increment of 20. Fu's (1996) F_S test of neutrality was also used to infer historic changes of population size using ARLEQUIN 1.1 (Schneider *et al.* 1997).

Phylogenetic relationships between haplotypes were reconstructed in PAUP* 4.01b applying the neighbour-joining method (Saitou & Nei 1987) with the best fitting model of DNA substitution. Node support was tested using one thousand bootstrap replicates. Haplotype networks may more effectively portray the relationships among sequences for populations with low sequence diversity (Crandall & Templeton 1996). A statistical parsimony cladogram (Templeton *et al.* 1992) was constructed using TCS 1.13 (Clement *et al.* 2000) considering gaps as a fifth state. Haplotypes in the resulting minimum spanning network were hierarchically nested to better visualize higher-order patterns of association (Templeton *et al.* 1987; Templeton & Sing 1993). A nested clade analysis (NCA) approach was used to test statistically for current and historic patterns of phylogenetic and geographic associations, as implemented in GeoDis 2.0 (Posada *et al.* 2000). NCA quantifies geographic data for each nesting clade as clade distance (D_C), which measures the geographic range of a clade, and as nested clade distance (D_N), which measures how a given clade is geographically distributed relative to its closest evolutionary sister clades (Templeton *et al.* 1995). For nested clades in which the tip/interior status is known and for which both tips and interiors exist, clade and nested clade distances $I\text{-}T_C$ and $I\text{-}T_N$ can be calculated. Association between phylogenetic and geographic position was tested by random permutation testing of D_C and D_N, and, if applicable, $I\text{-}T_C$ and $I\text{-}T_N$. For those clades for which the null hypothesis of random geographic distribution is rejected, the biological causes for association are inferred using Templeton *et al.*'s (1995) inference key.

Genetic differentiation between populations was assessed using three approaches. First, differentiation between pairs of populations was quantified in ARLEQUIN using Excoffier *et al.*'s (1992) ϕ_{ST} and tested with an exact test of population differentiation (Raymond and Rousset 1995) using 10, 000 Markov chain steps. Second, NJ trees were constructed using PHYLIP 3.572 (Felsenstein 1993) and based on the average sequence divergence between populations (Nei 1987). Mean sequence divergence between populations (d_{xy}) was corrected for mean sequence divergences within each population x and y, d_x and d_y. Finally the corrected sequence divergence $d_A = d_{xy} - (d_x + d_y)/2$ was calculated in ARLEQUIN 1.1 (Schneider *et al.* 1997).

5.2.4 Estimates of palaeogeographical change

The reconstruction of past habitat changes was based on a conception of changes in the altitudinal distribution of vegetation belts with changes in climate. The validity of using altitudinal boundaries to determine Afroalpine distribution is supported by a strong altitudinal variation within Ethiopia that affects climate, plant and animal distributions (Yalden & Largen 1992). These authors postulate that increasing aridity in Plio-Pleistocene times would have created the main vegetation types and the altitudinal zonation of vegetation that are seen today.

Current climate

Present Ethiopian wolf distribution closely follows that of its main rodent prey, which broadly corresponds to the *Wurch* zone or Afroalpine, from the tree-line at around 3,200m up to Ethiopia's highest peaks reaching ~4,500m (Gottelli & Sillero-Zubiri 1992; Sillero-Zubiri *et al.* 1995a,b; Marino 2003). These altitudinal boundaries were used to chart Afroalpine distribution under current climate, although presently many areas below 3,700m have been lost to agriculture throughout northern Ethiopia (Chapter 3).

Late glacial period

Evidence of the extension of glaciers and of lowered vegetation belts during the last glaciation in Ethiopia comes from fossil pollen and present landform-types. Lower glaciers in the Bale Mountains reached to 3,000-3,100m (Flenley 1979; Mohamed & Bonnefile 1998) but evidence indicates higher altitudes in the Arsi Mountains (Mt. Badda: 3800-3650m, Potter *et al.* 1976; Mt. Badda: 3,300m, Mt. Kaka: 3,400m, and Hunkolo: 3,200m, Nilson 1940) and the Simien massif (4,100m down to 3,750m, Hastenrath 1977). Flenley (1979) calculated that 15,000 years ago vegetation zones were depressed by 1,000m, and palynological data from Bale showed that between 13,000 to 10,000 years ago the forest limit was still well below 3,000m (i.e. pioneer treeless vegetation on the deglaciated landscape at 3,000m) (Mohamed & Bonefille 1998). Therefore, to model the distribution of the Afroalpine ecosystem during the glacial period, an upper and lower limit for the Afroalpine was respectively determined as the treeline at 2,200m and the glacier's boundary at 3,500m - an intermediate value. This may however be a conservative estimate of the extent that the Afroalpine ecosystem might have reached during the drier period of the Pleistocene between 50,000 and 12,000 BP (evidence reviewed in Yalden & Largen 1992).

Initial warming period

The beginning of the deglaciation in the Bale Mountains has been estimated at around 13,000-14,000 years BP (Mohamed & Bonnefile 1998), marking the onset of the glacial-interglacial period. The average global temperature warmed by about 7°C following the esnd of the last glacial maximum (Hurni 1982), but rates of warming do not necessarily remain constant throughout warming periods. More typically rates are high at the beginning of the episode and then decrease (Barnosky *et al.* 2003), so rapid changes in Afroalpine distribution may have occurred over a relative short period of time. Estimates of Afroalpine areas that may well represent the initial warming were defined by selecting a lower altitudinal boundary intermediate between the glacial and present climates (i.e. 500m above the late glacial level).

Patches of Afroalpine habitat at these three stages were identified on a Digital Elevation Model (DEM) of Ethiopia (U.S. Geological Survey). Small habitat patches were excluded from calculations, assuming a minimum area of 20km^2 for viable populations based on the evidence from two recent population extinctions (Marino 2003). To estimate population sizes, nearby patches connected by dispersal were grouped, assuming a maximum dispersal distance of 20km from empirical observations (Sillero-Zubiri & Gottelli 1995b; Z. T. Ashefani, pers. comm.; Z. Kibrit, pers. comm). The size of populations was estimated by extrapolation of an intermediate wolf density to the extent of each isolated patch or group of patches. A density range of 0.2-0.3 adult and subadult wolves/km^2 was chosen, which corresponds to wolf density in habitats with intermediate rodent prey biomass in Bale Mountains (Gottelli and Sillero-Zubiri 1992).

5.3 Results

5.3.1 Pleistocene range changes

During the late glacial period Afroalpine habitat was estimated to cover over 100,000km^2 and the Ethiopian massif appeared divided by the Great Rift Valley (Table 5.2, Fig. 5.1a). Afroalpine areas appeared in three main groups, separated by distances larger than the assumed dispersal range of Ethiopian wolves; 70% of the Afroalpine habitat was concentrated in the vast Central-Northern highlands, where notably the Blue Nile Gorge imposed a discontinuity that at least in parts was within the range of wolf dispersal.

Altitudinal boundaries (m ASL)	Late glacial 2,200 to 3,500	Post-glacial warming 2,700 to 4000	Current climate above 3,200
Extent of habitat (sq km)	**110,000**	**43,000**	**6,200**
North RV	*85,000 (77%)*	*31,000 (72%)*	*3,2000 (51%)*
SouthRV	*25,000 (23%)*	*12,000 (28%)*	*3,1000 (49%)*
Population size	**22,000-33,000**	**8,600-12,800**	**1,300-1,900**
NorthRV	*17,000-25,400*	*6,200-9,300*	*600-900*
SouthRV	*5,000-7,500*	*2,400-3,500*	*600-900*
Main habitat groups (=populations) and % of all habitat	Central-Northern high.70%	Central-Northeastern high. 51%	Mt Guna 2%
	South-Western high. 6%	Simien 7%	North Wollo 9%
	Southern highlands 22%	Chocke 8%	South Wollo 17%
		Southern highlands 26%	Shoa 8%
			Simien 10%
			Choke 5%
			Arsi 19%
			Bale 30%

Table 5.2 Habitat and population estimates since the last glacial age. Habitat groups defined as Afroalpine patches within wolf dispersal distance (<20km), each potentially home to an isolated wolf population. Populations South of the Rift Valley shaded in grey.

With the onset of the warm period the Afroalpine habitats disappeared from large areas at lower altitudes, including most of the south-western range, and the Simien and Choke ranges became isolated in term of wolf dispersal from each other and from the main northern massif (still containing around 50% of the habitat). Reaching current climatic conditions, the Afroalpine appeared deeply fragmented and constrained to the highest peaks; main reductions occurred in the lower-lying mountains of central Ethiopia (Shoa) and the habitat remaining was evenly distributed between the mountains north and south of the Rift valley. Only 5.6% of the habitat once available to wolves at the glacial age was estimated to remain by the time of current climatic conditions. Estimates of habitat change during the initial warming period already showed a reduction of 39% in suitable wolf habitats (Table 5.2). Inferred changes in wolf numbers were assumed as being proportional to changes in habitat available.

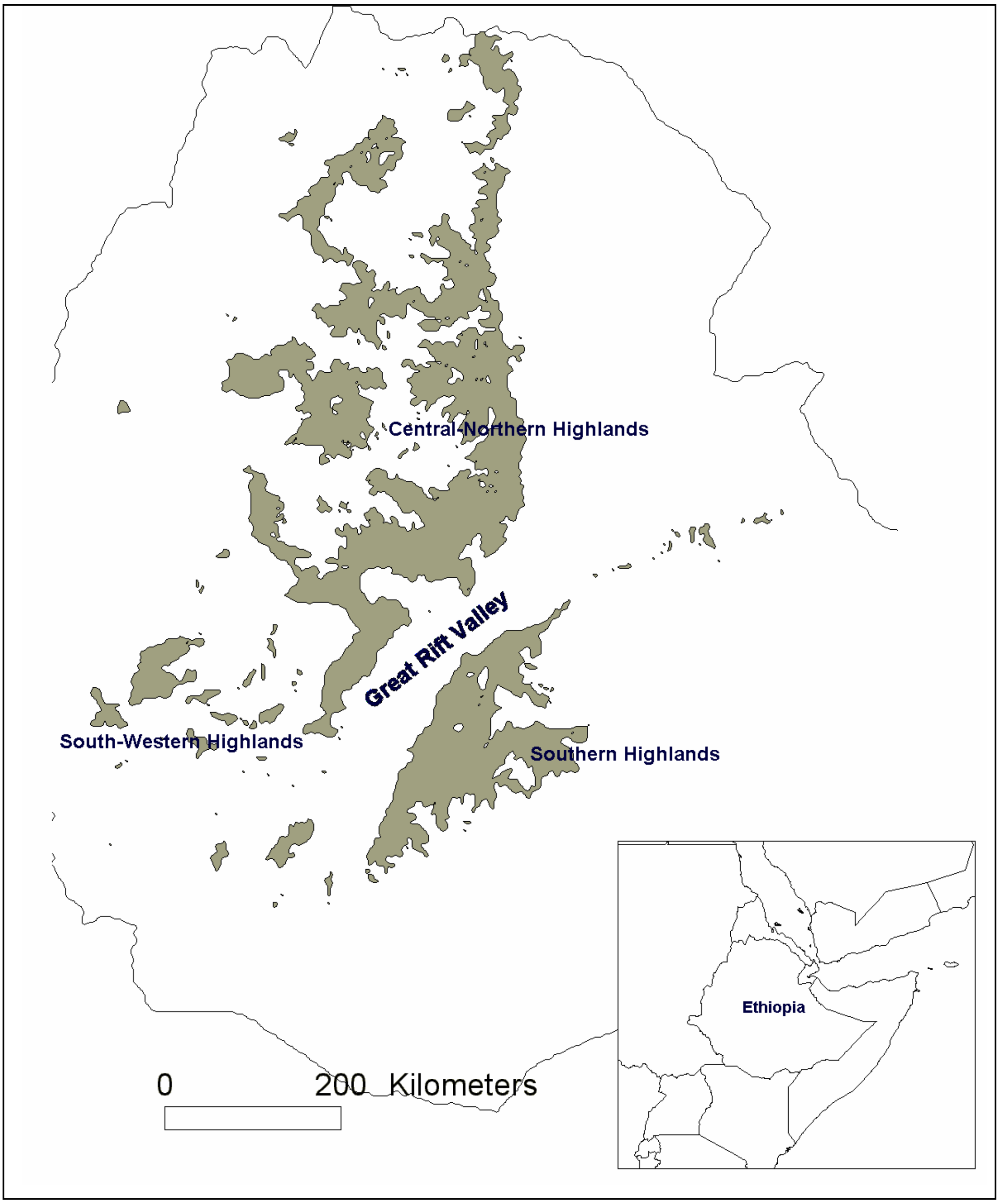


Fig. 5.1 a) Estimated distribution of Afroalpine habitats during the last late glacial period.

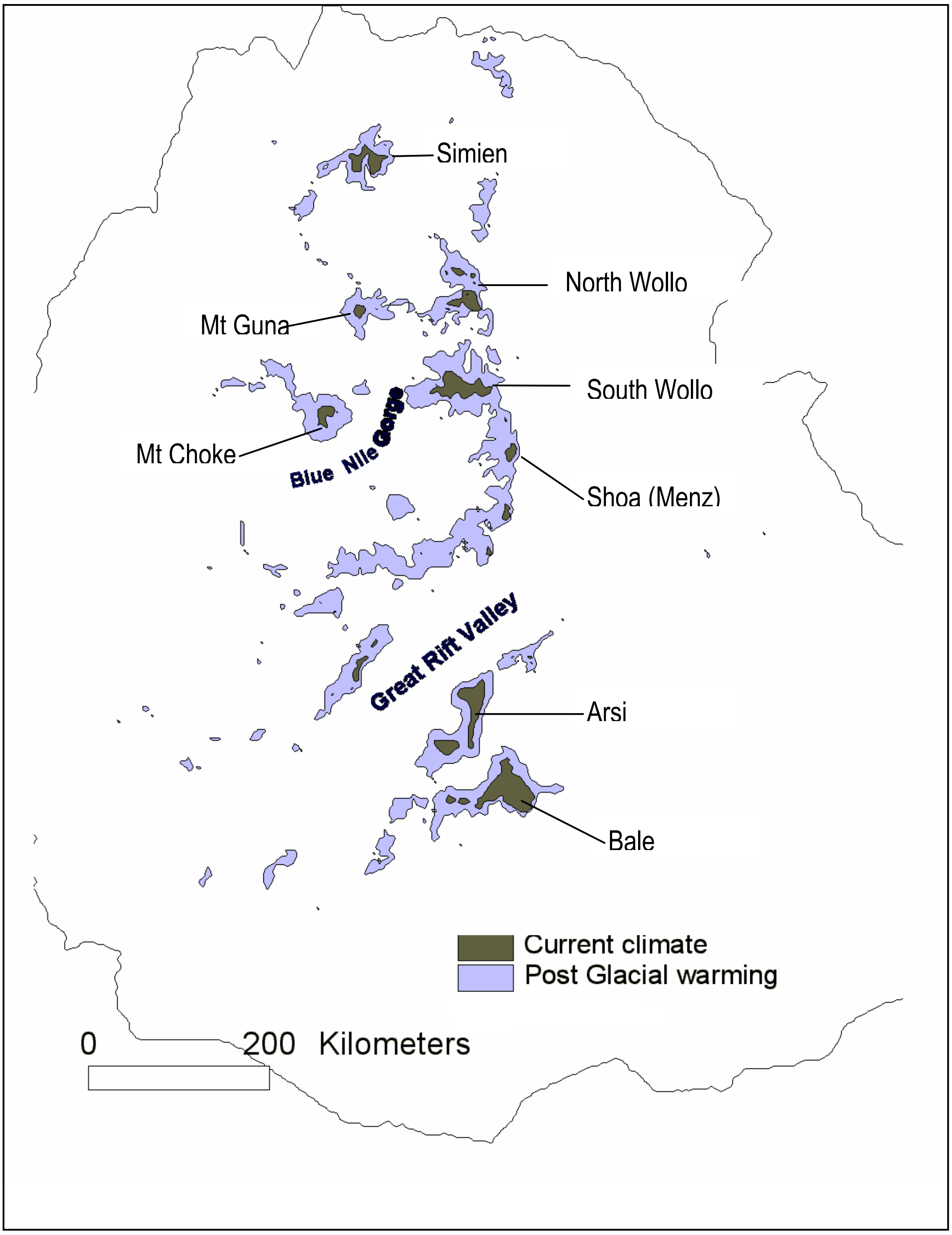


Fig. 5.1 b) Estimated distribution of Afroalpine habitats at an initial stage of late Pleistocene's warming period (=post-glacial warming) and under current climatic conditions. All extant populations are indicated; wolves in Mt. Choke became extinct around 100 years ago. Only South Wollo was not represented in the genetic sample.

5.3.2 Genetic diversity and population history

Ten variable sites defined ten control region genotypes in 66 Ethiopian wolf samples (Table 5.3). The variable sites included six transitions (*Ti*) and four indels. The hierarchical likelihood ratio test indicated that the model of substitution without rate heterogeneity (HKY) of Hasegawa *et al.* (1985) as the best fit for the data (-lnL = 355.45). No transversions (*Ts*) were observed. Including a grey wolf sequence, the hierarchical likelihood ratio test indicates the HKY model with Ti/Tv = 8.4 and without rate heterogeneity. Because no transversions were observed, this value of Ti/Tv was used for posterior estimates of the parameters θ and *g*.

Population	Sample	Haplotypes including indels											π
		N	CS01*	CS03*	CS04	CS05	CS06	CS02**	CS07**	CS08	CS09	CS10	
South of Rift Valley													
Arsi	6	2					5		1				0.0014
Arsi (historic)	8	4					4		2	1	1		0.0059
Bale	23	2					8		15				0.002
North of Rift Valley - western Mts.													
Mt Choke	3	3			1	1		1					0.0089
Mt. Guna	2	1										2	0
Simien	9	3	1			4						4	0.0043
North of Rift Valley - eastern Mts.													
N Wollo	5	1		5									0
NE Shoa	10	2		1							9		0.0009
Totals	66	10	1	6	1	5	17	1	18	1	10	6	0.0091

Table 5.3 Mitochondrial DNA genotypes and nucleotide diversity (π). Two pairs of haplotypes (* and **) collapse each into one haplotype when indels are excluded.

Nucleotide diversity (π) was 0.0091 (±0.0006) across all populations, but was larger for the two sampling populations composed only of historic samples. The estimation of *g* under the assumption of Ti/Tv=8.4 indicates population growth but this was not statistically significant (Table 5.4). Independent estimations of θ and *g* for the group of samples North and South of the Rift Valley indicated population growth and decline respectively, but these trends were not significant either. Assuming constant population size, the estimate of $\theta_{g=0}$ for the whole population was similar to that estimated from the nucleotide diversity (π) (Table 5.4). The estimated $\theta_{g=0}$ for the northern populations was significantly higher than in the populations South of the Rift Valley, indicating an almost ten-fold larger female effective population size in the North (Table 5.3). Similar values for θ, *g* and $\theta_{g=0}$ were obtained when Ti/Tv was varied between 5 and 50. Similarly, Fu's F_S test of neutrality, based on 5,000 simulated samplings, and including indels, was not significant for the total population (F_S=-1.36, P=0.31) and populations North and South of the Rift Valley (F_S=-0.36, P=0.40) (F_S= 0.18, P=0.43), indicating no population expansion or decline.

	Whole population		North of Rift Valley		South of Rift Valley	
Growth parameter	***g***	SD	***g***	SD	***g***	SD
	122.2	183.3	51.1	139.4	-103.3	511.6
Population parameter	$\theta_{g=0}$	C.I.	$\theta_{g=0}$	C.I.	$\theta_{g=0}$	C.I.
	0.0084	0.0060-0.0014	0.0097	0.0029-0.0141	0.0011	0.0003-0.0017

Table 5.4 Estimations of the growth parameter g and the population parameter θ assuming constant population sizes (g=0), as g values were not significantly different from zero (P> 0.05) C.I.= 95% confidence interval.

The mean sequence divergence within Ethiopian wolves was 1.0%, and assuming a divergence rate of 10% per million years for Canis control region (Vilà *et al.* 1999), coalescence of ≈ 102,602 years ago is implied. Assuming a mutation rate of ≈ 5 x 10-8 per nucleotide sites per year for Canis control region I (Vilà *et al.* 1999) and a generation time of between 3-5 years, a female effective population size of 36,000 to 60,000 is estimated from π=0.0091.

5.3.3 Genetic differentiation and phylogeography

Both population specific and ubiquitous genotypes were identified. Six haplotypes were exclusively found North of the Rift Valley and three haplotypes south of the Rift Valley (Table 5.3). Haplotype CS09 was prevalent in Shoa, north of the Rift Valley, and was found only once South of the Rift Valley. Both the NJ tree and the minimum-spanning network (Fig. 5.2) indicated a clear clustering of haplotypes from the North as compared to haplotypes from South of the Rift Valley. The NJ tree was poorly supported by bootstrap replicate trees and did not support reciprocal monophyly of the northern and southern haplotypes.

Fig. 5.2 shows the nested design obtained with the NCA analysis. The exact contingency analysis of 1,000 permutations of the whole cladogram rejected the null hypothesis of no association with geographical location (P < 0.001). All haplotypes in the partition of the minimum spanning network, labelled as the 2-step nesting *clade 2-1*, were from North of the Rift Valley, but the remaining two 2-step nesting *clades 2-2* and *2-3* both contained a mixture of northern and southern haplotypes.

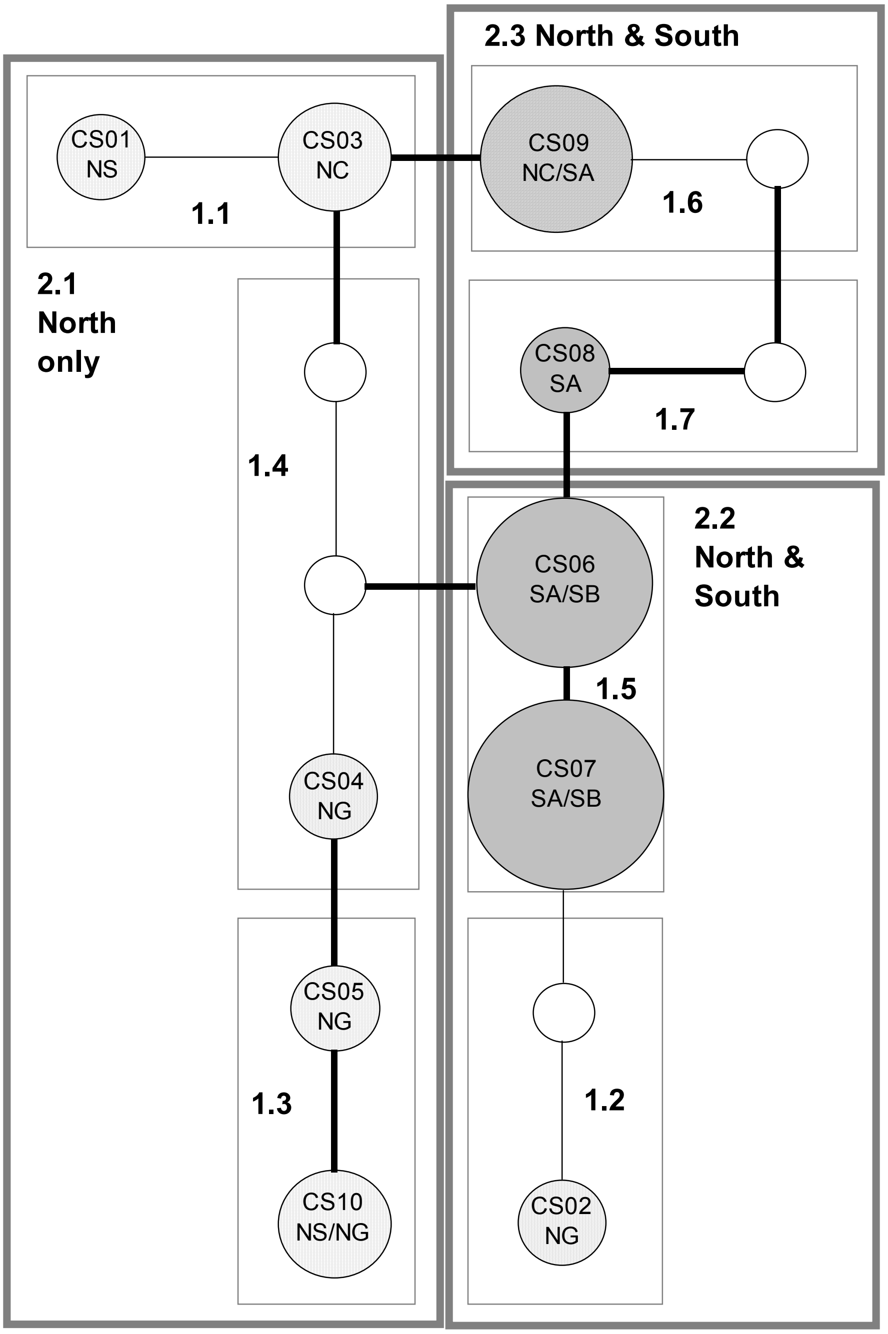
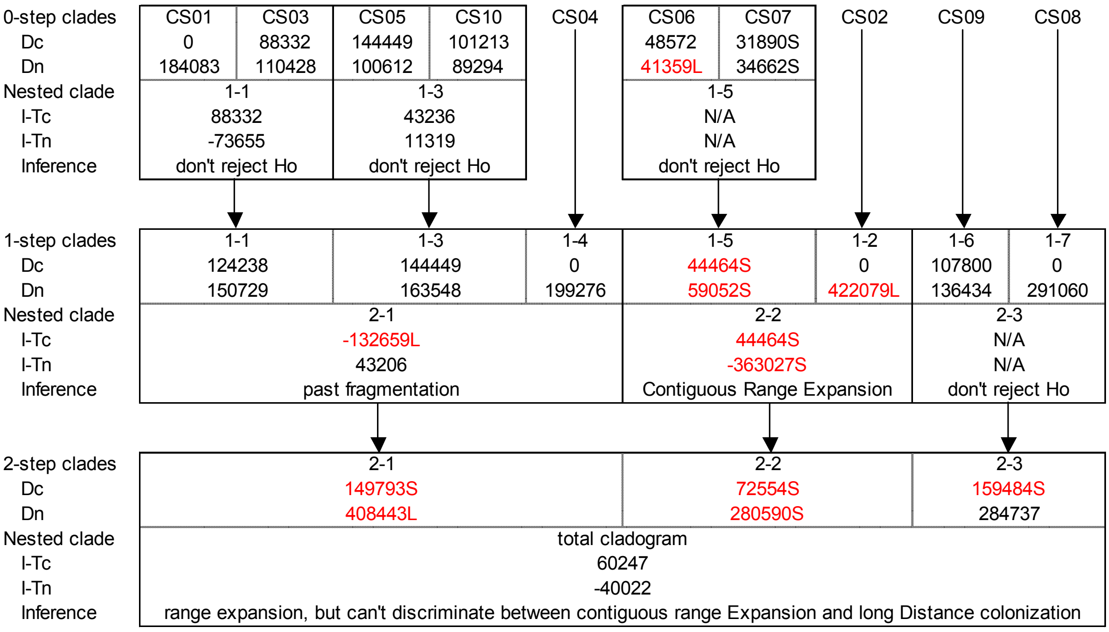


Figure 5.2 Phylogenetic relationships of Ethiopian wolf control region haplotypes. Minimum spanning network based on Templeton *et al*. (1987), Templeton *et al.* (1992) statistical parsimony. Each solid line represents one mutational step (simple solid lines for indels and thick solid lines for transitions). Nodes contain the haplotype number and haplotype frequency (Arsi, SA; Bale, SB, South of the Rift Valley and Wollo/Shoa, NC; Simien, NS and Mt. Guna/ Mt. Choke, NG, North of the Rift Valley); empty nodes indicate undetected intermediate haplotype states. The size of the nodes indicates the frequency of haplotype in the entire sample. The grey boxes indicate one-step nesting levels (1-1 to 1-7) and two-step nesting levels (2-1 to 2-3) for the nested clade analysis NCA.

Figure 5.3 presents the results of the NCA of geographic distances and describes the inferences drawn using the key given in Templeton *et al.* (1995) to the statistical results. These showed that both population structure and population history played an important role in determining the geographic associations (Fig. 5.4). The null hypothesis of no geographic association could not be rejected for all nested clades at the lowest nesting level (1-1, 1-3, and 1-5). Past fragmentation was inferred for the 2-step nested *clade 2-1* that exclusively involved northern haplotypes. Continuous range expansion was diagnosed for nesting *clade 2-2* including haplotypes from North and South. No geographic association could be inferred in *clade 2-3*, which involved haplotypes from mountain ranges bordering the Rift Valley both North and South (Wollo/Shoa and Arsi, respectively). At nesting level 3, which corresponds to the total cladogram, range expansion was inferred as the main cause of geographic association, but it was not possible to distinguish between continuous expansion and long-distance dispersal as the cause for expansion.



0-step clades	CS01	CS03	CS05	CS10	CS04	CS06	CS07	CS02	CS09	CS08
Dc	0	88332	144449	101213		48572	31890S			
Dn	184083	110428	100612	89294		41359L	34662S			
Nested clade	1-1		1-3			1-5				
I-Tc	88332		43236			N/A				
I-Tn	-73655		11319			N/A				
Inference	don't reject Ho		don't reject Ho			don't reject Ho				

1-step clades	1-1	1-3	1-4	1-5	1-2	1-6	1-7
Dc	124238	144449	0	44464S	0	107800	0
Dn	150729	163548	199276	59052S	422079L	136434	291060
Nested clade	2-1			2-2		2-3	
I-Tc	-132659L			44464S		N/A	
I-Tn	43206			-363027S		N/A	
Inference	past fragmentation			Contiguous Range Expansion		don't reject Ho	

2-step clades	2-1	2-2	2-3
Dc	149793S	72554S	159484S
Dn	408443L	280590S	284737
Nested clade	total cladogram		
I-Tc	60247		
I-Tn	-40022		
Inference	range expansion, but can't discriminate between contiguous range Expansion and long Distance colonization		

Figure 5.3 Nested cladistic analysis of geographical distances. Clade (D_C) and nested clade (D_N) distances are given for all nested clades containing with geographic and genetic variation. An S indicates that the distance is significantly small at the 5% level, and an L indicates that it is significantly large (significant results in red). Interior versus tip distances, D_C and D_N, are given for nested clades where the interior/tip status is known and for which both tips and interiors exist. Within the same nesting group, the clade name is shaded for interior clades. Inferences are given following Templeton *et al's* (1995) inference key.

Average pairwise ϕ_{ST} between populations was 0.64 and the exact test of population differentiation showed that all populations were significantly different from each other, except between the historic and recent sampled Arsi populations (*P*=0.49) and Mt. Guna and Mt. Choke versus Simien (*P*=0.30) (Table 5.5).

	Arsi recent	Arsi historic	Bale	MtChoke/Guna	Simien	NWollo
Arsi historic	-0.039					
Bale	0.296*	0.218*				
MtChoke/Guna	0.612**	0.488**	0.750**			
Simien	0.699**	0.603**	0.800**	-0.023		
NWollo	0.942**	0.688**	0.894**	0.739**	0.742**	
NEShoa	0.939**	0.767**	0.914**	0.831**	0.821**	0.851**

Table 5.5: Pairwise ϕST comparisons. (*= P < 0.05,**= P < 0.01).

The un-rooted NJ tree of average sequence divergence between populations suggested several population groupings (Figure 5.4). The Arsi/Bale, Wollo/Shoa, and Simien/Mt.Guna population pairs appeared tightly grouped, but the position of Mt. Choke was unclear.

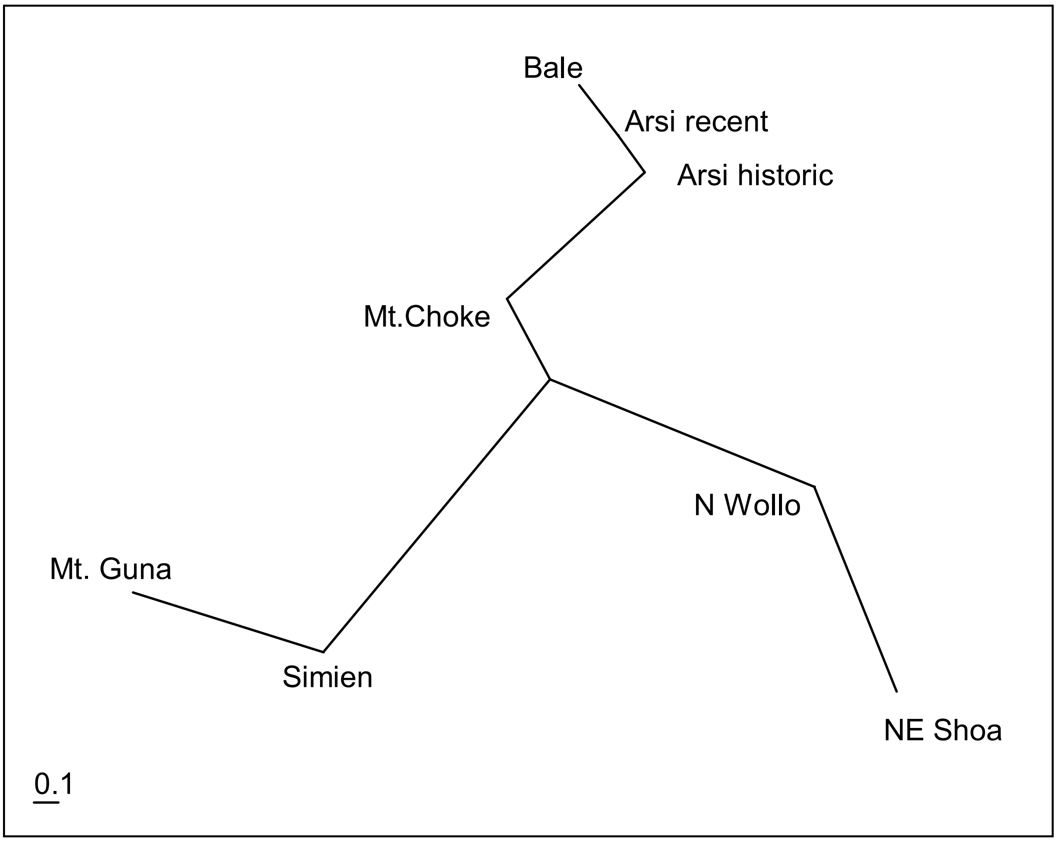


Figure 5.4 Neigbour joining tree of mtDNA sequence divergence.

The highest value of ϕ_{CT} (0.73) grouped populations according to their geographic proximity, differentiating a group southwards of the Rift Valley and two groups North of the Rift Valley, namely the Eastern and Western Highlands (Table 5.6). Mt. Choke was most strongly associated with the Western group (Simien and Mt. Guna). The grouping of all northern populations versus the southern populations obtains the lowest ϕ_{CT} value (0.39).

	Source of variation				
Groupings	among populations within groups ϕ_{SC}	within populations ϕ_{ST}	among groups ϕ_{CT}	% among groups	*P*
[Bale, Arsi] [Wollo, Shoa, Simien, Choke, Guna]	0.767	0.842	0.321	32.14	0.046
[Bale, Arsi, Choke] [Wollo, Shoa] [Simien, Guna]	0.505	0.85	0.697	69.68	0.014
[Bale, Arsi] [Wollo, Shoa, Choke] [Simien, Guna]	0.629	0.841	0.572	57.22	0.048
[Bale, Arsi] [Wollo, Shoa] [Simien, Choke, Guna]	**0.423**	**0.846**	**0.733**	**73.28**	**0.007**
[Bale, Arsi] [Wollo, Shoa] [Simien] [Choke, Guna]	0.457	0.841	0.706	70.63	0.026
[Bale, Arsi] [Wollo, Shoa, Choke, Guna] [Simien]	0.732	0.836	0.39	38.95	0.07

Table 5.6 AMOVA for groupings of populations estimated using ϕ-statistics based on mtDNA haplotype distances. In bold highlighted the group that displayed the highest ϕCT.

5.4 Discussion

5.4.1 Low genetic diversity and recent evolution

The lack of mitochondrial DNA variability in Ethiopian wolves contrasts with other species of wolf-like canids (Gottelli *et al.* 1994, Wayne *et al.* 1992). Only ten haplotypes were identified in a sample of 66 Ethiopian wolves, which represents all but one of the extant wolf populations. The calculated index of nucleotide diversity π (=0.0091) is amongst the lowest reported for carnivores, including those with relatively low variation (e.g. 0.0102 in African wild dogs *Lycaon pictus*, Girman *et al.* 2001; 0.18 in cheetahs *Acinonyx jubatus*, Menotti-Raymond & O'Brien 1993; 0.22 in giant pandas *Ailuropoda melanoleuca*, Lu *et al.* 2001; and 0.35 in North American pumas *Puma concolor*, O'Brien at al 1990).

The nucleotide diversity index π reflects recent population size, whereas the population parameter θ utilizes genealogical information and reflects historic population size. The lack of significant differences between them (θ=0.0084) and the growth factor *g* not significantly different from zero, would indicate that recent decline in Ethiopian wolf numbers has not yet caused a substantial reduction in levels of mitochondrial diversity. These results contrast with findings from other species of carnivores. In African wild dogs for instance, the comparison between π and θ (=0.0145) appears to indicate that recent population size is greater than the historical population size (Girman *et al.* 2001) and in grey wolves and coyotes, a 10-fold decrease in population size during the late Pleistocene (Vilà *et al.* 1999).

The low number of mtDNA haplotypes and the low sequence divergence between them thus reflects a recent evolution of Ethiopian wolves and relatively low population size compared to African wild dogs, grey wolves and coyotes. Based on the sequence divergence observed, coalescence was estimated at just over 100,000 years ago. Although considerable caution should be used in the literal interpretation of divergence times because of inaccuracies in the molecular clock (Gibbons 1998), this estimate of coalescence time is in agreement with the hypothesis that Ethiopian wolves diverged relatively recently from a grey wolf-like ancestor (Gottelli *et al.* 1994), which first appeared in Eurasia about 700,000 years ago (Kurtén 1968). Assuming panmixia in the ancient population, the female effective population size was estimated at between 36,000 and 60,000. This value is much higher than that inferred from habitat availability at the Last Glacial for the whole population (22,000 to 33,000 wolves). The over-estimation may be caused by the violation of panmixia, as the habitat reconstruction indeed indicates a certain degree of fragmentation of Afroalpine habitats at glacial times. It is also possible that habitat and population estimates under-represent the range of Afroalpine available at that time. It has been suggested that during some phase of the Pleistocene the climate was sufficiently cold and dry to bring the high-altitude grassland communities down to the floor of the Rift Valley at around 1,800m (Yalden & Largen 1992). Also the montane grassland habitat, known to harbour wolves in Bale, is found just below the treeline and thus was excluded from habitat calculations.

5.4.2 Population history and genomic structuring

The genetic structure of the surviving wolf populations seems to be a relict of a late Pleistocene expansion into Afroalpine habitat. Fragmentation and genetic drift over the last 10,000 years resulted in local loss of genetic variability but the species as a whole conserved genetic variability despite low numbers and fragmented populations. Habitat reduction after the estimated coalescence time, well before the end of the Last Glaciation, did not result in the fixation of a single mtDNA haplotype and most extant populations have retained more than one haplotype up to recently. The genetic structure observed today may reflect limited gene flow or historical events such as colonization or fragmentation. Distinguishing between these causes is inherently difficult specially when using nuclear markers. In principle, sequence-based markers (mtDNA) provide the analytical means to tackle the problem (Templeton 1995). Nested clade analysis allows one to deduce past population processes whereby different levels of nested clades correspond to different time periods (Templeton *et al.* 1987, 1995; Templeton & Sing 1993).

Range expansion is inferred as the main cause of geographic association during the most historic times, possibly immediately following the estimated coalescence time when the Afroalpine ecosystem expanded over large areas. This is indicative of a single colonization event and subsequent expansion. More recently, fragmentation of populations North of the Rift Valley, panmixia in the mountain ranges bordering both sides of the Rift Valley, and further expansion to the South was inferred. For the lowest nesting level, which corresponds to most recent times, the lack of geographic and genetic association indicates panmixia on a local scale. More recently however, human disturbance has further aggravated the reduction in population sizes, increasing the likelihood of local fixation of haplotypes, and the overall loss of haplotypes. This was exemplified by the comparison of historic and recent wolf samples from the Arsi population.

The observed loss of single haplotypes within the haplotypes network is consistent with a process of random fixation of alleles within isolated populations. Ecological and competitive interactions for limiting resources prevent dispersal in Ethiopian wolves, and both sexes show strong philopatry resulting in the formation of stable social groups (Sillero-Zubiri 1994; Sillero-Zubiri & Gottelli 1995b; Sillero-Zubiri *et al.* 1996a). In this scenario, rare alleles can become fixed within individual groups (Sugg *et al.* 1996a). As the same alleles are unlikely to become fixed in all groups, this process can increase the overall genetic diversity of the population, thus retaining higher levels of haplotype diversity than in a single panmmitic population. In summary, a complex pattern of phylogenetic and ecological relationships indicate a dynamic process of rapid expansion of a palearctic new-comer into new mountain areas, followed by subsequent isolation and divergence of populations. An apparent route for colonization is via the highlands extending towards Eritrea, linking to past land bridges across the Red Sea (Kingdon 1990) (Fig. 5.1a).

5.4.3 Genetics and biogeography

Parallelism between the processes of habitat change and genetic partitioning confirms the close relationship between Ethiopian wolves and their Afroalpine prey along the evolutionary history of the species. The initial population expansion occurred in a scenario of nearly continuous Afroalpine ranges, with the Great Rift Valley as the only main barrier. The ancient population was large and continuously distributed, and female-mediated gene flow would have been high along corridors between main mountain blocks. The population would then have become fragmented by extinction of intermediate populations as the climate warmed. The same pattern of population differentiation due to Ice Age isolation is still apparent in the brown bear (*Ursus arctus* Taberlet *et al.* 1995; Waist *et al.* 1998) and black bear *Ursus americanus* (Wooding & Ward 1997). Past fragmentation for the northern haplotypes coincides with the rapid loss of habitat at the onset of the late Pleistocene warming period, and the relatively early separation of Simien and Choke Mountains from the larger Central-Northern Highlands. The past history connecting current sampled populations to previous larger and more continuous ones overall agrees with the phylogenetic differentiation of populations South of the Rift Valley (Bale and Arsi), populations in the North that remained connected for longer periods (Wollo and Menz), and populations that separated earlier (Simien and Choke). It is unclear whether the Blue Nile Gorge that encircles the Gojjam Highlands (Mt. Choke) acted as an almost complete barrier to wolf dispersal. From a biogeographical perspective it seems probable that contemporary populations on both sides of the Rift Valley were sufficiently separated to explain the observed grouping of northern haplotypes. However, the lack of reciprocal monophyly of the northern and southern clades does not support the criteria for a two subspecies division. The sharing of haplotypes CS09 and CS02 between populations North and South of the Rift valley also contradicts this taxonomic differentiation. The morphological differences found in the craniomorphology of wolves on both sides of the Rift Valley are however indicative of adaptations to prey on the large giant molerat (*Tachyoryctes macrocephalus*) in the Bale population (Dalton 2001). Large sample sizes may be needed to confirm the extent and distribution of such phenotypic differences, but this may not necessarily be accompanied by genetic change. The more recent admixture found among populations on the edges of the Rift valley could be explained by the rapid and short return of cooler/dryer conditions of the Younger Dryas (10,000 BP) (Hewitt 1996) which may have allowed wolves to disperse along new corridors of suitable habitat for a period of ~ 1,000 years.

5.4.4 Conservation implications

The levels of genetic diversity in the Ethiopian wolf are very low. However, the current level of haplotype diversity mirrors ancient rather than recent population densities. Most of these populations have retained more than one haplotype up to recently, but the impact of human disturbance further aggravates isolation and reduced population sizes, particularly in the North, leading to concerns that, with historic patterns of gene flow disrupted, small populations will lead to diminished genetic variability. Until recently conservation efforts have been focussed on the larger population of Bale Mountains. This study highlights the need for protecting the northern populations, identified as the main reservoir of genetic variability - largely exceeding that of the southern populations - and where human pressures have also reached critical levels. Management to restore or maintain variation in genetically-at-risk populations could be effective while still maintaining genetic patterns by means of translocations among contiguous regions or closely related populations (see Sillero-Zubiri & Macdonald 1997 for detailed meta-population management proposals). The most likely genetic partitioning corresponds to three mountain groups, namely Arsi/Bale, Wollo/Shoa, and Simien/Mt.Guna.

CHAPTER VI

Trends, dynamics and resilience of an Ethiopian wolf population

Abstract

The analysis of trends in the abundance of Ethiopian wolves is essential for understanding the dynamics of populations and for devising management and conservation actions. This study analyzes time series of count data from a long-term monitoring programme in the Bale Mountains of southern Ethiopia, home to the largest population, spanning over 17 years (1983- 2000). Marked variations in wolf abundances were associated with disease epizootics and high wolf densities, and were unrelated to trends in the levels of other potential agents of decline, such as livestock, domestic dogs and human abundances within the population ranges. The stability of populations in the absence of disease and their return to previous levels after disruption gives evidence of population regulation. Negative density dependence was evident above a threshold density (carrying capacity), but at the lower extreme of densities, the rate of population increase was inversely density-dependent. The interpretation of these results supports the notion of intra-specific competition for the rodent prey as a major force in regulating populations of the Ethiopian wolf, whereas delays in the formation of new breeding units appear to limit the capacity for rapid recovery at reduced levels of competition. While stability and resilience are good omens for the conservation of these endangered canids, the risk of infectious disease and the increase of grazing within wolf ranges deserve well-planned conservation measurements to prevent further declines.

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6.1 Introduction

Knowledge of population dynamics is vital for the understanding of the behavioural ecology, the evolution of behavioural patterns, or the conservation of a species. Population ecologists have traditionally been concerned with the factors and processes that contribute to population regulation and hence make it likely that the population does not become excessively large nor goes extinct (e.g. Sinclair 1989; Begon *et al.* 1990; Hanski 1990; Turchin 1995). Population regulation is commonly used in the sense of a return tendency, due to density-dependent processes, towards an equilibrium density - or a stationary distribution of population densities. Density dependence is understood to be any dependence of per capita growth rate on present and/or past population densities.

The equilibrium-oriented, density-dependent paradigm, however, neglects the role of environmental changes and the quality of individuals. Models of simple dynamics, such as the logistic model for example, often failed to predict the way populations behave, even if allowing for stochasticity. The mechanistic paradigm is an alternative approach that focuses on mechanisms controlling populations such as disease, predation, food shortage and territoriality (Krebs 1995; Sinclair & Pech 1996). The mathematical models of population extinction exemplify well the relative utility of these paradigms. Dealing with mechanisms of extinction in stationary environments - such as demographic and environmental stochasticity - these models are not often very helpful in predicting the fate of natural populations, because the actual causes of extinction often involve environmental changes, most notably habitat loss and change in habitat quality. Caughley (1994) has drawn attention to this contrast, making the point that although population biologists have traditionally worked in the realm of the small-population paradigm, assuming a stationary environment, what we really need is a theory for the declining population paradigm, which deals with the causes of decline and its cure.

This succinct overview of the paradigms in population biology is particularly relevant for the study and conservation of carnivore populations. The need for monitoring to understand the dynamics of these populations has been amply acknowledged in the recent literature, in response to the increasing concern about the status and distribution of terrestrial carnivore populations throughout the world (e.g. Schaller

1996). Changes in land-use practices, habitat loss and fragmentation, human persecution, declines in natural prey populations, disease, and increased competition within carnivore guilds have brought about dramatic declines in several carnivore populations over the past few hundred years (Woodroffe 2001). Disease in particular has emerged as a central issue in carnivore conservation (Macdonald 1993b) with a number of dramatic population declines occurring since the beginning of the 1990s (e.g. African wild dogs *Lycaon pictus,* Hofmeyr *et al.* 2000; grey wolves *Canis lupus,* Weiler *et al.* 1995; lions *Panthera leo,* Roelke-Parker *et al.* 1996; black footed ferrets *Mustela nigripes,* Williams *et al.* 1988). However, the long-term effects of disease on wild populations have not been well documented and long-term data are clearly needed for a better understanding of disease dynamics and the resilience of carnivore populations.

The problem is that, with some notable exceptions (e.g. cheetah *Acynonix jubatus*, Serengeti lions), there is general lack of long-term carnivore population studies. The collection and analysis of long-term count data are often complicated by the limitations inherent to extensive surveys, such as measurement error and missing data (Thomas 1996), and in addition most carnivores are secretive, nocturnal, or far ranging. Among the examples of such studies, many are from populations of canid species that live in temperate environments and prey on long-lived mammals that often exhibit fluctuations and oscillations. Interactions between sociality and food dynamics or abundance were implicated in the dynamics and recovery of these populations (e.g. grey wolves, Hayes & Harestad 2000; kit foxes *Vulpes macrotis* Dennis & Otten 2000; Arctic foxes *Alopex lagopus*, Loison *et al.* 2001; coyotes *Canis latrans*, Windberg 1995; Windberg *et al.* 1997). Other studies in Africa identified natural predators and intra-guild competition as major factors in the dynamics of populations of several social carnivores (e.g. African wild dogs, Creel & Creel 1996; jackals, Loveridge & Macdonald 2003; cheetahs (Kelly *et al.* 1998).

Seventeen years of monitoring in the largest population of Ethiopian wolves (*Canis simensis*) provides a case to reveal population processes in medium-sized carnivores that depend on small, abundant prey and, more specifically, the role infectious disease play in the dynamics of populations. The answers are potentially important to the theory of population biology and conservation because this is an endangered species occurring in fragmented, small populations (Chapter 3).

Monitoring in the Bale Mountains, between 1989 and 2000, included wolf populations that differed in the availability of prey and wolf density, and a period of severe mortality due to rabies that affected wolves in two high-density populations in the early 1990s (Sillero-Zubiri *et al.* 1996b). During a rabies epizootic 77% of known wolves in the Web Valley population, including whole packs, died or disappeared over a short period of time in 1992 (Sillero-Zubiri *et al.* 1996b). A similar rapid decline was registered on the Sanetti Plateau population where 54% of known individuals among three packs died or disappeared in 1990, although a definitive confirmation of disease as the cause of mortality could not be achieved (Sillero-Zubiri *et al.* 1996b). Transmission from domestic dogs has been the most parsimonious explanation for the epidemic of rabies in wolves (Sillero-Zubiri *et al.* 1996b; Laurenson *et al.* 1997, 1998; Malcolm & Sillero-Zubiri 1997). Five years later, in 1996, the populations affected had shown no sign of recovery (Stephens *et al.* 2001).

This natural 'perturbation experiment' permits us to explore whether populations are regulated (i.e. if they return to the equilibrium after a perturbation) and if regulation is mediated by density dependence mechanisms. Given the simplicity of the biological system (e.g. a super-abundant food resource monopolized by a species with no natural predators), classical population models would predict populations regulated via density-dependent mechanisms. This is because intra-specific competition is expected among individuals that utilize a common resource that is in short supply. Pure ecological factors can then explain reduced survival at high densities because of increasing levels of interference and/or depletion when there greater numbers of competitors for the food resource (Caughley & Sinclair 1994). In turn, high rates of population growth would be expected after severe reduction, because prey availability will be high and competition for food negligible at low wolf densities. In social cooperative species, however, the intrinsic ability to convert that extra energy into enhanced fecundity and diminished mortality could be limited by behavioural mechanisms (e.g. wild dogs). The quantification of the simultaneous levels of other factors that can affect prey availability (e.g. grazing pressure) or wolf foraging efficiency (e.g. disturbance by humans) can suggest causes of limited recovery or low rates of population growth. Their identification as putative agents of decline will depend on their levels changing in directions consistent with trends in the abundance of wolves (Caughley 1994; Sutherland 1996a).

This study updates previous analysis of monitoring data from Bale (Hillman 1986; Sillero-Zubiri 1994; Malcolm & Sillero-Zubiri 1997; Stephens *et al.* 2001) by incorporating a longer dataset and stratification by habitat type. The stratification accounts for differences in wolf density and the degree of exposure to potential agents of decline. Firstly, the utility of line-transect counts to estimate wolf abundances and trends is evaluated and validated. Secondly, trends along time series of wolf abundances are described and patterns of population change derived from a shorter time series of population sizes. Finally, trends in the levels of potential agents of decline are evaluated from time series of counts of livestock, people and domestic dogs.

6.2 Study Areas

The highlands of Bale in southeastern Ethiopia (7°S, 39°45'E) are protected within the Bale Mountains National Park (BMNP). Wolves in Bale have been regularly monitored in the high altitude plateau of Sanetti (3,800-4050m) and in the broad valley bottom of the upper Web Valley (3,450-3,550m) (Fig. 6.1). The Afroalpine climate in these areas is characterized by a dry season (October to March) with extremely cold nights and warm days, and a warmer wet season (April to September) that experiences 70% of the annual rainfall with peaks in April-May and September. On the bases of empirical associations between vegetation types, rodent abundances and wolf densities (Gottelli & Sillero-Zubiri 1992; Sillero-Zubiri 1994), the four study sites have been classified as *optimal*, *good* or *marginal* habitats for wolves. In the field, these habitat categories were easily identified by rather abrupt transitions between main vegetation types and major topographic features. There follows a brief description of the study areas (see Chapter 2 for more details):

Web Valley and **Central Sanetti** are typical *optimal* habitats. In these open and flat landscapes Afroalpine meadows and grasslands dominate, sustaining exceptionally high rodent biomasses (~ 27kg/ha) and wolves at densities of around 1.2 adults and subadults/km^2.

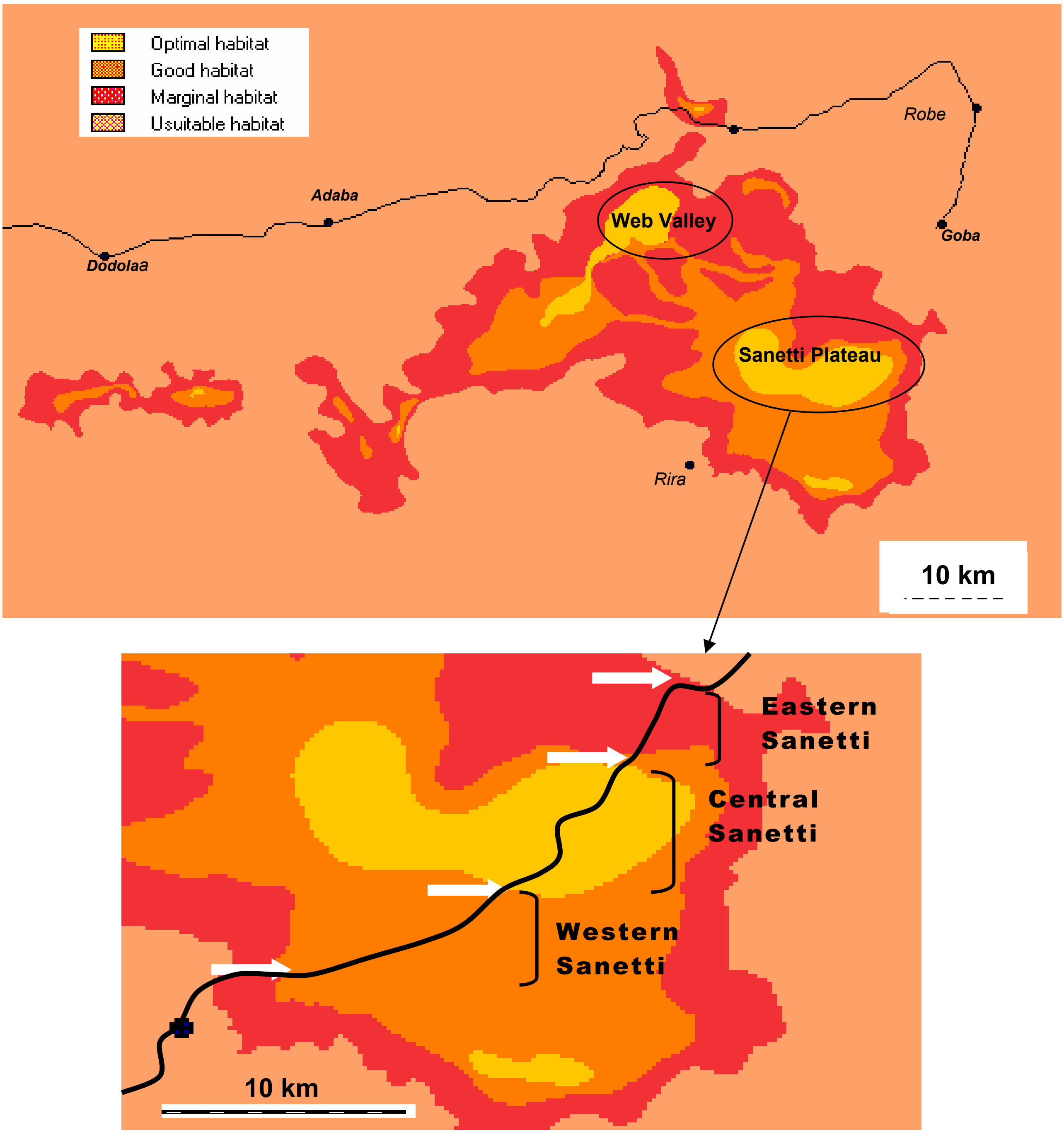


Figure 6.1 Bale Mountains showing distribution of Ethiopian wolf habitats and study areas. Insert shows details of Sanetti line-transect along Goba-Rira road.

Western Sanetti (or Tullu Demtu) is an area of *good* wolf habitat, along the drier southern slopes of the plateau. The characteristic *Helichrysum* heaths have a rodent biomass of around 1/5 of that in *optimal* habitat and wolves live at densities ca. 0.25/km2.

Eastern Sanetti is an area of *marginal* habitat for wolves. In the dominant ericaceous heaths, formed by *Erica* spp. and *Phillipa* spp. bushes, prey abundance is relatively low and wolves uncommon.

Unlike the northern highlands of Ethiopia, the Bale Mountains have never been heavily populated. Wolves in the Web Valley however have coexisted with Oromo pastoralists and their livestock (Malcolm & Sillero-Zubiri 1997). Their traditional use of Afroalpine pastures follows the pattern of rains, resulting in highest stock densities at the peak of the rainy season and lowest abundances in the dry season (Sillero-Zubiri 1994). The extreme climatic conditions in Central Sanetti have deterred human settlement and prolonged grazing seasons in the upper plateau, but people living lower down the mountain slopes utilize the *Helichrysum* and ericaceous heaths for grazing livestock. Unlike other areas of BMNP (Stephens *et al.* 2001), human encroachment and cultivation did not occur within the study areas, eliminating habitat loss as a potential agent of decline in the study populations.

6.3 Methods

6.3.1 Monitoring strategy and count data

Regular surveys of wolves and livestock (sheep/goats, horse/mule/donkeys, cattle) started in Bale in 1983 by the Bale Mountains Research Project (Hillman 1986) and continued until present, with an interruption in the mid-1990s due to civil unrest. Regular monitoring activities were re-established in 1996 by the Ethiopian Wolf Conservation Programme (EWCP - Williams & Sillero-Zubiri in press). Severe wolf mortality occurred over a short period of time in Central Sanetti (April-June 1990), and Web Valley (October 1991-February 1992) towards the end of the first monitoring period. Table 6.1 summarizes the type of data and the monitoring period covered in the present study.

	83	*84*	*85*	*86*	*87*	*88*	*89*	***90***	*91*	**92**	*93*	*94*	*95*	*96*	*97*	*98*	*99*	*00*
Line-transect counts (n=counts per year)																		
Sanetti Plateau*	4	24	19	22	23	28	23	**5**	8	3		8	8	3	7	10	10	11
Web Valley						2	3	5	5	**6**				3	6	11	11	12
Total counts (x= years with total counts)																		
Central Sanetti					X	X	X	**X**								X	X	X
Web Valley					X	X	X	X	X	**X**				X	X	X	X	X

Table 6.1 Wolf monitoring data for Bale Mountains (disease epizootics indicated in bold). * Since 1985 Sanetti transect was subdivided by habitat type, into Central, Eastern and Western Sanetti.

Wolf and livestock counts along fixed line-transects followed a standard protocol consistently applied in successive years. The longest time series exists for the Sanetti Plateau, starting in 1983. Regular monitoring commenced in Web Valley in 1988. Domestic dog and people counts were incorporated more recently, when their relevance for wolf hybridization and disease transmission was realized. Line transects did not approach villages or houses, thus encounters of domestic dogs and people were not directly associated with human settlements but instead reflected their presence within wolf ranges. Total wolf counts in Central Sanetti and Web Valley were conducted as part of a detailed study of the species' behaviour started by C. Sillero & D. Gottelli in 1987. The territories of these focal packs overlapped with the area traversed by the line transect in these two study areas. The animals encountered thus belonged to those focal packs, enabling direct comparisons between the two methods. Ancillary information on the persistence/extinction of focal packs for the period of discontinuous monitoring came from short visits by C. Sillero (April 1995, October-November 1996, unpubl. data) and Edriss Ebu (March and August 1996, unpubl. data).

Line transect counts

Animals and people in Sanetti were counted along the Goba-Rira road that traverses the plateau in an almost straight line for 31km. This covered the altitudinal range between 3,400-4,100m and traversed the three main vegetation zones recognized as distinctive wolf habitat types (section 6.2). Since 1985 counts were discriminated by habitat type, subdividing the road into three sections: a 6.7km section in ericaceous heaths (=*Eastern Sanetti,* marginal habitat); a 10km section in Afroalpine formations (=*Central Sanetti*, optimal habitat) and 14.3km-section in *Helichrysum* heaths (=*Western Sanetti,* good habitat) (Fig. 6.1). Counts were conducted from a vehicle driving at approximately 20km/hour, with two or more observers including the driver. The time spent in a count varied between 1.5-2.5h and observers varied across periods, with at least one experienced observer present at each count. Counts occurred during daytime and at all seasons, and were initially conducted twice per month, but cut down to once monthly later on (Table 6.1).

Counts in Web were conducted along a specifically designed line-transect, a 20kmcircuit that sampled over 30km^2 of optimal wolf habitat. Counts were made on horseback and lasted 5-7h, starting early morning and completed by early afternoon, with 1-4 observers, including at least one experienced observer. Counts were initially conducted quarterly and more recently monthly, with a three year-gap in the mid 1990s (Table 6.1).

Total counts

Total wolf counts through direct observation of focal packs provided data on the number and size of packs in Central Sanetti and Web Valley. Population size was expressed as the sum of all wolves older than one year in the focal packs (i.e. adult and subadults) and *floaters* (i.e. solitary females not associated to family groups), during the reproductive season (November to March). Wolves were directly observed through binoculars at 20-500m, on foot or from horseback. During the period 1988-1992 all individuals were recognized using records of coat patterns and a tag system (Sillero-Zubiri 1994, 1996; Sillero-Zubiri & Gottelli 1994, 1995b). From 1996 onwards field work was less intensive and total counts were achieved by complete pack enumerations during the November-March period of focal pack observations. Complete pack enumerations were achieved by keeping records of all wolves seen around the den, during social greetings and patrols, until no new individuals were observed and the list was completed (Greenwood 1996). Total wolf counts were facilitated by the inherent stability of packs and territories (Sillero-Zubiri & Gottelli 1995b), the concentration of pack members' activity around the den during the reproductive season, and the easy recognition of members of each sex and of the dominant pair from behavioural observations.

6.3.2 Wolf abundance index

The existence of repeated counts and stratifications per habitat type was capitalized on to increase the validity, usefulness, and precision of wolf counts from line-transects (Macdonald *et al.* 1988). Sampling error can be reduced for example by increasing the size of the sample (Macdonald *et al.* 1988; Thomas 1996; Thompson *et al.* 1998). Therefore repeated wolf counts over a year period were therefore combined into a simple index of relative abundance. The A*nnual Abundance Index* (AAI) was calculated as the annual average of wolf counts for each transect (= ∑wolves sighted /number of counts in the year).

Preliminary analysis revealed clearer trends along time series of the annual index of wolf abundance than along the series of single counts. Trends in wolf abundance were obscured by the noise arising from variations among closely repeated counts –for example, counts on consecutive months sometimes gave markedly different results, and zero counts were occasionally recorded in areas and periods for which wolf density was known to be high. The different number of wolves sighted by chance in a line-transect thus appeared as a major source of sampling variance. This variability was then integrated into the standard deviation of the annual average of wolf counts (=AAI).

Among other factors that may affect the probability of animals being encountered and seen along transects, errors from variations in the time of the day and season of the counts are unlikely, because wolves live in stable, all-year round territories where they forage intermittently during daytime hours (Sillero-Zubiri 1994; Sillero-Zubiri & Gottelli 1995b). Biases due to the different ability of the observers to detect wolves were minimised by the presence of at least one experienced observer in each count. Differences in terrain and vegetation structure however can affect visibility and the detection of animals in different habitat types (e.g. short Afroalpine meadows versus *Helichrysum* heaths). Given also that wolves exist at different densities in different habitats - probably determining different probabilities of encounter - stratification of counts per habitat type was the strategy of choice. The lack of standardization meant that quantitative changes in wolf abundance could be assessed only within study areas.

To be of any utility, an index of abundance has to relate to the actual number of animals in some simple way; ideally via a positive, linear relationship with slope constant across habitats and over time (Thompson *et al.* 1998). In a validation exercise the values of the index were compared to contemporary total counts based on observations of focal packs. Validation data were available for nine years in Web and three years in Sanetti (Table 6.1). Regression was used to test for linearity in the relationship between total numbers of wolves (response variable) on the abundance index (explanatory variable). The effect of sampling frequency (i.e. number of counts averaged per year) was analysed in scatter plots versus the index standard deviation.

The index *Coefficient of Variation* (CV) was used to explore the effect of animal density on the index accuracy by comparing study areas.

6.3.3 Time series analysis

To detect trends in wolf abundance, a simple function was constructed to fit the time series of wolf counts in each study area (Minitab 13.3 Trend Analysis program). Segmental analysis was also conducted for subsets of the sequence (e.g. before and after an epizootic) to enhance the detection of shorter-term variations. The realized rate of population change (*r*) was calculated from the series of total population sizes. The shape of the function relating the rate of population change with increasing population size was used to describe patterns of population growth and detect density dependence.

Counts of people, domestic dogs and livestock were first standardized as their numbers per unit of distance (= individuals sighted per km of line-transect traversed). To account for the effect of seasonality in the use of pastures by livestock, and the associated movement of people, a decomposition method was used to separate the time series into linear trend and seasonal components (Minitab 13.3 Trend Analysis program). The data were averaged in three-month season blocks: namely: *dry season* (January to March); *early wet season* (April to June), *mid wet season* (July to September), and *late wet season* (October to December) (n= 1-8 counts per season). The decomposition analysis produced two main outputs: a time series of de-trended data and a time series adjusted by seasonality. A 'seasonal only' decomposition analysis was then run on the de-trended time series in order to assess the strength of the seasonal component. *The Mean Absolute Percentage Error* (MAPE) was used to assess the accuracy of the seasonal model fitted by the program. A MAPE <50% was chosen as indicative of significant seasonality based on the range of observed values. When a 'significant' seasonal component was detected, the time series of the seasonally adjusted data was used for trend detection.

6.4 Results

6. 4.1 Assessment of the index of wolf abundance

Index validation

The index of wolf abundance was validated against the actual size of the populations in Web Valley and Central Sanetti as recorded in the total counts. During validation years a rather constant proportion of all the animals present was detected in both populations (23% SE 2.8, n=11 years). The regression of population size on the index showed a significant positive relationship that explained 73% (R-square) of the observed variation (Fig. 6.2a). The equation fitted was: 1.99 (SE 0.38) x + 15.05 (SE 0.71); ANOVA F(1,10)=26.88, P<0.001). An unusual high count occurred in Web in 1989, producing a large negative residual (Fig. 6.2b). In that year, nearly half of the population was on average counted along the line-transect (48%). Excluding this data point, detectability was slightly lower and less variable (21% of the population, SE 1.8, n=10 years) and the regression provided a better fit for the abundance-index relationship: 3.09 (SE 0.30) x + 8.90 (SE 2.44), R-square: 0.92; ANOVA F(1,9)=98.17, P=<0.001 (Fig. 6.2c).

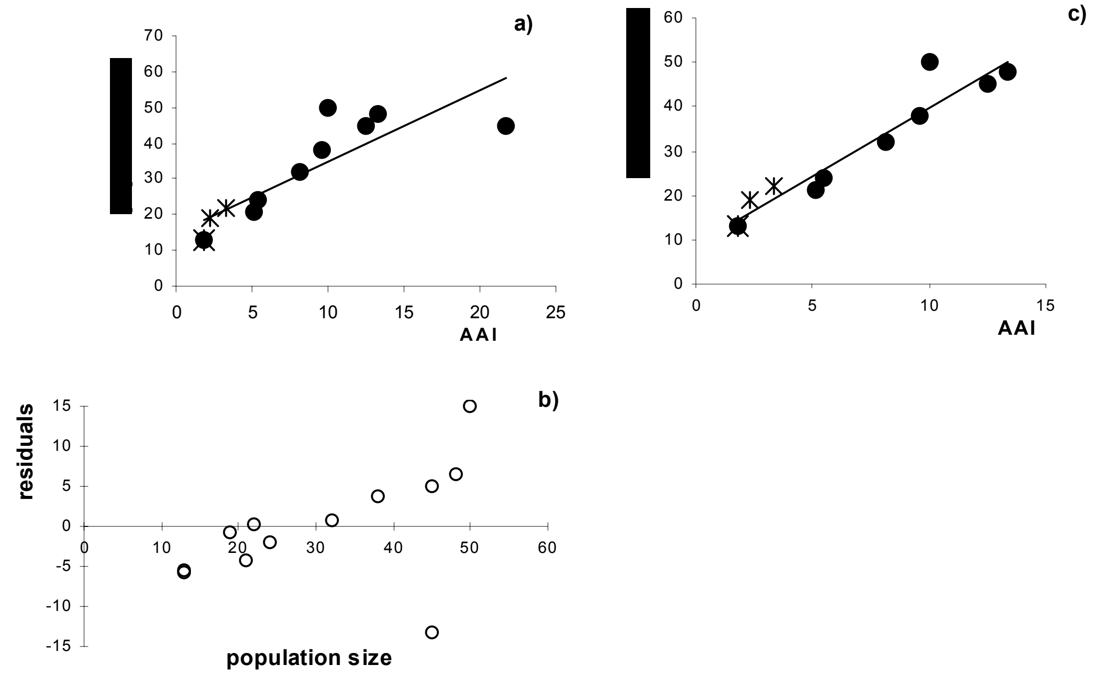


Figure 6.2 Index validation: a) Regression of population size on the wolf index (AAI) and b) plot of the residuals versus population size. c) Regression after removing the extreme point Web-1989. Stars are data points from Central Sanetti and circles from Web.

Index variability

Correlations between the index standard deviation and the number of counts per were not significant (Pearson's coefficients of correlations Web Valley r=0.29, P=0.41, n=10; Central Sanetti r=0.33, P=0.23, n=15; Western Sanetti r=0.23 P=0.44, n=13; Eastern Sanetti r= -032, P=0.60).

The index CV stabilized at around 0.5 when 10 or more repeated counts were averaged per year in optimal habitats (Fig. 6.3); two years with unusually large CVs were years of low wolf density after epizootics (1992 in Web and 1995 in Sanetti).

The effect of animal abundance in the index accuracy was evident when comparing areas: indices with largest CVs corresponded to good and marginal habitats, where wolf density is at least four times lower than in optimal habitat (even with 10 or more counts per year; Table 6.2). The index CV changed consistently with increasing numbers of wolves sighted by transect (Fig. 6.4): accuracy decreased dramatically when on average less than one wolf per transect was encountered (all counts in marginal habitat and some in good habitat); above that level, variability rapidly levelled off from intermediate CV values in good habitat to a relatively low and stable CV in optimal habitats (Table 6.2).

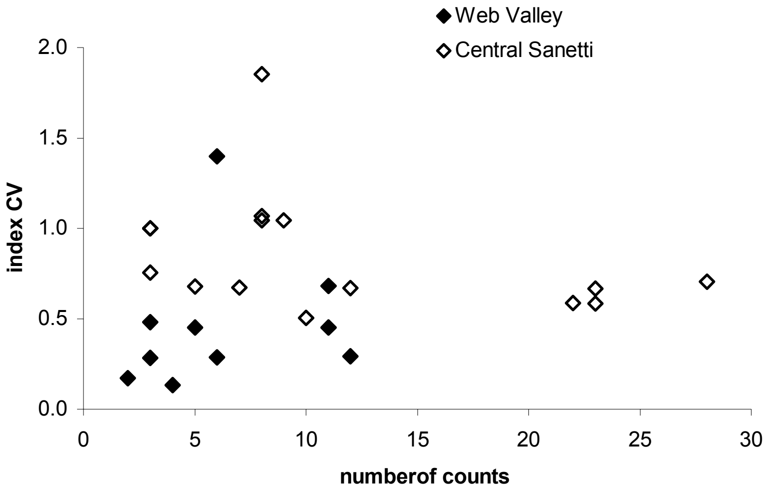


Figure 6.3 Plot of the index coefficient of variation (CV) versus sampling intensity (=number of counts per year) in the two optimal habitat areas.

		Coefficient of variation CV			
		All years		Years with 10 or more counts	
Study area	Habitat type	AV	n (=years)	AV	n (=years)
Web Valley	optimal	0.46	10	0.47	3
Central sanetti	optimal	0.86	15	0.62	6
Western Sanetti	good	1.39	15	1.27	7
Eastern Sanetti	marginal	2.77	6	2.89	4

Table 6.2 Average of the index coefficient of variation (CV) in habitats with different wolf density and for a subset of the years with more than 10 repeated counts.

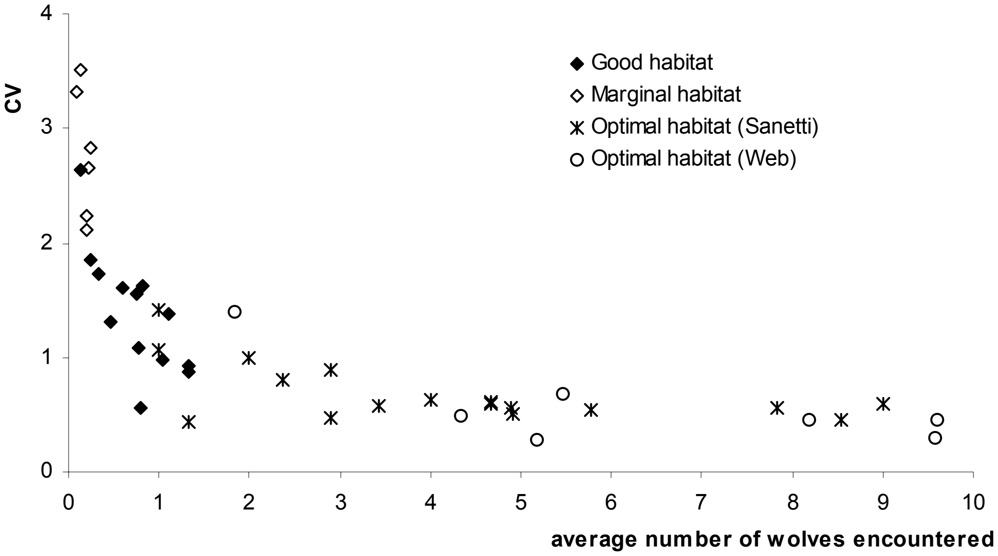


Figure 6.4 Changes in index variation (CV) with the number of wolves sighted along line transects. Index variability increased abruptly at low wolf densities (i.e. marginal and good habitat), and decreased and stabilized towards higher densities (i.e. optimal habitat).

6.4.2 Trends in wolf abundance and patterns of population change

The index of wolf abundance was used for trend detection in all study areas. An overall declining trend was detected in Sanetti's optimal habitat (1985-2000: slope= –0.20 SE 0.06; R-square= 0.45, ANOVA F(1,13)=27.02, P=0.006) (Fig. 6.5a). This long-term decline was not fully explained by the decline recorded in 1990, as the segmental analysis detected a significant declining trend for the period 1983 – 1989 (slope= –0.55 SE 0.12; R-square=0.83; ANOVA F(1,4)=21.04, P=0.021). After the epizootic in 1990, counts had increased by 1992, but were low again when monitoring re-started in 1994, followed by another small drop in 1995. By the end of the monitoring period in 2000 the population had recovered to pre-epidemic levels, yet still below the maximum of the early 1980s. It is pertinent to notice that the index in

1992 had a high CV and this point was influential in determining the steepness of the post-epizootic recovery in 1992 and the subsequent decline in 1995. There is a possibility that these short-term fluctuations were exacerbated by this year count.

Wolf counts in good habitat showed much less variability than in optimal habitat, with slight fluctuations and no overall trend. There was no conspicuous decline in good habitat at the time of the population decline in Central Sanetti, and counts in these two areas were uncorrelated (Pearson r=0.31, P=0.26, Fig. 6.5b). Wolf counts in marginal habitat were very low (Fig. 6.5c). All animals sighted between 1987-1991 almost certainly belonged to the single pack whose territory was traversed by this section of transect. The extreme rarity of wolf sightings between 1992-2000 coincided with the extinction of this pack around 1992, and solitary wolves seen twice in 1998 may have been transient wolves or in excursions from packs in the contiguous optimal range.

Population trends in Web Valley were analyzed from total counts, available for the whole monitoring period in this study area (1987-2000). This shorter time series, compared with that from Sanetti, mainly showed the fall and subsequent rise of wolves following the epizootic in 1992 (Figs. 6.6a and 6.6b). Before the population crash, population size fluctuated slightly with no significant trend, showing positive and negative annual changes (a mean rate of 5.0 ± 10.4 SD wolves per year over five years). When monitoring restarted, four years after the epizootic, there were no signs of population recovery. Since then however, wolf numbers increased consistently with positive annual changes in all years (average 8.0 ± 5.9 SD wolves per year over five years), reaching pre-reduction levels by 2000.

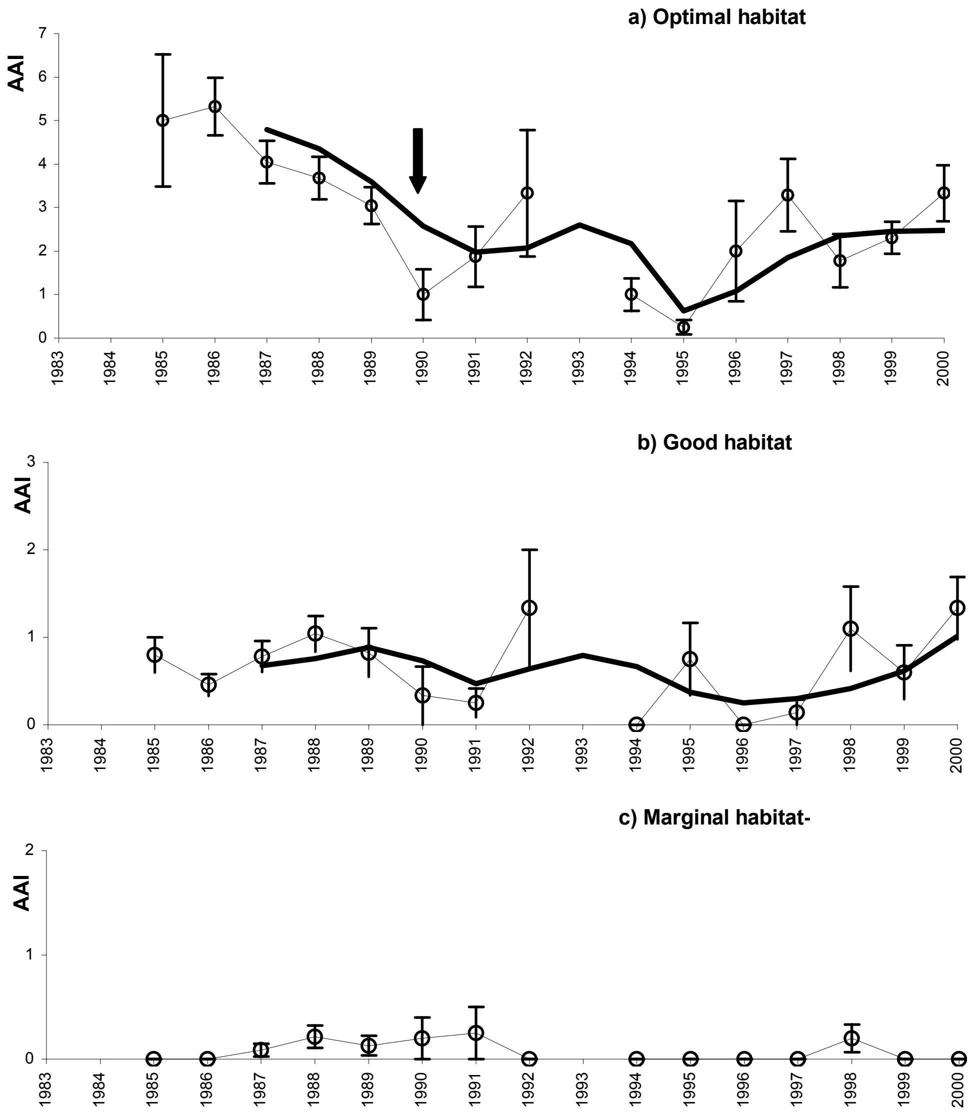
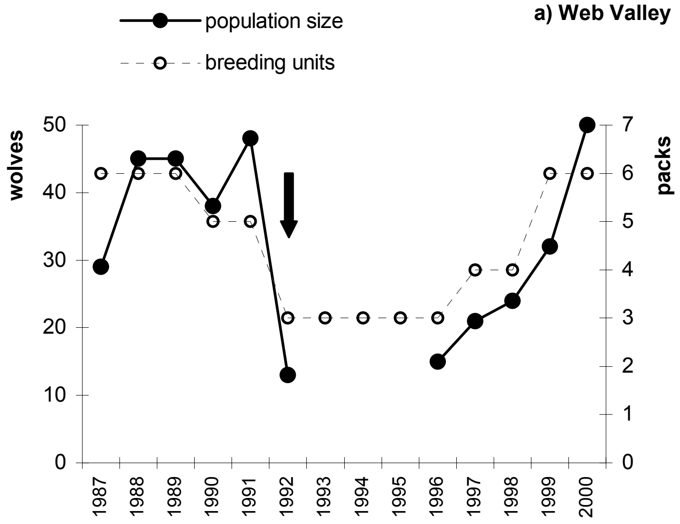


Figure 6.5 Time series of wolf abundance index in Sanetti's a) optimal, b) good and c) marginal habitat. Dark lines are the moving averages fitted to the time series. The arrow indicates the year of the documented, epizootic causes, population decline. AAI=annual abundance index. Y error bars are standard errors.

The recovery of the Web Valley population was mediated by the formation of new breeding units. Three out of five packs survived the epizootic in Web and the number of packs increased to six by 1999 (Fig. 6.6a), although the first new pack only formed four years after the population crash. On Sanetti, in contrast, the recovery of wolves after the high mortality of 1990 occurred solely through the enlargement of the two packs in the study area, after a third pack decimated by disease in 1990 finally disintegrated in 1992 (Fig.6. 6b). During the final three years of total counts in Central Sanetti (1998-2000) the population increased from 13 to 21 wolves (a mean rate of 4.0 ± 1.4 SD wolves per year).



b) Central Sanetti

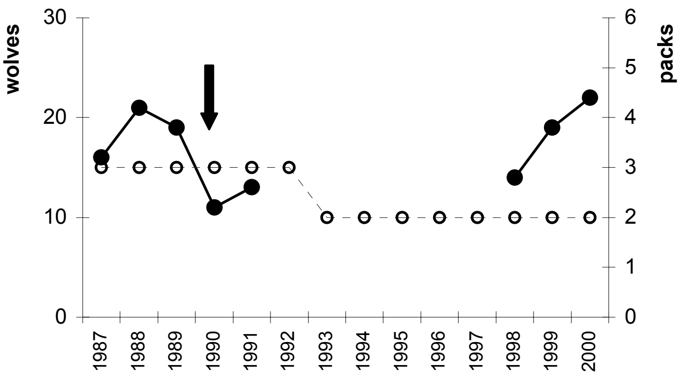


Figure 6.6 Time series of population sizes and pack numbers from total counts in the Web Valley (a) and Central Sanetti (b). Arrows indicate epizootics.

The relationship between the rate of population change (*r*) and increasing population size in the Web Valley fitted a quadratic function with the shape of an inverted-U (R-square= 0. 70; ANOVA F(2,5)=5.80, P=0.05). In Central Sanetti the relationship approached a negative linear function (R-square= 0.88; ANOVA F(1,2)=14.4, P=0.063) (Fig. 6.7). These results indicated that above certain size, population growth decreased with increasing population size (i.e. negative density dependence), but in Web the rate of increase was reduced at small population sizes after the epizootic, and actually increased with increasing population size (i.e. inverse density dependence).

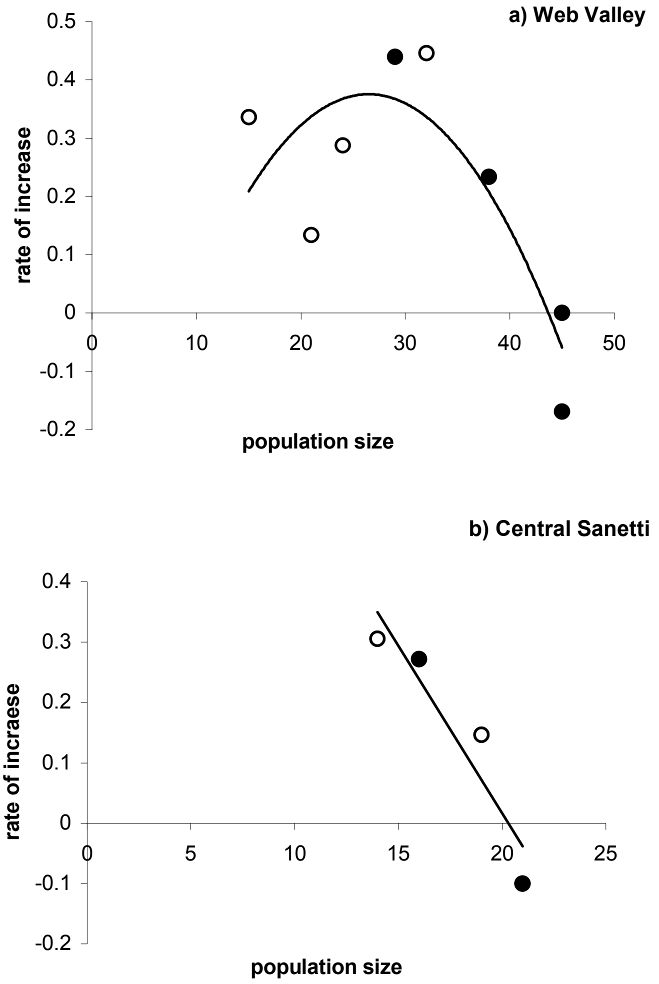


Figure 6.7 Relationship between the realized rate of population increase (*r*) and the size of the populations in (a) Web Valley (n=8 years) and (b) Central Sanetti (n=4 years). Black circles are years before an epizootic and empty circles years after epizootics, the year of the epizootic excluded.

The value at which population growth became zero was considered an indicator of the carrying capacity of that population (e.g. 45 wolves in Web and 20 in Central Sanetti). A percentage carrying capacity (%K) was then calculated for each year. This was used as surrogate for population size in order to explore a more general relationship between population size and the rate of change by combining the two populations. An inverted-U quadratic function also fitted the data (e.g. R-square: 76.5%, ANOVA F(2,9)=14.61, P=0.001) (Fig. 6.8): maximum population growth occurred at intermediate densities, it declined towards higher densities above 70% of the carrying capacity, and it was lower again below that threshold in Web. The data points on the density dependence side of the graph corresponded to the years before the epizootics in Web Valley and Central Sanetti, and the three years of final recovery in Central

Sanetti. The data points on the inverse density dependence side corresponded to the years of reduced density after the epizootic in Web.

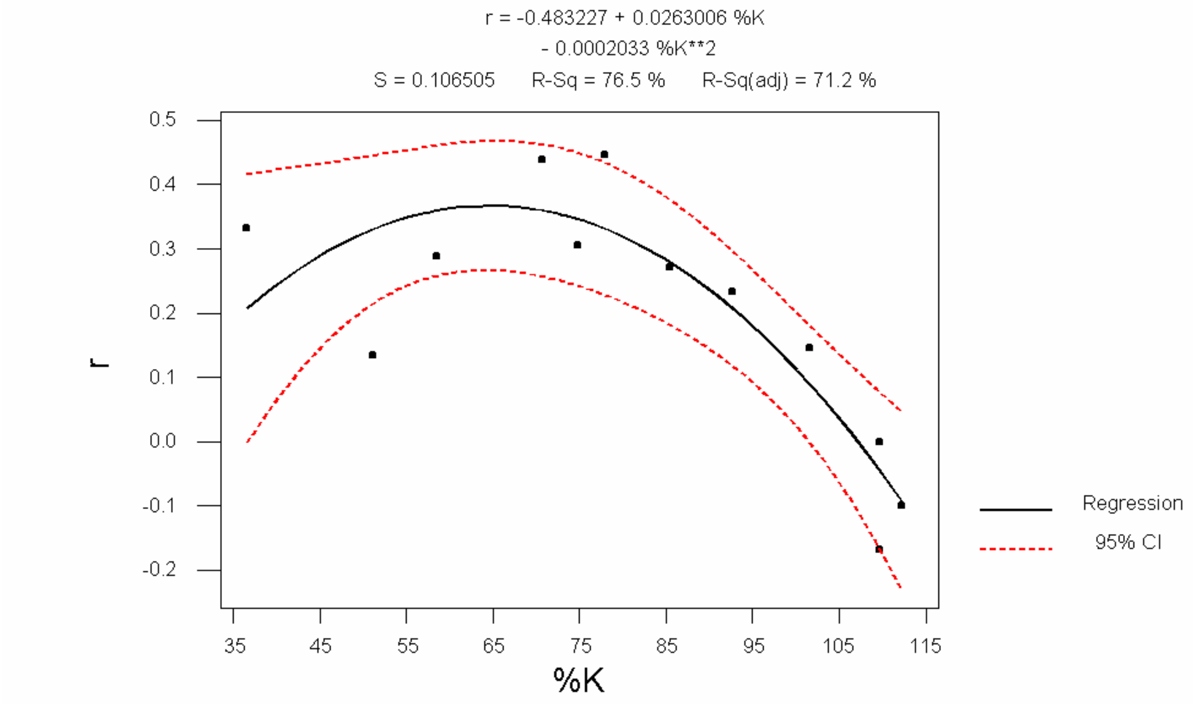
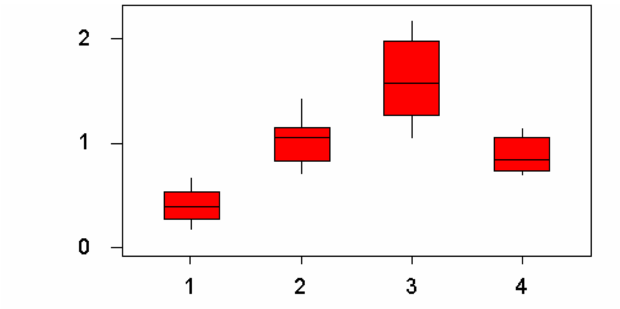


Figure 6.8 Relationship between the realized rate of population increase (*r*) and the percentage carrying capacity K (n=12 years).

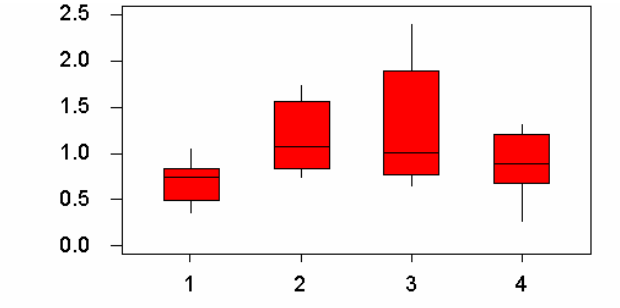
6.4.3 Agents of decline

Seasonal patterns were identified in the time series of counts of livestock and people in the Web Valley. Numbers of cattle, horse/donkeys and people increased from a minimum in the dry season to a maximum in the wet season, with intermediate values in the early and late wet seasons (*seasonality type A*, Fig. 6.9a)(Mean Absolute Percentage Error MAPE: 25.6%, 28.3%, 38.1% for cattle, horse/donkeys and people time series respectively; the smaller the value the better the fit). Counts of sheep and goats in Web showed a similar pattern - lowest counts in the dry season- but without a marked peak in the mid-wet season (*seasonality type A1*, Fig.6.9b) (MAPE: 38.6%). No evidence of seasonality was found in the time series of counts elsewhere with the exception of people counts in Eastern Sanetti, which were lowest in the dry season and again at the peak of the rainy season (*seasonality type B*, Fig. 6.9c, Table 6.3)(MAPE: 41%).

a) Seasonality type A: cattle in Web Valley



b) Seasonal type A1: sheep and goats in Web Valley



c) Seasonality type B: people in eastern Sanetti

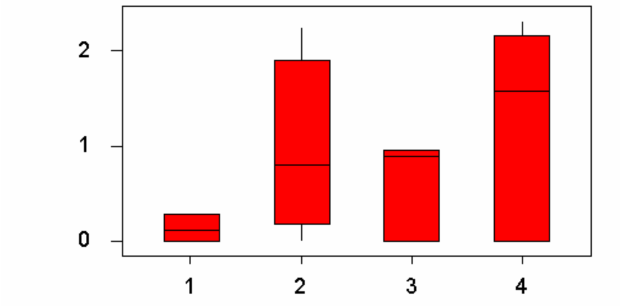


Figure 6.9 Seasonal patterns in count data: mean raw seasons (*) along the y axis and seasons along the x axe (1=dry season, 2=early wet season, 3=mid wet season, 4=late wet season). *The 'row seasonal' measures the difference between data point values in the de-trended time series and data point values on a moving average of seasonal length.

Livestock abundances increased consistently along the monitoring period in all the study areas with the exception of sheep and goats in Web Valley. Significant linear fits explained between 14% and 62% of the variation. Table 6.3 summarizes the results from trend detection analysis. Where seasonality was identified, the time series of the seasonally adjusted data was used for trend detection.

	Regression slope	R-square	F	P	n
Optimal wolf habitat					
Web valley					
Cattle	**0.495**	23.20%	(1,31) 9.34	**0.005**	50(17)
Sheep & goats	0.032	0.70%	(1,31) 0.23	0.637	50(17)
Horses & donkeys	**0.085**	24.60%	(1,31) 22.99	**0.000**	50(17)
Domestic dogs	**-0.002**	14%	(1,31) 5.81	**0.030**	50(17)
People	**0.008**	20.60%	(1,31) 7.01	**0.013**	50(17)
Central Sanetti					
Cattle	**0.046**	26.60%	(1,33) 11.96	**0.002**	57(22)
Sheep & goats	*not encountered*				57(22)
Horses & donkeys	**0.001**	25.00%	(1,33) 10.92	**0.002**	57(22)
Domestic dogs	*only one dog encountered*				24(8)
People	0.006	14.20%	(1,14) 2.32	0.150	24(8)
Good wolf habitat: Western Sanetti					
Cattle	**0.193**	62.00%	(1,33) 54.89	**0.000**	57(22)
Sheep & goats	**0.305**	31%	(1,14) 6.36	**0.024**	24(8)**
Horses & donkeys	**0.023**	42.50%	(1,33) 24.40	**0.000**	57(22)
Domestic dogs	*rarely enocuntered*				24(8)
People	**0.028**	52.70%	(1,14) 15.61	**0.001**	24(8)
Marginal wolf habitat: Eastern Sanetti					
Cattle	**0.200**	46.80%	(1,33) 29.09	**0.000**	57(22)
Sheep & goats	**0.126**	20.00%	(1,33) 8.25	**0.007**	57(22)
Horses & donkeys	**0.009**	26.10%	(1,33) 17.64	**0.002**	57(22)
Domestic dogs	*only one dog encountered*				24(8)
People	0.008	10%	(1,14) 1.58	0.2	24(8)

Table 6.3 Linear models adjusted to the time series of livestock, people and domestic dogs counts. P=significance level; N= time series length in number of seasons with missing seasons between brackets. ** The series of sheep and goat counts in good habitat was shortened to exclude an initial period with zero counts. Variations in sample sizes otherwise reflect the shorter period of people and domestic dog counts.

Highest and lowest livestock abundances were registered in the two *optimal* habitat areas, Web Valley and Central Sanetti respectively. No sheep/goats were found in Central Sanetti, cattle were rarely encountered and the few horses/donkeys sighted were associated to people travelling along the road. On the other hand, in the Web Valley all livestock types were over four times more abundant than elsewhere. To help visualize differences in the abundance and steepness of the increase the adjusted regression lines are shown in Fig. 6.10. Numbers of cattle and horses/donkeys in Web showed the most rapid increment of all, but sheep/goat abundances did not change significantly over the study period (Table 6.3). In Eastern and Western Sanetti (good and marginal habitats) cattle abundance was similar and increased at the same rate; sheep and goats showed a more rapid increment in the ericaceous heaths of Eastern Sanetti, where this type of domestic stock was absent until 1996.

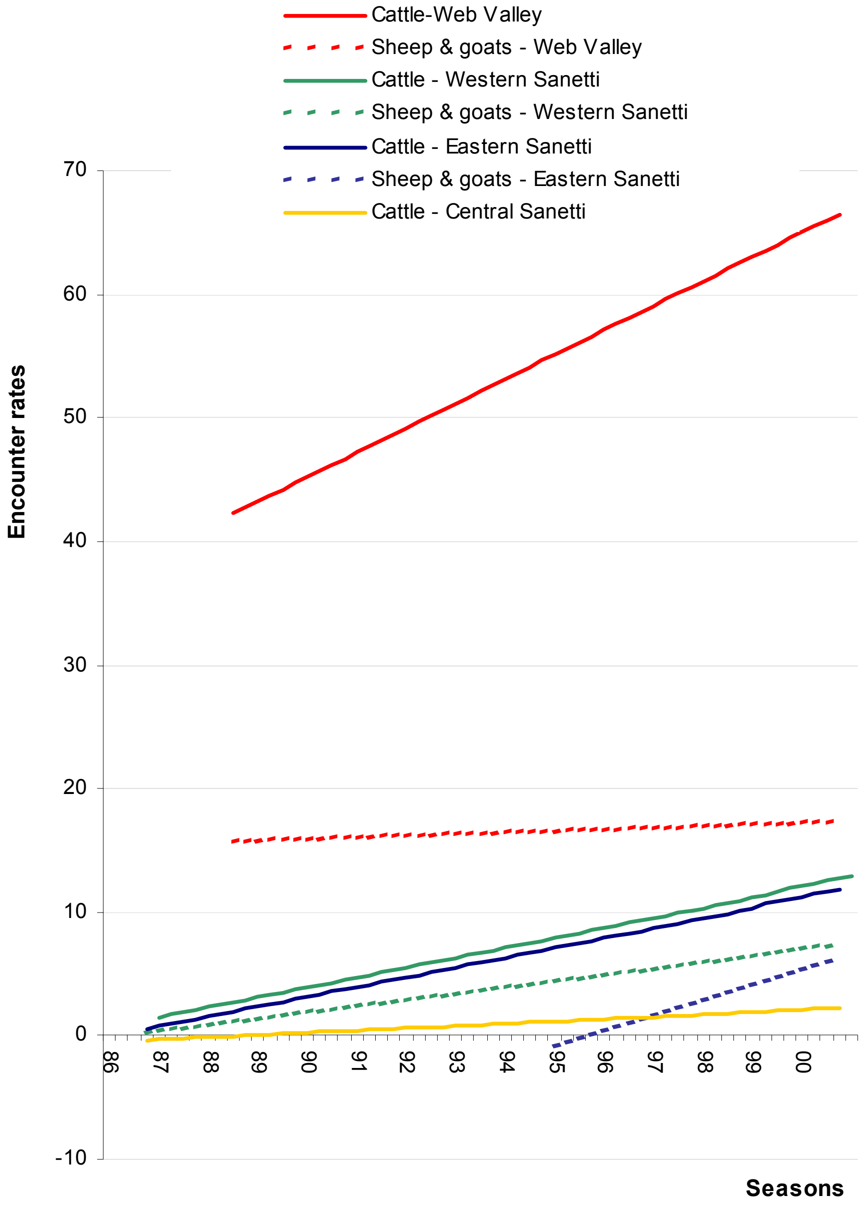


Figure 6.10 Regression lines fitted to the time series of abundances of cattle (solid line) and sheep & goat (dotted lines) encountered along line transects. All trends were positive and significant with the exception of sheep and goats in Web Valley that showed no significant trend.

More people were sighted in the Web Valley (encounter rates 3-7 times higher than in other study areas), but they were encountered at significantly increasing frequencies in all the study areas with the exception of Central Sanetti. Dogs were almost absent in Central Sanetti and were rarely seen in the other two study areas in the plateau. Although counts declined over the monitoring period, domestic dogs were most frequently encountered in the Web Valley (Table 6.3, Fig. 6.11). There was a rapid drop in dog counts in 1992 at the time of the rabies epizootic, and a more recent decline coincided with a dog vaccination and a public education campaign implemented by EWCP in villages around the wolf range in Web valley since 1997.

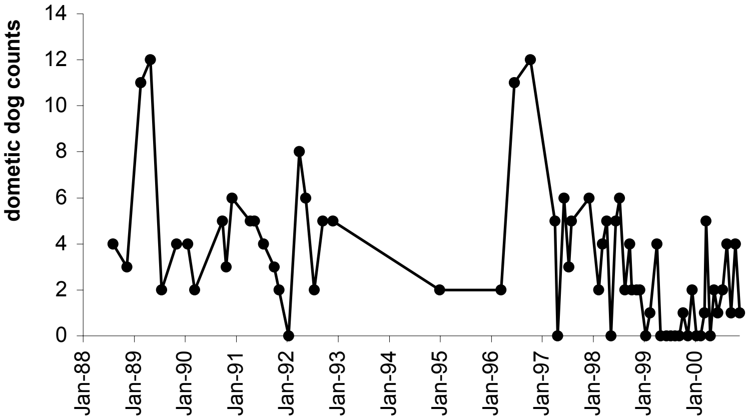


Figure 6.11 Counts of domestic dogs along the Web Valley line-transect.

6.5 Discussion

6.5.1 Population trends and agents of decline

The long-term monitoring programme in the Bale Mountains provided adequate data for the detection of trends in wolf abundance and enhanced our understanding of local threats. Major fluctuations in abundance occurred in the two populations in optimal habitat in association with well-documented declines driven by disease and sporadic shooting in the early 1990s (Sillero-Zubiri *et al.* 1996b; Laurenson e*t al.* 1998). While wolf numbers recovered fully by the end of the study, their levels in Central Sanetti were still below the historical maximum of the mid 1980s. Wolf numbers in the poorer habitat remained relatively stable, with slight fluctuations and no signs of severe mortality at the time of the epizootics or otherwise. On the other hand, the single pack in marginal habitat went extinct and this territory remained vacant until the end of the study in 2000.

Despite disruption to the dataset due to political unrest at the time, it was possible to observe the response of wolf populations to drastic reduction. A recovery gap before continuous population growth was evident in the populations disrupted by disease. In Central Sanetti there was an apparent immediate recovery followed by a lesser population drop in 1995, but these short-term fluctuations may not reflect proportional changes in wolf numbers because of the fewer and more variable counts during that period. An epidemic of canine distemper virus was detected among domestic dogs in the Web Valley around 1994 (Laurenson *et al.* 1997), but it was not possible to establish whether distemper spilled over to the wolf population (Laurenson *et al.* 1998). Indeed, there was no evidence of further wolf mortality due to human persecution or disease in Bale since the early 1990s events up the 2000 (EWCP unpubl. data).

In general, trends in abundance were not associated with trends in human counts, domestic dogs or livestock. Seasonality in livestock counts data impeded direct correlational studies, but no parallel was found between the approximated linear increment in livestock heads and trends in wolf abundance across populations. For example, a long-term decline was evidenced in Central Sanetti where livestock is virtually absent, and a rapid increase in grazing intensities in Western Sanetti contrasted with the relatively stability of wolf numbers. Moreover, the recovery of the disrupted populations occurred in the two areas where relative livestock abundances were highest, in Web Valley, and lowest, in Central Sanetti. A link between increasing numbers of livestock and the lack of an immediate recovery of wolves in Bale has been suggested (Stephens *et al.* 2001), but the study failed to account for the markedly different livestock densities in the two populations affected by disease. Previous studies had already shown that the activity of wolves was not significantly affected by presence of humans and livestock (Sillero-Zubiri & Macdonald 1997; Ashenafi 2001). Still, evidence of any negative impacts on wolves by increasing livestock grazing is equivocal. It is widely believed that overgrazing of high altitude pastures negatively affects wolves through unfavorable impacts on rodent populations (Nievergelt *et al.* 1998; Wehrli 1999; Ashenafi 2001) although studies in Bale and Menz found no supporting evidence (Sillero-Zubiri *et al.* 1995b; Ashenafi 2001).

Disease therefore emerged as the main cause of decline in wolf numbers. It is expected that high wolf densities, high contact rates between and within packs, and the presence of sympatric domestic dogs, all increase the likelihood and potential severity of a disease epizootic in Bale (Sillero-Zubiri *et al.* 1996b; Laurenson *et al.* 1997). This study would suggest that wolf density is actually more important than the abundance of sympatric domestic dogs for the spread of disease, particularly rabies. Evidence in support of this hypothesis is the absence of dogs in Central Sanetti and the lack of signs of simultaneous declines in the populations on poorer habitats where wolves occur at much lower densities. This interpretation concord with observations made in populations of other canids (e.g. jackals Loveridge & Macdonald 2001; Rhodes *et al.* 1998; red foxes *Vulpes vulpes* White *et al.*1995) and with predictions of epidemiological models, based on inter-group contact probabilities over a range of population densities (Woodroffe *et al.* in press).

6.5.2 Population dynamics

Absolute counts of wolves in the two populations in optimal habitats provided a natural experiment on the dynamics of populations affected by catastrophic events. Population sizes in the Web Valley were known for two 4-year periods before and after the epizootic, separated by a 3-year period of seemingly no change, and for a shorter period in Central Sanetti. Population dynamics were characterized by an initial period of relative stability at high density until the epizootic, followed by a period of recovery towards pre-epizootic levels with consistently positive population growth.

Population stability at a relatively fixed high density and the return of populations to pre-epizootic levels strongly suggest the existence of mechanisms regulating population size (Caugley & Sinclair 1994). Density dependence above a carrying capacity threshold was consistent with expectations of intraspecific competition for the rodent prey as a regulatory mechanism in populations of the Ethiopian wolf. The Afroalpine rodents constitute a very rich, predictable and rapidly renewable food resource (Sillero-Zubiri *et al.* 1995a) and wolves are able to locate the same prey at all times of the year (Sillero-Zubiri & Gottelli 1995a). Stability in the absence of disease and the recovery of populations to previous levels are indications of a stable food resource, and the absence of synchronous fluctuations in close local populations illustrated the minor role of environmental stochasticity in the dynamics of populations in Bale. This contrasts with results of studies of carnivore populations that rely on migratory or cyclic prey, or have a seasonally variable diet. Examples of density dependence in rates of population growth in carnivore populations are indeed uncommon (e.g. grey wolves Hayes & Harestad 2000). In most cases, variations in prey abundance - or environmental correlates - and interactions with density dependence and sociality were involved in the dynamics and recovery of carnivore populations (e.g. kit foxes Dennis & Otten 2000); Arctic foxes (Loison *et al.* 2001);

coyotes (Windberg 1995; Windberg *et al.* 1997), grey wolves, Hayes & Harestad 2000) and cheetahs (Kelly *et al.* 1998).

At the lower extreme of population densities, however, the population in Web showed inverse density dependence in the rate of increase at small population sizes. This limited capacity of wolves to exploit the greater amount of food available per animal requires an explanation. Two out of five packs disintegrated and went extinct in Web Valley during the epizootic; the subsequent formation of new packs was a phenomenon unique to this period and area. The first new pack however, only formed four years after the population crash, and in Sanetti the population recovered solely by the enlargement of surviving packs, after one went extinct shortly following the population drop. Consequently, the capacity for rapid recovery appeared limited by the processes of pack formation, limiting the numbers of breeding units. Limitations to population recovery from low densities have been observed in other species of obligate cooperative carnivores, such as African wild dogs (Courchamp & Macdonald 2001; Courchamp *et al.* 2002). Field observations and models suggest this might result from the need for helpers for survival and/or reproduction, possibly accompanied by the existence of a critical pack size. Such an Allee effect could explain the inverse density dependence observed (Courchamp *et al.* 1999; Stephens & Sutherland 1999).

6.5.3 Conservation implications

Habitat loss and range contraction have historically been a major cause of decline in Ethiopian wolf numbers across the species' distribution (Marino 2003). On the other hand, Ethiopian wolf populations appear to be relatively stable and resilient to catastrophic events, or to habitat modification by grazing. Still population viability models predict that rabies and canine distemper will cause substantial fluctuations and substantial population extinction risks in small populations of Ethiopian wolves (Haydon *et al.* 2002). Concerns of the risk of disease epizootics among wolves are rooted in the fact that rabies affects domestic dogs and livestock in all known wolf ranges (Marino 2000; Ashenafi 2001) and the expectation that, with increasing contacts between wolves and people, the risks of disease transmission from domestic animals will increase. In addition, populations with inverse density dependence will have even lower probabilities of recovery if driven to low population sizes by such catastrophic events.

The Ethiopian Wolf Conservation Programme works to control infectious diseases in wolves through the vaccination and sterilization of domestic dogs around wolf ranges in the Web Valley and by research aimed at confirming the role of domestic dogs as a major reservoir of rabies in Bale and on the effects of vaccine intervention in dogs (Laurenson *et al.* 1998). This study further highlights the importance of the differential vulnerability to disease in local populations of wolves in Bale. It is apparent that vulnerability will be higher in optimal habitats with high wolf density, particularly, although not necessarily, where wolves are in closer contact with people and their domestic dogs (Web Valley). Having returned to density levels similar to those at the time of the last epizootic, the populations in Central Sanetti and Web are newly at risk. Indeed, an epizootic has been detected in Web in October 2003 and diagnosed as rabies (K. Laurenson, pers. comm.); to date over half of the wolf population there has died (S. Williams, pers. comm.).

The increasing use of wolf ranges for livestock grazing in Bale also deserves a word of caution. High livestock numbers and their steady increase in the Web Valley do not appear to have had negative effects on wolves and on the capacity of population to recover. Similar livestock pressures in the high altitude plateau of Central Sanetti could however be problematic - as with virtually no livestock, rodent and wolf abundances are presently similar to those in the Web Valley. It appears inevitable that with the increasing density of humans in the highlands of Bale, the use of high altitude pastures for grazing could soon reach levels with negative consequences for wolves. Not only are livestock densities increasing but also grazing regimes are changing and not all areas are used for grazing on seasonal bases. There is an obvious need for further research to understand and predict the potential effect of grazing on wolf populations. It can be expected that primary productive and rodent abundance will be more severely affected in unproductive than productive environments, with implications for the persistence of wolf populations inhabiting habitats of poor prey quality.

It follows that regular wolf monitoring should remain an important component of conservation efforts aimed to reduce the risk of future declines in wolf populations. Wolf counts along line-transects can successfully capture trends in local populations when repeated counts are conducted over several years, and to measure the levels of potential agents of decline. Overall, the resolution of the index of wolf abundance could be improved either by increasing the distance traversed by the transect - therefore encountering more animals - or by increasing the number of repeated counts in each year. With 10 or more counts per year, coefficient of variation CV for the annual index of abundance fell within the levels described for small and medium-size mammals (50-100% CV) and approached the levels of other groups, including large mammals (25-50%CV) (Gibbs 2000). Although counts are less accurate in areas with low wolf density, monitoring in poorer habitats, or areas peripheral to human settlements, gathers useful information on the circumstances and timing of local extinctions or wolf range contractions. The monitoring programme in Bale also has potential as an early warning system, by detecting in real time departures from population trends.

CHAPTER VII

The fall and rise of Ethiopian wolves: a natural experiment on population dynamics and regulation

Abstract

The fall and rise of Ethiopian wolves (*Canis simensis*) in the Bale Mountains constituted a revealing natural experiment on dynamics of populations of a highland endemic, social carnivore. Demographic, structural and spatial parameters at pack and population levels were compared in two stages: a pre-epizootic period of relative stability at high density, and a post-epizootic period of continuous recovery from low densities. The data come from focal observations of packs in two local populations under similar environmental conditions that experienced declines of different magnitudes. High adult survivorship was observed all along, whereas recruitment (i.e. the rate of pup survival in their first year) was higher during the recovery period. Larger litter sizes also facilitated the recovery, but delays in the formation of new breeding units in the more severely reduced population constrained reproduction and lead to inverse-density dependence in the rate of population growth. There was no evidence of a causal Allee effect at pack level. Density dependent survival contributed to regulate populations at the upper extreme of animal densities. At the lower extreme, packs expanded spatially and augmented in size but new breeding units only formed once a pack was large enough (group size 14) to allow for splitting, or when sufficient dispersers coalesced (3 to 5) to defend a new territory. Expansionism and delayed dispersal prevailed below carrying capacity levels, and later territory holders benefited from budding part of their natal range. The findings have important implications for our understanding of the selective forces underlying sociality in the Ethiopian wolf.

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7.1 Introduction

Knowledge of the biology of populations is a prerequisite to understanding a species' behavioural ecology and evolution, and to develop conservation solutions. Ecologists have long debated the role of density dependence (the return of a population to an equilibrium) and stability (a relative constancy in population size) in the dynamics of populations (Bonsall et al. 1998). Most studies focus on the importance of negative density dependence at high densities and the mechanisms imposing an upper limit to population size. The demonstration of density dependence at some stage in the life cycle of a species may result from competition for resources or space, the effect of predators, parasites or diseases (Caughley & Sinclair 1994). Also longstanding is the idea that there might be a minimum density for a species to maintain itself in nature. As W.C. Allee noted, "under-crowding, as well as overcrowding, can be limiting" so that a species can suffer a decrease in the per capita rate of increase when populations reach small sizes (Allee et al. 1949).

Such an 'Allee effect' in cooperative species can be a consequence of a reduction in social interactions when individuals are scarce, as a critical number of helpers sometimes appear necessary for significant reproductive success or survival in species of cooperative carnivores (e.g. wild dogs *Lycaon pictus* (Malcolm & Marten 1982), banded mongooses *Mungo mungo* (Cant 1998) and dwarf mongooses (Creel & Creel 1991)). Empirical evidence in support of the Allee effect in cooperative carnivores is an increase in reproductive success and/or survival with increasing group size (e.g. in dwarf mongooses *Helogale parvula* (Rood 1990), suricates *Suricata suricatta* (Clutton-Brock et al. 1999a), black-backed jackals *Canis mesomelas* (Moehlman 1979), and lions *Panthera leo* (Packer et al. 1988)). When populations become small Allee effects can lead to inverse density dependence in the rate of population growth (Stephens & Sutherland 1999), but an empirical test is still needed to demonstrate the mechanism by which an Alle effect at the group level affects population-level phenomena (Courchamp et al. 2002).

Allee effects are good examples of 'intrinsic' mechanisms of population regulation. In general, the social structure of mammals can act in such a way as to disrupt the reproductive physiology of some females, thus affecting reproduction, or to influence access to resources, affecting mortality. Clearly a more explanatory and predictive understanding of population change can be achieved if the behavioural bases of demographic change are taken into consideration. Very few population studies succeeded in the difficult task of integrating detailed understanding of the dynamic of social groups (but see Clutton-Brock et al. 1999b). Natural experiments, such as those driven by catastrophic events, are very rare opportunities in which regulation can be detected, because populations exhibit a broad range of density variation. This study made use of the fall and raise of Ethiopian wolves (*Canis simensis*) in the Bale Mountains as such an experiment on populations of a highly social, cooperative carnivore.

Two local populations that existed at high-density were drastically reduced by epizootics and persecution in the early 1990s. Social groups became smaller and some went extinct (Sillero-Zubiri et al. 1996b). Wolf numbers recovered to pre-epidemic levels by 2000, but pack formation took time and the rate of population growth was inversely density dependent at lowest densities (Chapter 6). The objective of this study is to identify patterns and processes of population change and the underlying mechanisms, including density dependence and Allee effects. Spatial, structural and demographic data, both at pack and population levels, were compared between two stages: a period of population 'stability' at high density (i.e. before the epizootic) and a period of 'recovery' from small numbers (i.e. after the epizootic), when populations showed positive annual changes in every year. To account for intrinsic factors affecting regulation this study combined population-level analysis with the dynamics of social groups. In populations of social species such as the Ethiopian wolf, intrinsic regulation, if occurring, is expected to be mediated by dispersal, territoriality and reproductive suppression (Wolff 1997). While the capacity for self-regulation is not in itself an evolutionary strategy, these factors can all be adaptive at the individual level. By testing ways in which these behaviours affect population-level phenomena this study advances our understanding of the adaptive value of social strategies in the Ethiopian wolf.

Ethiopian wolves show an intricate social system seemingly adapted to space constraints in the distribution of their prey, the high-altitude rodent fauna. The patterns of delayed dispersal and reproductive suppression shown by Ethiopian wolves are common among social canids particularly when space and/or breeding opportunities are limited (Moehlman 1983; Creel & Creel 1991; Sillero-Zubiri at al. 1996a). Before the decline, wolves in the study populations occupied all suitable habitat in a tight mosaic of tessellated territories (Sillero-Zubiri & Gottelli 1995b). The lack of vacant territories and of reproductive opportunities favoured the delayed dispersal of young with the formation of groups of close kin (Sillero-Zubiri at al. 1996a). Following population crashes, windows for territorial colonization and independent reproduction suddenly opened, with possible concomitant changes on the selective pressures for sociality and cooperation.

Although Ethiopian wolves forage alone, all pack members help to defend a territory and to raise the pups of the dominant pair (Sillero-Zubiri & Gottelli 1995b). Subordinate females are at most times reproductively suppressed and their chances of accessing reproductive status are very low. Most disperse at maturity, when they become *floaters* or face long-distance dispersal. Males are phylopatric and experience a higher turnover of the reproductive position; they also benefit from male-coalitions to access extra-pack copulations during the short mating season. Thus under conditions of habitat saturation, the size and composition of social groups was mainly determined by births and deaths -the few immigrants were *floaters* or females from adjacent packs- and by the tendency for females to disperse long distances (Sillero-Zubiri & Gottelli 1995b), determining a male-biased sex structure.

At reduced densities, following the epizootic, subordinate females in particular are expected to attempt independent reproduction, either by budding (a subordinate female once attempted to split a pack unsuccessfully) or by dispersing individually into a pool of dispersers that can eventually merge into a colonizing group. The provision of dispersers could be constrained if at reduced densities small packs do worse than larger pack in terms of survival and reproduction, slowing the capacity for population growth. A previous study by Sillero-Zubiri *et al.* (2004) produced no evidence of enhanced reproductive success with increasing numbers of helpers at the den or the presence of an allo-suckler; still helpers reduced the reproductive workload of the dominant pair, and may just ‘pay to stay’. Thus the benefits of cooperative breeding in Ethiopian wolves remain elusive. The communal defence of a limited food resource appears as the most obvious advantage of sociality: larger packs do better at territorial contests, so that larger packs tend to defend larger territories, and whenever possible a pack would expand spatially for example after the extinction of a neighbouring pack (Sillero-Zubiri & Gottelli 1995b). If persistent at reduced densities, this 'expansionist' strategy (*sensu* Kruuk & Macdonald 1985) could raise the costs of settlement for colonizing pairs or groups, because expanding packs can remove the vacated areas and interstices (as observed in a disrupted population of red foxes *Vulpes vulpes*, Baker et al 2000). The establishment of an exclusive territory appears to be a prerequisite for independent reproduction. If there is a certain pack size requirement for new groups to defend successfully a new territory, it can potentially influence the formation of packs and the speed of recovery.

7.2 Methods

7.2.1 Study populations

The Bale Mountains in southern Ethiopia (7ºS, 39º45'E) make up the largest Afroalpine range in Africa and contain more than half of the surviving Ethiopian wolves. The two local populations studied occurred in the *Web Valley* (3,450m) and the *Sanetti Plateau* (4,000m), where wolf and rodent prey biomass are exceptionally high. Twenty kilometres of suboptimal habitats separate the populations, which remained closed to immigration during the years previous to the decline (Sillero-Zubiri & Gottelli 1995b). The collection of data from focal packs was initiated by C. Sillero-Zubiri & D. Gottelli (1987-1992) and continued by the Ethiopian Wolf Conservation Programme (1996 to present), after a gap of a few years due to political unrest in the region. Between three and six packs occupied *ca.* 35km^2 of Afroalpine habitat in the broad valley of the upper Web River and two to three packs *ca.* 20km^2 of similar habitat in the Sanetti Plateau. Two separate epizootics, combined with persecution in Sanetti, affected these populations in the early 1990s; 77% of known wolves in the Web Valley died or disappeared over a few months in 1991-1992, including whole packs, and 54% died or disappeared in Sanetti in 1990 (Sillero-Zubiri *et al.* 1996b). At the end of the monitoring period in 2000, populations had recovered to pre-epizootic levels.

7.2.2 Count data

Direct observation of focal packs provided data on pack numbers, their size and composition. Total counts were conducted by direct observations during the breeding season (October to March). Wolves were directly observed through binoculars at 20-500m, on foot or from horseback.

During the period before the decline (1987-1991) wolves were individually recognized by ear-tags and coat patterns. During the period of recovery (1996-2000) total counts relied upon complete enumerations of pack members (Greenwood, 1996): records were kept of all wolves seen around the den, during social greetings and patrols, until no new individuals were observed and the list was completed. Pack enumerations were facilitated by the inherent stability of packs and territories (Sillero-Zubiri & Gottelli 1995b), the concentration of pack members' activity around the den during the reproductive season, and during patrols and greetings, some animals with unique coat patterns, and the easy recognition of age and sex classes and of the dominant pair from behavioural observations. Wolves were classified into three age categories: pups (from emergence at three weeks of age until they became subadults the next season); subadults (1-<2 year old, the surviving pups from the previous breeding season); and adults (≥ 2 years old, all sexually mature animals) (Fig 7.1). A successful breeding attempt was considered when pups emerged from the pack's den. New packs were recognised as a new group that bred successfully in a newly established territory, which could be part of a territory formerly occupied by a different group.

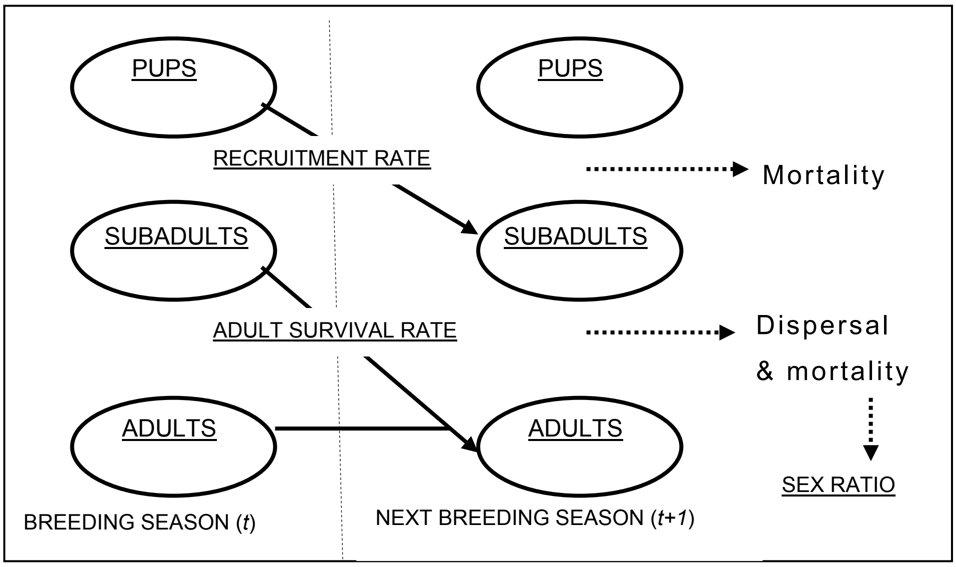


Figure 7.1 Representation of the life cycle of the Ethiopian wolf (underlined the parameters measured)

7.2.3 Structural and demographic parameters

Population size: total number of adult and subadult wolves in the study area at the time of the pup emergence.

Pack size: number of adult and subadults within a pack.

Sex ratio: ratio of male to female wolves in a pack or population (adults and subadults).

Litter size: number of pups at the time of emergence from the den.

Total reproduction: number of pups born in the population in one year.

Recruitment rate: survival of pups into the next breeding season, when they become subadults ($=\text{subadults}_{t+1} / \text{pups}_t$) (Fig. 7.1).

Adult survival rate: the combined survival of subadults and adults into the adult category on the next breeding season ($=\text{adults}_{t+1} / (\text{subadult+adults})_t$) (Fig. 7.1).

Survival rates were calculated from a simple life-table method or 'current life table' (McCallum 2000). The table is constructed from a snapshot of the population or pack in successive years, from which the annual survival for each age class is calculated (Fig 1). It was not possible to determine subadult survival as no further age classes were identified after sexual maturity at age 2. The assumption of closed populations and accurate age identification were safely sustained, as the broad age classes were easy to recognize and there was no immigration, at least during the first period.

7.2.4 Spatial parameters

Pack home ranges were calculated using ArcView's Animal Movement program (Hooge & Eichenlaub 2000) using restricted minimum convex polygons (5% outlier locations removed). Sillero-Zubiri & Gottelli (1995b) previously validated the utility of minimum convex polygons to represent the home range of a pack, by pooling the locations of all individuals in that pack between October and March (i.e. the dry season, matching the biological breeding-through-independent period). The location data were independent observations of wolves, excluding pups; location data was very scarce for the last season 1999-2000 and this year was excluded from spatial analysis. The area of occupancy of a population was calculated as the minimum convex polygon of all location points for each year's dry season period. Population density is the number of adult and subadult wolves/km^2 of the area of occupancy, and territorial density the number of adult and subadult wolves/km^2 of pack home range.

7.2.4 Data analysis

Field or natural experiments are usually called 'quasi-experiments'. These result from some treatment applied to individuals or, more often, to habitats containing individuals, which are not under direct control of the investigator. Although a strict cause and effect relationship cannot be addressed by a quasi-experiment, the strength of inference related to some cause is still much stronger than in a simple observational study in which there is no manipulation or treatment (Thompson *et al.* 1998). The drastic decline of wolves in Bale was used as a quasi-experiment to compare data in two time blocks: a pre-epizootic period of 'stability' at high density, and a post-epizootic period of 'recovery' with continuous population growth from low density. The dataset covered five years in each period in Web (1987-1991, 1996-2000) and three years in each period in Sanetti (1987-1989, 1998-2000) excluding the year of population decline (1992 and 1990 respectively). The non-parametric Mann-Whitney U-test is a two-sampled un-paired test of significance and was used to test the null hypothesis of no difference in pack-level variables between periods. The test compares the ranks of a parameter average (e.g. the average size of litters of each pack) in the two periods. Samples sizes were, before and after the epizootic respectively: n1=6 packs and n2=5 packs in Web, and n1=3 packs and n2=2 packs in Sanetti. Population-level parameters were compared by contrasting parameter averages and standard deviations in the two periods.

Density dependence effects on demographic parameters (response variable) were tested using regression-based statistical methods, which rely on a range of density values (predictor variable) being available (McCallum 2000). Density dependence was tested both at the level of packs and populations.

7.3 Results

7.3.1 Pack numbers and the formation of new groups

Pack numbers remained remarkably constant during the years previous to the epizootics (Fig. 7.2 and Fig. 7.3). There were three packs in Sanetti between 1988 and 1990 (*BBC, Nyala and Crane Lakes*) and five packs in Web between 1987 and 1991; a sixth (*Terapesa*) disintegrated after the death of its alpha female in 1989 (Sillero-Zubiri & Gottelli 1995b). Three out of the five packs went extinct in Web during the 1992 epizootic(*Wolla, Fincha and Sodota*), and in Sanetti the *Crane Lakes* pack left with only three wolves in 1990, eventually disintegrated in 1993 (when only two wolves remained, one male and one female). Only in the Web Valley was pack formation a component of the recovery process. The first pack appeared in 1997, four years after the epizootic, and by 1999 numbers had reached the previous maximum of six packs (Fig 7.2).

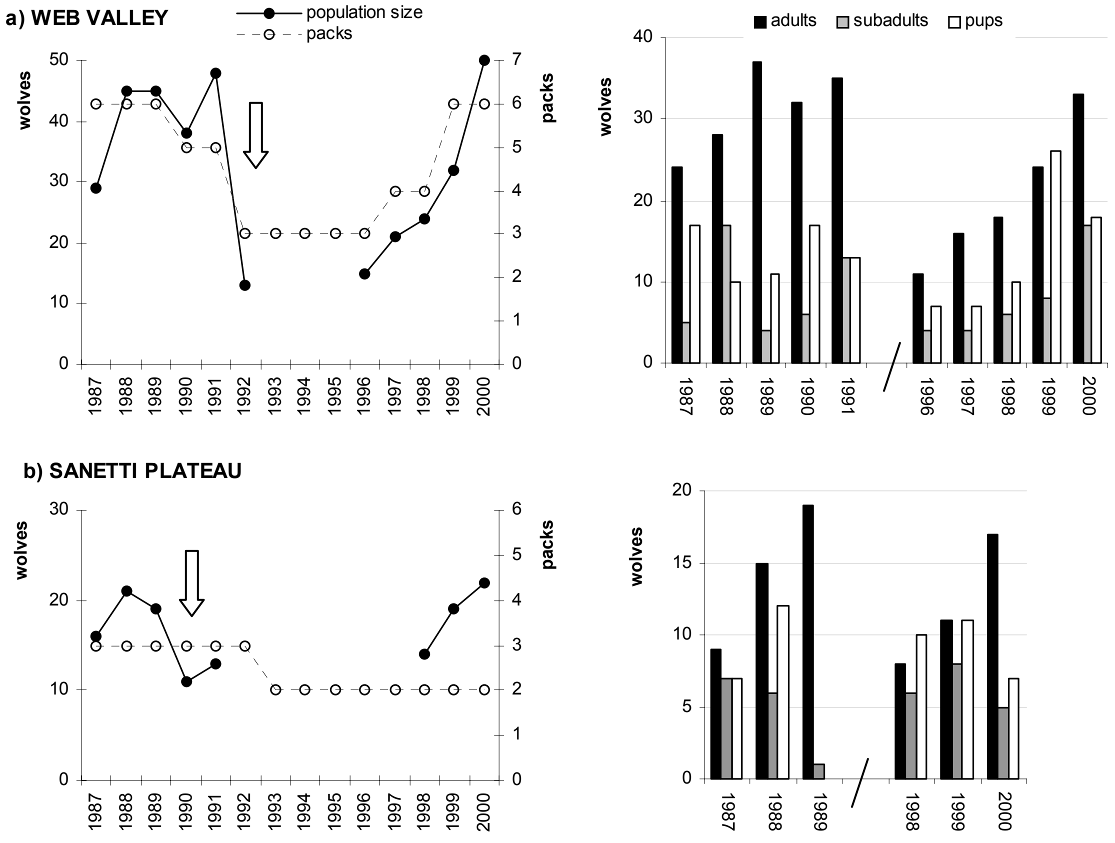


Figure 7.2 Time series of population sizes, pack numbers and age classes in the Web valley (a) and the Sanetti Plateau (b). Arrows indicate the year of the population decline.

New packs formed by three mechanisms (Fig. 7.3):

<u>'Reorganizations'</u> occurred after pack disruptions in the transitions between *Sodota, Hybrid* and *New Fincha*, when immigrants joined wolves from a disrupted pack. Survivors from *Sodota,* which included two dog-wolf hybrids, reorganized immediately after the epizootic and formed the *Hybrid* pack in that same year. The two hybrid males disappeared in 1998 and the surviving female joined two males of unknown origin to form *New Fincha.*

<u>'Pack fission'</u> accounted for the origin of *Darkeena* from *Mulamu;* the split of *Mulamu* was the first successful fission registered. A subordinate female observed to be pregnant, denned on the fringes of her natal territory accompanied by other members of the pack and gave birth to four pups. Of the original 14 adults and sub-adults, nine remained in *Mulamu* and five formed *Darkeena*. Another Other attempts did not succeed: in 1991 a subordinate female in Web attempted to split a pack but her litter died, most probably killed by the dominant female, and the break-away group rejoined the natal pack (Sillero-Zubiri & Gottelli 1995b). A splitting attempt in 1999 by a group of wolves from the *BBC* pack in Sanetti ended in a similar fate.

<u>'Coalescence of dispersers'</u> resulted in the formation of *New Sodota* (1997) and *Megity* (1999). The origin of every pack member remained unclear, but two wolves in the new pack *Megity* were known to be from *Kotera* (one male and one female). The analysis of pack demography (see below) also confirmed that established packs provided at least some of the dispersers involved in pack formations (see below).

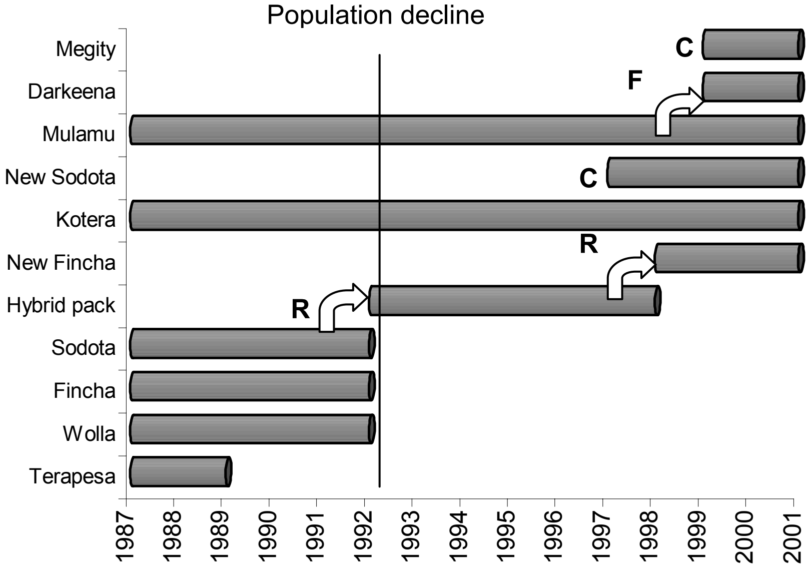


Figure 7.3 History of Ethiopian wolf packs in the Web Valley. Arrows indicate connections between established and newly formed packs: via reorganization of members after disruption (R), pack fission (F) or coalescence of dispersers of various origins (C).

7.3.2 Size and structure of groups and populations

Populations were maintained within a narrow range of high densities before the decline, averaging 1.4 (SD 0.2) wolves/km^2 across 5 years in Web, and 0.9 (SD 0.1) wolves/km^2 during 3 years in Sanetti. Age classes fluctuated in size with no significant trend, with the exception of the adult class in Sanetti that grew consistently, but not the population as a whole (Fig. 7.2). During the recovery, populations increased in size each year. The adult class grew consistently at a rate of 5.2 ± 0.7 adults per year in Web (linear regression R-sq 0.95; ANOVA, F(1,3)=54.81, P=0.01), and in Sanetti from 8 to 17 adult wolves (insufficient data to fit a model). The subadult class also increased consistently in Web (3.0 ± 0.95 subadults per year, linear regression: R-sq 0.77; ANOVA F(1,3)=10.1, P=0.05)(Fig. 7.2).

Packs fluctuated in size during the pre- epizootic period, with the exception of *Sodota* that grew consistently (Fig. 7.4). Fluctuations were asynchronous among packs, with the exception of the first year (1997-1998) when most packs augmented and the populations appeared to recover from a previous decline (Fig. 7. 2). In contrast, packs showed a clear tendency towards group augmentation during the post-epizootic period (Fig. 7.4). Although in 1991, coincident with the formation of two new packs, two 'old' packs did not grow (*Kotera* and *Mulamu*) and one declined (*New Sotoda),* suggesting that they provided at least some of the dispersers. *New Fincha* was exceptional in that this pack persisted with only three wolves in any given year. The sole female in this pack never reproduced nor showed signs of pregnancy or denning behaviour, probably because of reduced fecundity as she descended from dog-wolf hybrids in the *Hybrid* pack (two other hybrids identified later in the *Mulamu*'s litter in 1998 were soon sterilized).

The Sanetti population recovered via pack augmentation only, and the size of social groups ranged from 5-8 and 6-13 before and after the decline respectively (packs with more than 8 wolves only occurred during the recovery) (Fig.7.4.b and Table 7.1). In the Web Valley the packs that survived the epizootic also attained large sizes (up to 9 and 11), whereas colonizing packs started small (with 3, 4 and 5 wolves) and increased rapidly in size (*Megity* and *Darkeena* augmented to 9 and 11 wolves on their second year) (Fig. 7.4a). Consequently, the average size of packs was not significantly different between periods (Table 7.1, Mann-Whitney test P=0.243).

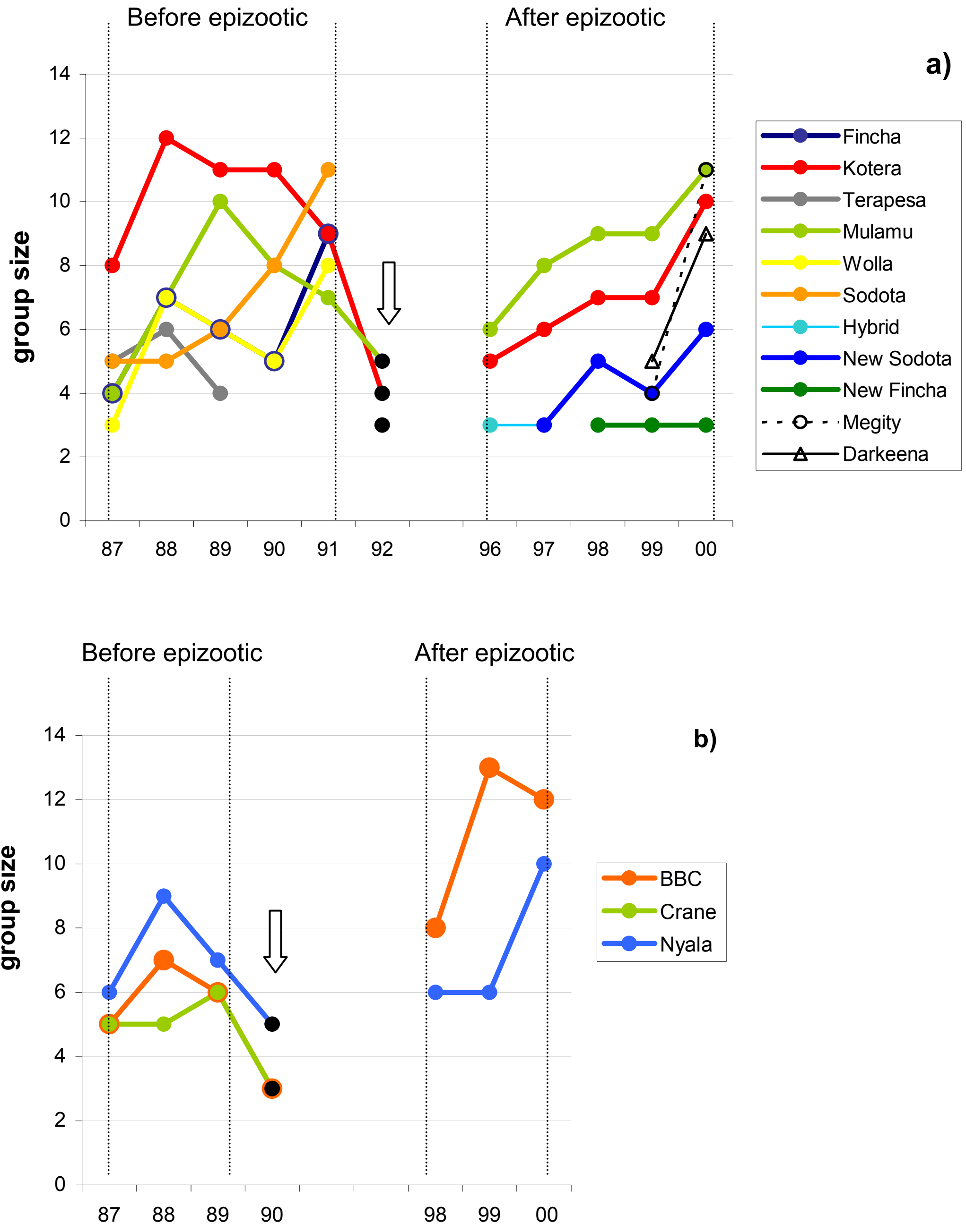


Figure 7.4 Time series of pack sizes in (a) Web Valley and (b) Sanetti. Arrows indicate the year of the population decline (data points in black)

Most packs contained in most years one or two adult females (Table 7.1). The average numbers of adult females per pack did not differ significantly between periods (Table 7.1, Mann-Whitney test P=0.365). Larger packs tended to have more adult females (linear regression, R-sq 0.46, ANOVA F(1,64)=48.722, P<0.001) but packs with three or four adult females were rare (13% of 65 pack/years). Interestingly, the three attempts at pack fission (i.e. Sodota-1991, Mulamu-1999 and BBC-1999) occurred within large groups (with 11, 12 and 13 adults and subadults) that had three or four adult females.

The population sex ratio was on average less biased towards males during the recovery, particularly in Sanetti, which had a highly biased sex structure before the decline. Sex ratios, before and after the decline respectively, averaged 2.0(SD 0.2) and 1.8(SD 0.1) in Web and 3.1(SD 0.6) and 1.2(SD 0.3) in Sanetti. At the level of packs too sex ratios were less biased toward males during the recovery (Table 7.1, Mann-Whitney test, P=0.023), an indication that a relatively lower proportion of females faced long distance dispersal but instead remained as part of the large, expanding groups, or as members of new groups.

7.3.3 Spatial organization

At the beginning of the recovery period, in 1997, the three packs that had survived the epizootic in the Web Valley had expanded their territories to occupy an area similar to that used by five packs before (Fig. 7.5). New packs later colonized areas on the fringes of the longer-established packs. In the Web Valley, the packs that survived the epizootic tended to have larger territories (up to 10.7 and 11.7km^2) than the newly formed packs in the Web Valley (minimum size at the time of colonization 2.0 and 3.4km^2) (Fig 5 and Table 1). Differences between periods were not significant (Table 1, Mann-Whitney test P= 0.185) but territories were more variable during the recovery period than before (Table 1, Mann-Whitney test P=0.038). This variability reflected the re-adjustment of territorial boundaries in response to the formation of new packs. For example *New Sodota* contracted its territory from 10.5 to 2.0km^2 the year of the formation of two new packs, and *Mulamu* from 11.7km^2 to 9.4km^2 when this pack split. The two packs that survived the decline in Sanetti also expanded to incorporate the area vacated by the extinction of *Central Lakes*.

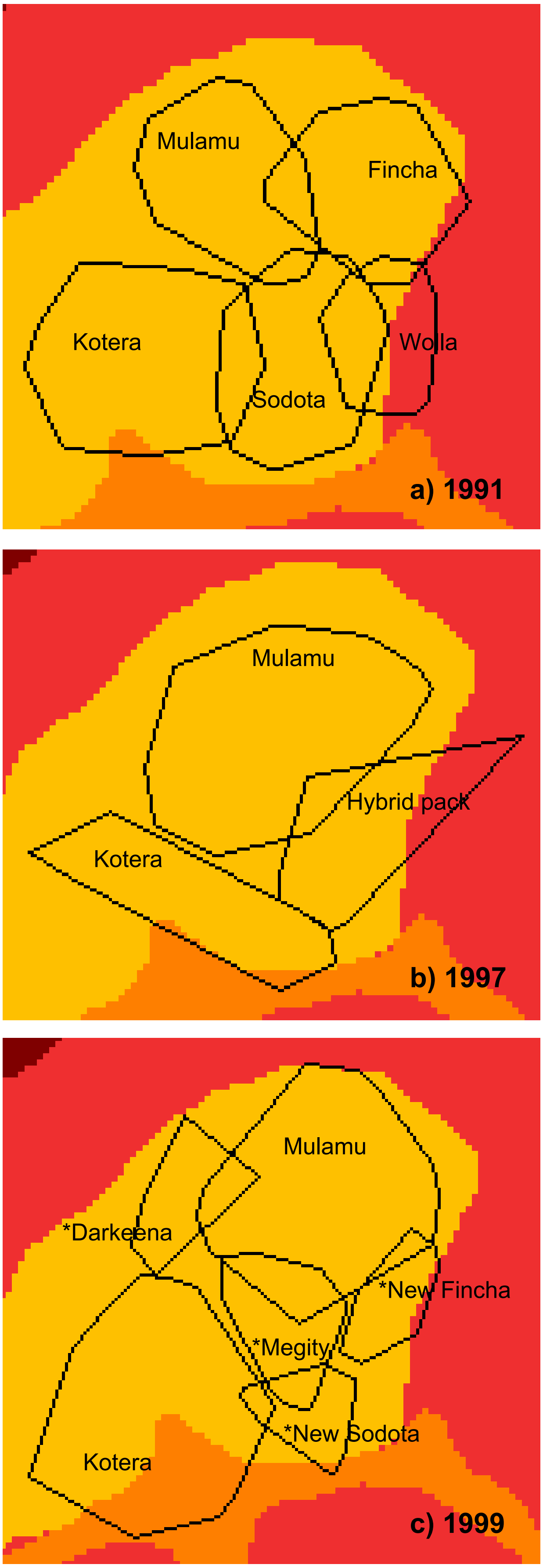


Figure 7.5 Spatial dynamics of territories in the Web Valley

a) Home ranges of the five focal packs just before the epizootic

b) Home ranges of three packs that persisted through the epizootic, four years later

c) Home ranges of the six packs eight years after the epizootic. * New packs.

Note: The areas in yellow are ‘optimal’ wolf habitats (*sensu* Gottelli & Sillero-Zubiri 1992) with Afroalpine meadows and grasslands. The areas in red are ‘marginal’ habitats, mainly ericaceous moorlands along the valley walls. ‘Good’ habitats, in orange, of intermediate quality.

	Litter size						Recruitment rate						Adult survival rate						Sex ratio						Adult sex ratio					
	Before			After			Before			After			Before			After			Before			After			Before			After		
	AV	SD	*n**	AV	SD	*n**	AV	SD	*n**	AV	SD	*n**	AV	SD	*n**	AV	SD	*n**	AV	SD	*n**	AV	SD	*n**	AV	SD	*n**	AV	SD	*n**
WEB VALLEY																														
Fincha	**3.20**	2.39	*5*				**0.77**	0.25	*3*				**0.89**	0.14	*4*				**2.06**	1.17	*5*				**2.30**	1.57	*5*			
Kotera	**2.20**	2.17	*5*	**3.40**	2.07	*5*	**0.83**	0.29	*3*	**0.84**	0.19	*4*	**0.84**	0.08	*4*	**0.85**	0.12	*4*	**2.34**	0.76	*5*	**2.26**	0.25	*5*	**2.44**	0.44	*5*	**2.70**	1.20	*5*
Terapesa	**2.00**	1.41	*3*				**1.00**		*1*				**1.00**		*1*				**1.75**	0.35	*3*				**1.75**	0.35	*2*			
Mulamu	**3.00**	1.87	*5*	**4.20**	1.48	*5*	**0.76**	0.21	*3*	**0.54**	0.33	*4*	**0.87**	0.19	*4*	**0.86**	0.19	*4*	**2.24**	0.62	*5*	**1.42**	0.33	*5*	**2.40**	0.42	*5*	**2.02**	0.90	*5*
Wolla	**2.20**	2.17	*5*				**0.60**	0.53	*3*				**0.87**	0.09	*4*				**2.20**	1.05	*5*				**2.60**	0.89	*5*			
Sodota	**2.20**	2.39	*5*				**0.78**	0.19	*3*				**0.97**	0.17	*4*				**2.44**	1.47	*5*				**2.46**	1.05	*5*			
New Sodota				**3.50**	1.29	*4*				**0.61**	0.35	*3*				**0.87**	0.23	*3*				**2.13**	0.63	*4*				**2.25**	0.50	*4*
Megity				**4.00**	5.66	*2*				**0.88**		*1*				**1.00**		*1*				**1.40**	0.57	*2*				**1.00**	0.00	*2*
Darkeena				**4.00**	0.00	*2*				**0.75**		*1*				**1.20**		*1*				**1.75**	0.35	*2*				**1.50**	0.71	*2*
SANETTI PLATEAU																														
BBC	**2.67**	3.06	*3*	**4.33**	1.15	*3*	**0.50**	0.71	*2*	**0.75**	0.35	*2*	**0.93**	0.10	*2*	**0.89**	0.16	*2*	**3.83**	1.26	*3*	**1.20**	0.20	*3*	**3.67**	1.53	*3*	**1.17**	0.29	*3*
Crane	**1.33**	1.15	*3*				**0.50**	0.00	*2*				**0.90**	0.14	*2*				**1.67**	0.29	*3*				**1.17**	0.29	*3*			
Nyala	**1.33**	1.53	*3*	**5.33**	1.53	*3*	**0.50**	0.71	*2*	**0.52**	0.12	*2*	**0.94**	0.08	*2*	**0.75**	0.35	*2*	**4.83**	1.26	*3*	**1.33**	0.76	*3*	**4.67**	1.53	*3*	**1.60**	1.15	*3*

	Pack size						Adult females						Pack home range					
	Before			After			Before			After			Before			After		
	AV	SD	*n**	AV	SD	*n**	AV	SD	*n**	AV	SD	*n**	AV	SD	*n**	AV	SD	*n**
WEB VALLEY																		
Fincha	**6.20**	1.92	*5*				**1.60**	0.55	*5*				**5.87**	1.91	*3*			
Kotera	**10.20**	1.64	*5*	**6.50**	2.07	*5*	**2.40**	0.55	*5*	**1.40**	0.55	*5*	**8.95**	1.07	*4*	**8.60**	3.10	*3*
Terapesa	**5.00**	1.00	*3*				**1.67**	0.58	*2*				**1.80**		*1*			
Mulamu	**7.20**	2.17	*5*	**8.00**	2.19	*5*	**1.60**	0.55	*5*	**2.40**	1.34	*5*	**5.35**	0.21	*2*	**10.60**	1.15	*3*
Wolla	**5.80**	1.92	*5*				**1.20**	0.45	*5*				**3.70**	0.65	*4*			
Sodota	**7.00**	2.55	*5*				**1.80**	0.84	*5*				**4.90**	1.61	*4*			
New Sodota				**4.50**	1.29	*4*				**1.00**	0.00	*4*				**6.25**	6.01	*2*
Megity				**7.50**	4.95	*2*				**2.00**	0.00	*2*				**3.40**		*1*
Darkeena				**7.00**	2.83	*2*				**1.50**	0.71	*2*				**2.60**		*1*
SANETTI PLATEAU																		
BBC	**6.00**	1.00	*3*	**11.00**	2.65	*3*	**1.00**	0.00	*3*	**3.33**	1.15	*3*	**4.30**	1.98	*2*	**6.70**	3.68	*2*
Crane	**5.33**	0.58	*3*				**1.67**	0.58	*3*				**2.60**	0.28	*2*	**6.20**	3.25	*2*
Nyala	**7.33**	1.53	*3*	**7.33**	2.31	*3*	**1.00**	0.00	*3*	**2.00**	1.00	*3*	**5.20**		*1*			

Table 7.1 Parameter values used to compare pack composition and demography before and after the population decline with the Mann-Whitney test * *n* are numbers of years averaged by pack in the correspondent period. Grey shadow highlights new packs.

Territory size was positively correlated with group size throughout the study period and across populations (Spearman rank r: 0.67, P<0.001, n= 38 packs/years) (Fig. 7.6). In other words, larger packs tended to use larger territories. This result confirmed that expansionism was prevalent across a wide range of population densities and habitat saturation levels. In particular, the packs that survived and expanded spatially after the epizootic in the Web Valley showed comparatively larger territories for their group sizes (empty circles, Fig. 7.6), and the newly formed packs were among the smallest groups with smallest territories (gray circles, Fig. 7.6). Overall, territorial density was not significantly different between study periods (Mann-Whitney test P= 0.266)

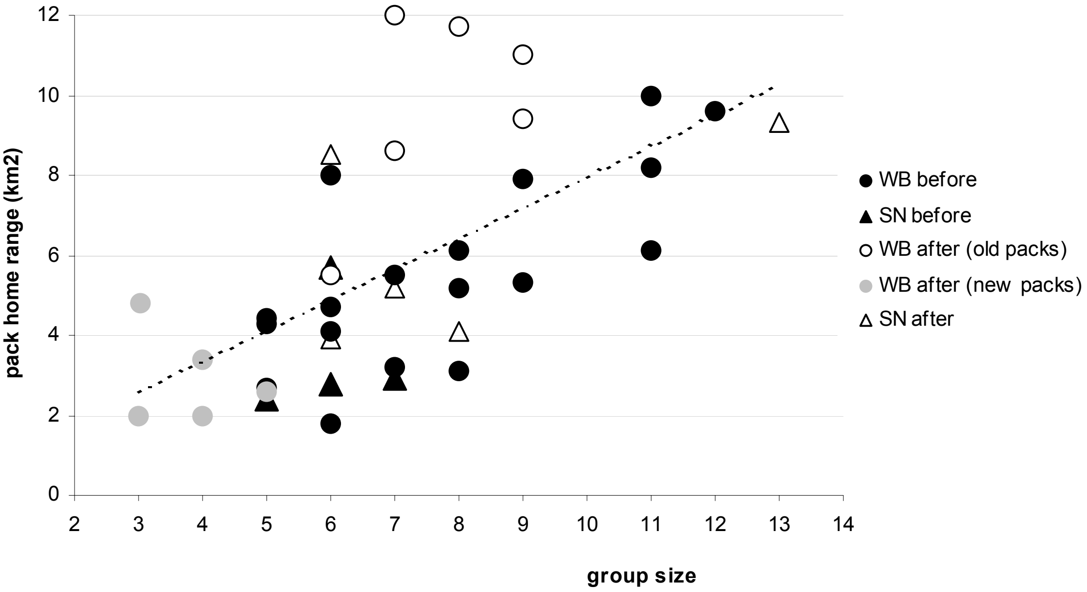


Figure 7.6 Variation in home range size with increasing group size (n=48 pack/years)

7.3.4 Demography: survival and reproduction

Populations were characterized by high survivorship of the age classes older than one year old (adult survival rate, Fig. 7.7), a relatively lower and more variable survival of the young in their first year (recruitment rate, Fig. 7.7) and variable total reproduction (number of pups born annually, Fig. 7.2). Within this general pattern some differences were evident between the stages of population stability and recovery.

At high population densities, annual recruitment rates were more variable than during the recovery (coefficient of variation: 38% and 18% in Web, and 117% and 40% in Sanetti before and after the epizootic respectively). Comparatively, adult survival rates were stable across periods and populations (coefficient of variation ranged from 10.3% to 0.2%, Fig. 7.7). Thus fluctuations at high density were associated with inter-annual variations in recruitment rate and the total production of pups as well (see 'pups' in Fig 7.2). Events of failed reproduction were also commoner during the recovery (pups emerged from dens in 80% and 94% of the pack/years before and after the decline respectively).

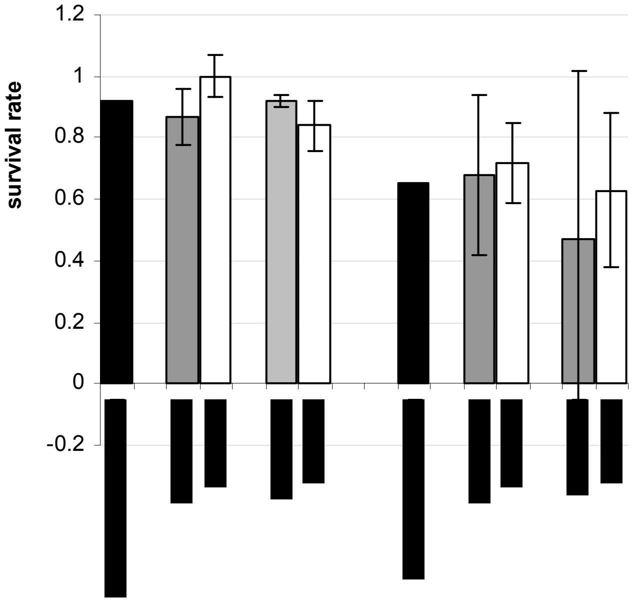


Figure 7.7 Population adult survival rate and recruitment rate before and after the epizootics. Error bars are standard deviations.

The average recruitment rate was comparatively higher during the recovery period than before, as well as and the average adult survivorship in Web (Fig. 7.7). Two years with survival rates above one confirmed the immigration of at least two adult wolves into the Web population, one in 1997 and one in 2000; no immigration was recorded before the decline. Enhanced reproduction also contributed to the recovery in Sanetti, 19 and 27 pups were born over a 3-year period before and after the decline respectively. In Web similar numbers of pups were born in each period (68 and 64 pups before and after the decline respectively), but during the recovery reproduction increased with the number of packs (Spearman rank r: 0.64, P=0.048, n= 10 years), from its lowest value in 1996 towards a peak in 1999 when the breeding units increased from four to six. Larger litter sizes during the recovery (Table 1, Man-Whitney test P= 0.001) in part compensated for the fewer number of reproductive events (fewer pack/years) during the recovery in both populations.

At the level of packs the demography was also characterized by high adult survivorship (range 0.75-1.2), lower recruitment rates (range 0.50-1.00), and variable litter sizes. Litter size ranged from 1 to 8 (litters of 7 and 8 were very uncommon) and averaged 2.8 (SD 2.2) and 3.2 (SD 2.4) pups per litter in Web and Sanetti respectively. The level of variation in litter size was similar across packs in the two periods (Table 1, Mann-Whitney test P= 0.744). At high population densities, fluctuations in pack sizes were also explained by a more variable recruitment rate in comparison with the period of recovery (Table 1, Man-Whitney test P= 0.037; excluding years with no recruitment due reproductive failures on the previous season). The survival of adults in the longer-established packs of Web declined in 1999 when two new packs formed, providing independent evidence that they provided at least some of the dispersers that coalesced into new packs. Pack adult survival rates exceeding one coincided with observations of one female floater joining *Sodota* in 1989 (Sillero-Zubiri *et al.* 1996a) and one subordinate female from *Darkeena* rejoining her natal pack *Mulamu* in 2000. Differences in pack-level adult survival were only nearly significant (Table 1, Man-Whitney test P= 0.064) and not significant for pack recruitment rates (Table 1, Man-Whitney test P= 0.648). These results contrast the finding of differences in population-level survival rates, possibly because pack parameters needed to be average across years for individual packs.

7.3.5 Density dependence and Allee effects

Survival rates changed consistently with population density in the previous season (Fig. 7.8). A percentage carrying capacity (%K) was calculated for each year to be able to merge data from the two populations (with K defined as the population size at which growth was nil). Actual densities were used for density dependent analysis in Web, but small sample sizes precluded this type of analysis for Sanetti. Delayed responses made sense in biological terms because conditions in a given season were bound to affect the survival of wolves into the next season.

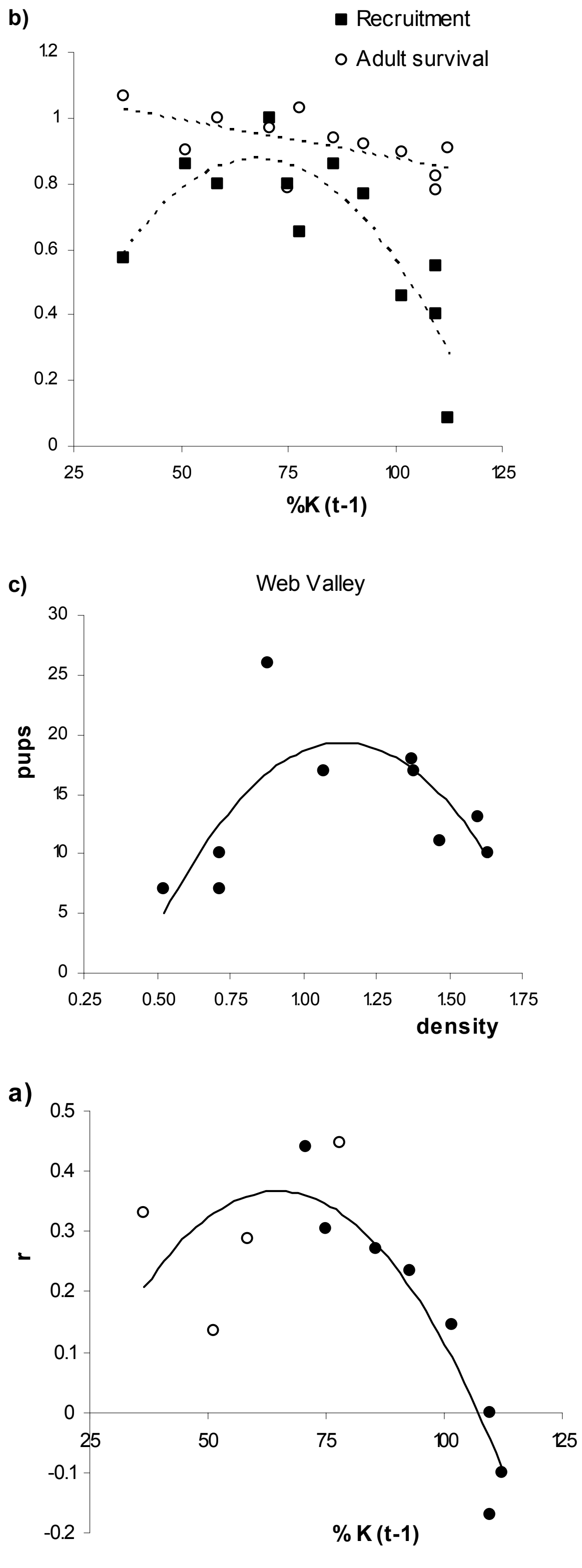


Figure 7.8 Density dependent changes: a) adult survival and recruitment rates; b) total reproduction in Web Valley; and c) the intrinsic rate of population change ($r=\ln N_t - \ln N_{t-1}$), as described in Chapter 6. The empty circles are years after the epizootic in Web; %K (t-1)= percentage carrying capacity in the previous season.

Adult survival rates decreased linearly with %K in the previous year (R-sq 0.38, ANOVA F(1,10)=6.578, P=0.028), or density in the previous year in Web (Fig 7.8b). Variation in recruitment rate followed a U-shaped quadratic function (R-sq 0.81, ANOVA F(2,9)=19.977, P<0.001)(Fig 8b), but one year with low recruitment at low density seemed to affect this relationship; after removing this point a negative linear relationship still explained 60% of the variation (R-sq 0.59, ANOVA F(1,11)=5.401, P=0.042).

Annual reproduction in the Web Valley varied with population density via a quadratic function (R-sq 0.50, ANOVA F(2,7)=3.80, P=0.076) that matched closely the pattern of change in population growth described in Chapter 6 (Fig 8a and 8c): inverse density dependence (left hand side of the graphs) occurred during the years following the epizootic, and above a threshold of around 1 wolf/km^2 (or ca. 70% of the carrying capacity) annual reproduction and population growth started to decrease with increasing density (right hand side of the graphs).

There was no evidence of Allee effects at level of packs that could explain the phenomenon of inverse density dependence. No significant correlations were found between group size and litter size (Spearman's rank r=-0.042, P= 0.749, n=60pack/years), group size and pack recruitment (Spearman's rank r=0.120, P=0.460, n=39pack/years), or group size and adult survival rates (Spearman's rank r=0.186, P=0.276, n=44pack/years). Neither of these parameters changed consistently with territorial density in that year or the previous. Litter size tended to decrease with increasing territorial density on the previous year (liner regression, ANOVA F(1,26), P=0.066, n=28 pack/years), a relationship close to statistical significance but that only explained 12% of the variation (Fig. 7.9a). This relationship was much clearer for the pack with the longest dataset, *Kotera* (n=6 years) (Fig. 7.9b). Also, seven of the eight cases of reproductive failure (and the four litters with only one pup) occurred in packs with densities above 1 wolf/km^2 in that breeding season or the previous. That density dependence was otherwise not evident at pack level is possibly the result of the need to average pack parameters across periods for statistical analysis, but also because territorial density was not necessarily lower during the recovery (e.g. new territories could be crowded). Still, 'noise' from inter-pack variations did not obscure patterns of density dependence at the population level.

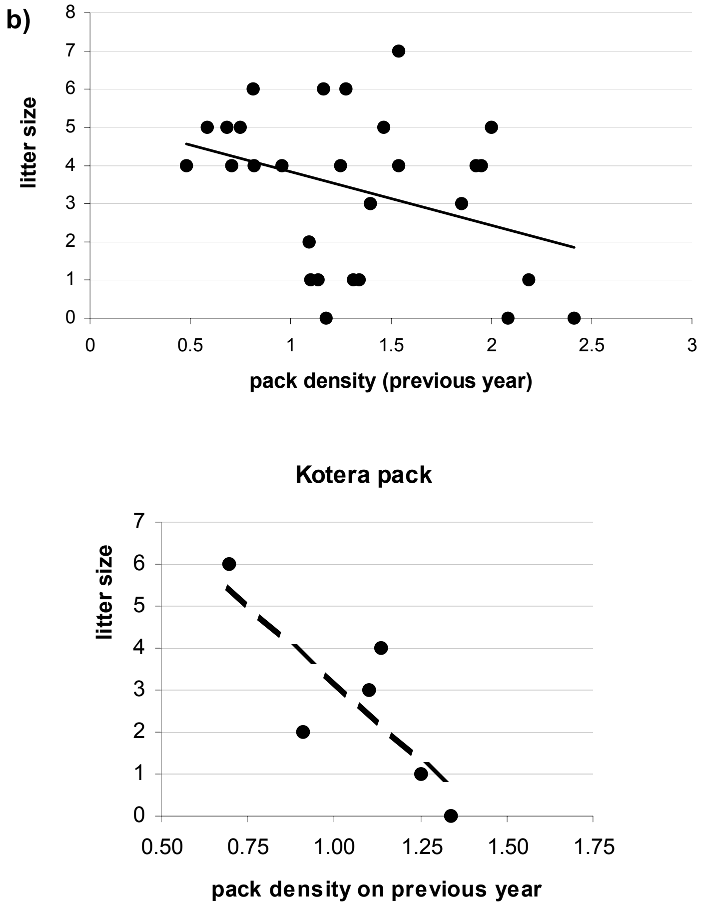


Figure 7.9 Variations in litter size with increasing pack size across years and populations (n=65 pack/years) (a) and for the *Kotera* pack only (b) (Note: several points with same values cannot be seen in the graph).

7.4 Discussion

7.4.1 Regulation at high densities

It is difficult to determine whether the size of populations at high density is primarily stabilized by trophic interactions or by behavioural mechanisms. Due to their specialized requirements, Ethiopian wolves compete strongly for a limited number of suitable territory vacancies within the Afroalpine ‘islands’ they inhabit. Food distribution and abundance will undoubtedly affect optimal territory size and consequently the number of breeding territories, but reproductive suppression by limiting the number of breeding females may halt population growth before reaching the stage of resource depletion. Territoriality not only limited offspring rearing space for females but offspring of both sexes delayed dispersal, resulting in the formation of groups of close kin. Delaying dispersal however does not always pay: low-ranking subordinate females with very low chances of breeding within the pack -typically when there are more than two females- dispersed long distances and possibly died.

Additionally, the finding of density dependent survival gives weight to the notion of regulation mediated by ecological factors -as predicted by increasing levels of interference and/or depletion when there are greater numbers of competitors for a critical resource (Caughley & Sinclair 1994). The wolves' rodent prey is a very rich, predictable and rapidly renewable resource (Sillero-Zubiri, Tattersall & Macdonald 1995) but this is geographically restricted and at high demand (denning sites, access to water or shelter are not critical). Starvation is the most obvious cause of mortality in pups at the time they become independent and stop receiving food from other pack members (Sillero-Zubiri *et al.* in press). Marked variations in pup survival were associated with fluctuating population sizes at high density. Asynchronous fluctuations in the size of packs preclude climatic-induced changes in food availability as a cause for these variations. Reproductive failures and smaller litter sizes also limited growth at high-densities. It is possible that physiological stress affected the body condition and fecundity in dominant females, as Sillero-Zubiri *et al.* (2004) observed smaller litter sizes to be associated to social tension between dominant and subordinate females, and social unease in the pack.

The evidence indicates that in the absence of disease populations of Ethiopian can be relatively stable (Haydon *et al.* 2002, Chapter 6) and characterized by high adult and juvenile survivorship. The result is the production of a considerable surplus of individuals relative to the number of territorial vacancies. Maintaining a stable breeding population would actually require the survival of a small percentage of pups. Yet it was the capacity for additional members of the population to assume reproductive functions at reduced densities that contributed to the resilience of the populations

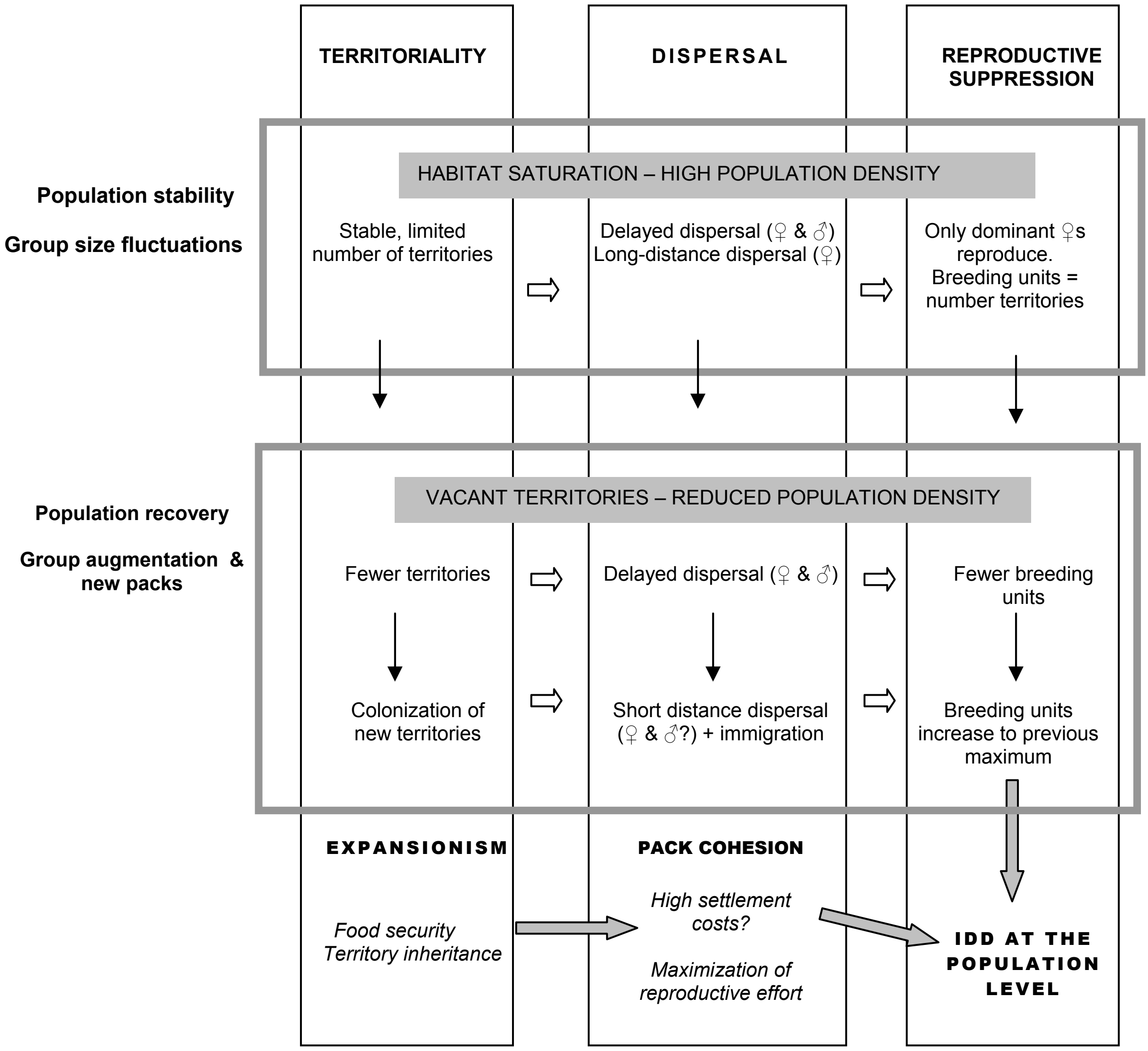
7.4.2 Mechanisms of population recovery

Populations recovered via pack augmentation and by the formation of new packs in one population only. Larger litters also contributed to the recovery, possibly the result of more relaxed social relationships when wolves exist at lower density (new packs also bred profusely in spite of their relatively small size). Enhanced survival was consistent with density dependence changes as driven mainly by competition for food. The enhanced survival of pups in their first year necessarily implied lower mortality because young do not disperse until they become adults at 2 years or shortly before (Sillero-Zubiri 1994; Sillero-Zubiri *et* al.1996a). In addition to mortality, other factors could affect the calculation of survival rates for the older age classes. Immigration occurred in one population at least; the two confirmed immigrants most likely coalesced with the local dispersers to colonize new territories. Changes in the sex structure also evidenced that fewer females dispersed long-distances in the recovering populations. Females that would otherwise leave the population at saturation were accommodated as part of the expanding packs that attained large sizes (e.g. in Sanetti) or in the newly formed groups (e.g. in Web).

Populations recovered fully to pre-epizootic levels but the rate of growth was inversely density dependent in the population more severely affected by disease. Limited recovery from low densities has been described in species of obligate cooperative carnivores such as the African wild dogs (Courchamp & Macdonald 2001; Courchamp, Rasmussen & Macdonald 2002), in which case an Allee effect was suspected because of the existence of a critical pack size for significant survival and reproduction (Courchamp, Clutton-Brock & Grenfellet 1999; Stephens & Sutherland 1999). We found no evidence of such Allee effects in groups of Ethiopian wolves. As the population began to recover, the surviving packs expanded spatially and grew via delayed dispersal, but the number of packs did not increase immediately, so the increase in group size had little effect on the total number of emerging litters, which was mainly determined by the number of groups. In consequence, the rate of population recovery was initially slow, and increased as new packs formed. Slow recovery as a result of delays in the formation of new groups has also been described for one population of suricates (Clutton-Brock *et al.* 1999b). Where few females emigrate and the rate at which groups are established is low, populations of social species may be slow to recover from period of population decline induced by food shortage or disease.

7.4.3 Behavioural mechanisms and social strategies

The combination of population analysis with the dynamics of social groups helped to identify the role of dispersal, territoriality and reproductive suppression in the regulation of wolf numbers. The diagram below summarizes how these behaviours influenced the stability or recovery of populations, leading to inverse density dependence (IDD) at low densities.



Wolves that survived the epizootics faced reduced levels of competition and spatial constraints. The failure of non-breeding females to emigrate and colonize vacated areas suggests that habitat saturation is not necessary for dispersal to be delayed. In evolutionary terms, dispersal must have been always a costly option for Ethiopian wolves. It is therefore conceivable that sociality benefits pack members with medium or long-term advantages that are not obvious in immediate conditions –for example soon after a population decline.

In saturated populations, Sillero-Zubiri (1994) observed that remaining at home increased the female subordinate's future chance of gaining high quality breeding sites, either by inheritance of the natal territory itself, or by gaining a competitive edge in contents for openings that may arise. At reduced densities, pack cohesion and expansionism brought to territory holders the benefit of increasing food security and the prospect of future group augmentation. Initially, the advantages of strength of numbers appeared to outweigh the benefits of independent reproduction, but territory owners eventually benefited by dispersing and budding part of the natal territory.

By expanding spatially, the surviving packs also removed the interstices available for outside colonizers, which only later mated with local dispersers and formed new packs. The settlement costs involved in carving out and defending a territory against expansionist neighbouring packs, probably limited the establishment of colonizing pairs. Packs of as few as three wolves succeeded in colonizing a territory but these grew rapidly, increasing their strength in numbers to defend the newly established territory.

The females' decision to disperse appeared to depend more on the number of dominant competitors 'in line' to inherit, than on prevailing circumstances beyond (e.g. reduced population density) (Macdonald & Carr 1989). Independently of the level of saturation, packs typically contained one or two adult females. Above that threshold, the chances of low ranking females to access breeding status within the packs must be very small. Dispersing females may become floaters, face the high risks of long distance dispersal, or integrate new packs if populations are bellow carrying capacity.

It was also apparent that subordinate wolves did not disperse until conditions for successful colonization were given. This happened when one pack was large enough to allow for splitting, or when a sufficient number of dispersers met and colonized a new territory. This strategy can serve to maximize reproductive success by conserving reproductive effort. It also pre-empts the possibility of pack extinctions, which characterizes the recovery of African wild dog populations at low density. In that case the logical explanation is that small packs produce fewer dispersers and new packs cannot persist because of their small size (Courchamp *et al.* 2002). This study would indicate that cooperative breeding does not impose such constraints in Ethiopian wolf populations. Small packs did not do worse than larger packs in terms of reproductive success or survival, and the new, relatively small packs (three to five wolves) succeeded in breeding and maintaining their new territory.

In conclusion, behavioural regulation of Ethiopian wolf numbers appears the result of adaptations to strong levels of competition for a critical food resource. Sociality must have been an evolutionary stable strategy that enabled specialized wolves to colonize and persist in small isolated habitats. This study supports the thesis that the long-term maintenance of a known area of good quality must have been a crucial selective force for sociality.

CHAPTER VIII

Ecological bases of group size and territory size in the Ethiopian wolf

Abstract

Local resource abundance leads to varying social and spatial structure in the mountain specialist Ethiopian wolf (*Canis simensis*): wolves in areas with low rodent density occur mostly as pairs, with territories at least twice as large as those defended by larger groups in rodent-rich habitats. This study tests for ecological explanations of such intraspecific variation using empirically–defined habitat types as a proxy for rodent availability within territories. Territories across study areas were configured as to contain similar amounts of the two richest habitat types (i.e. with high abundance of giant molerats *Tachyoryctes macrocephalus* and/or Murinae rats) in variable combinations, independently of the area of a third poorest habitat type. Territories in the less productive area included relatively constant amounts of the richest habitat type (that with high abundance of the preferred prey, giant molerat), distributed within a matrix of poor habitat. The poor habitat occupied on average 60% of the home range (n=4 packs), compared with 6% to 20% (n=3 and 10 packs) in the more productive areas. The results coincide with the prediction of larger territories when key habitats are more dispersed, but differences on group size could not be explained by differences in the absolute amounts of key habitats within territories. Analyses of habitat composition were also conducted within the more productive areas, where group size and territories were positively correlated ('expansionist' strategy). In this case, larger territories showed proportional increments in the area of rodent-rich habitats, and the area per wolf increased with territory size. The high aggregation of food thus appears to shift the balance of costs and benefits towards sociality in an arms race to secure a portion of a high-quality area. In contrast, the costs of expanding an already large territory to include more rich patches may be too high -and the benefits for the primary pair minimal- in the less productive area.

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8.1 Introduction

8.1.1 Behavioural and ecological bases of sociality in territorial species

Territory holding by animals is often interpreted as an adaptation to defend a limiting resource, often food (e.g. Brown, 1964, 1982; Davies & Houston 1984). Since territoriality involves costs (e.g. defence against conspecifics) as well as benefits, territories are expected to be of the minimum size required to satisfy the requirements of all the occupants (further enlargement would bring extra costs without net benefits). When territories are held by groups larger than a single individual or a mated pair, functional advantages of group living may derive directly from their collective presence (e.g. cooperative hunting, alloparental care, etc).

Since territory size sets limits upon group size, the benefits of defending a territory of a given size are affected by the existence of this varied suite of advantages and disadvantages of group living (Kruuk & Macdonald 1985). Under some circumstances, however, group territoriality appears to be a result of the pattern of resource distribution in the environment – patterns that facilitate co-occupancy by obviating its costs – and functional advantages of group living, if they exist, may be only secondary (e.g. the Resource Dispersion Hypothesis of Carr & Macdonald 1986).

Being a diverse group, the Carnivora have provided a fruitful arena for the study of the behavioural ecology of sociality and the relationships between body size - and thus metabolic needs - prey and home range size (e.g. Gittleman 1989). Intraspecific variations in the size of groups and territories in carnivores have been correlated with different prey productivity (e.g. coyotes *Canis latrans*, Bekoff & Wells 1980; red foxes *Vulpes vulpes*, Macdonald 1981). The simplest ecological model is that increases in overall prey abundance will lead to increases in habitat quality per unit-area, thus resulting in higher animal densities and, pro rata, typically smaller ranging areas (Gittleman & Harvey 1982; Reiss 1988). This however raises question of why larger groups do not shed members in order to form smaller groups in smaller territories while maintaining their former per-capita intake rate (Kruuk & Macdonald 1985)

Carnivores - the majority of which are non-social, have home range sizes consistently predicted by allometric relationships. Social species, however, appear to violate the well-established allometric scaling of home range, which assumes randomly distributed resources (Johnson *et al.* 2002) – only one carnivore study has produced contradictory results (Baker & Harris, 2004). The Ethiopian wolf (*Canis simensis*) is among the group of small and medium sized carnivores with smaller home ranges than those predicted by the group metabolic needs (Johnson et al 2002). These species rely on small prey -which tend to be abundant and easy to catch (Carbone *et al.* 1999), and patchy food types which are rapidly renewed or locally abundant (Johnson *et al.* 2002). In the case of Ethiopian wolves, the Afroalpine rodent prey on which they depend exist at unusually high biomass (Chapter 2), and their home ranges are among the smallest, and their density among the highest, reported for all eight *Canis* species (reviewed in Ginsberg & Macdonald 1990; see also Macdonald & Sillero-Zubiri in press).

It remains to be seen whether social group formation at the extremes of resource dispersion operates through particular mechanisms such as the Resource Dispersion Hypothesis (RDH), which predicts group formation will be determined largely by the dispersion and abundance of the resources available (Carr & Macdonald 1986). When the food resource is very rich, reduced feeding competition can permit overlapping home ranges and the consequent formation of 'spatial groups' (Kruuk & Parish 1982; Macdonald 1983; Wrangham 1993; Creel & Macdonald 1995). The lowered costs of sharing resources in a territory will shift the cost-benefit balance towards group living and permit the formation of groups even in the absence of direct benefits (Carr & Macdonald 1986; Blackwell 1990). Ultimately, this study aims to answer the fundamental question of whether group living in Ethiopian wolves is mainly favoured by the advantages of cooperation (mainly the communal defence of a territory) or by the pattern of prey distribution.

8.1.2 The Ethiopian wolf study case

Local resource abundance led to different types of society in the Ethiopian wolf. In the Bale Mountains of southern Ethiopia, wolf packs in areas with low rodent density exist mostly as pairs (Sillero-Zubiri & Gottelli 1995b) with territories at least twice as large as those defended by larger groups in rodent-rich habitats. The size of groups determines the outcome of territorial boundary clashes in the more productive areas, and larger groups defend larger territories (Sillero-Zubiri & Macdonald 1998). In species with such 'expansionist' strategy, the benefits of cooperative territorial defence have significant consequences for food security, and food security may be the major selective pressure for sociality (Chapter 7; Kruuk & Macdonald 1985). In Ethiopian wolves, the maintenance of a high quality range is believed to be the greatest advantage of sociality (Sillero-Zubiri *et al.* 1996a, in press), but the benefits of group living appear to operate within a framework of constraints, which this study explores by focusing on resource availability within territories. Two main comparisons are made:

a) Between poor and highly productive areas (Tullu Deemtu versus Web-Sanetti), where territory and group size vary independently
b) Within the more productive area (Web-Sanetti) were pack size is positively correlated with territory area

The quantification of prey abundance required for testing ecological theories is notoriously difficult. The wolf prey in Bale, however, is closely associated to different habitat types (Sillero-Zubiri *et al.* 1995a,b, in press) and it is this predictability that may explain the wolves' pack territoriality as a food-resource defence strategy and an optimization of its feeding efficiency (Sillero-Zubiri 1994). Rodent-habitat associations were therefore used to develop an objective classification of habitat quality types that could be validated and readily mapped. To the extent that habitat types are a good index of prey abundance, their distribution will reflect the pattern of prey availability within a territory; the underlying assumption being that abundance is a good proxy for availability. This task is simplified because wolf prey in Bale comprises essentially just two main types of rodent: the rat-sized Murinae rodent and the larger, preferred giant molerat (*Tachyoryctes macrocephalus*) (Sillero-Zubiri & Gottelli 1995a). The RDH (Macdonald 1983) predicts that, all else being equal, and most obviously when food patches are distinctive, the dispersion of patches will determine territory size and shape, whereas group size will be determined by their richness (specifically, the abundance of available food during a bottleneck period in total food abundance).

One plausible hypothesis is that habitats with giant molerats –or with larger giant molerat abundances- will be paramount in determining the configuration of wolf territories. However, since wolves' abundance is known to correlate with the abundance of the two types of prey, separately (Sillero-Zubiri 1994; Sillero-Zubiri *et al.* 1995a,b), this hypothesis may be too simple. Perhaps instead territories could be configured to contain a certain amount of rodent rich-habitat types, combining in variable proportions those needed to support both categories of prey. Within the population of expansionists, wolves are expected to live in groups with a larger membership than could be sustained by the minimum territory (Kruuk & Macdonald 1985); that which encompassed the minimum amount of a key habitat. This would evidence that the extra costs of territorial defence are outweighed by the advantages (whatever they may be) of larger group size. An equal probability of availability over a given area will determine that an increase on group biomass will demand an increase in home range size to maintain per capita intakes (Gittleman & Harvey 1982; Reiss 1988).

The first part of the chapter is devoted to the definition, validation and mapping, of habitat quality types on the bases of rodent-habitat associations. The second part compares measurements of the habitat composition of territories across study areas, and within the more productive areas, to test these ecological-based predictions of variations in the size of territories and social groups in Ethiopian wolves.

8.2 Study areas

The three study areas are located within the Afroalpine belt of the Bale Mountains: the *Web Valley* (3,450m) in the west, the *Sanetti Plateau* (3,800-4,000m) in the East, and *Tullu Deemtu* (up to above 4,300m) in the drier southern declivity of the plateau (Fig. 8.1). The first two represent typical Afroalpine habitats, open and with short vegetation, with high prey biomass and wolves at densities of up to 1.2 wolf/km^2. Tullu Deemtu represents another common habitat type, the *Helichrysum* dwarf-scrub, which sustains lower prey biomass and wolves at densities *ca.* 0.25/km^2.

In Tullu Deemtu mated pairs were the basic social unit; groups included one or two associates and home ranges were between 1.5 and 5 times larger than those in Afroalpine grassland. This difference was explained by the different biomass of prey, which in Tullu Deemtu was estimated a fifth of that in the Afroalpine grasslands and meadows of Web Valley and Sanetti Plateau (Sillero-Zubiri *et al.* 1995a,b), mostly concentrated along drainage lines and bogs.

In Web and Sanetti, but not in Tullu Deemtu, home range sizes and group sizes were positively related (Sillero-Zubiri & Gottelli 1995b). This 'expansionist' strategy (*sensu* Kruuk & Macdonald 1985) was supported by territorial expansion whenever a reduction on group size in a neighbouring pack allowed it.

Wolf distribution in Bale follows that of their diurnal rodent prey, giant molerats and Murinae grass rats, which in turn correlates with vegetation types (Sillero-Zubiri *et al.* 1995a,b, reviewed in Chapter 2). Optimal habitats for rodents and for giant molerats in particular, are the valley floors, swamp shores and herbaceous communities (Sillero-Zubiri *et al.* 1995b), with vegetation kept in permanent pioneer stages by the activity of rodent and frost-induced soil movements. Short herbs and grasses dominate (e.g. *Alchemilla abyssinica*, *Polygonum plebejum*, *Trifolium acaule*, *Anthemis tigrensis*, and *Poa muhavurensis*), specked by *Helichrysum* and *Artemesia* bushes (Miehe & Miehe 1993). Rounded mounds, known as *mima* mounds, are common along drainage lines and correlate with giant molerat abundance. Other areas, with thin soils, are sub-optimal areas for molerats (Gottelli & Sillero-Zubiri 1992). In Tullu Deemtu, *H. splendidum* shrubs (up to 50 cm tall) dominate, but leave open space for tussock grasses to grow (e.g. *Agrostris quinqueseta* and *Festuca richardii,* Miehe & Miehe 1993) and the more productive Afroalpine habitats are restricted to drainage lines and bogs.

8.3 Methods

8.3.1 Habitat quality types

Logic

Extensive field surveys were conducted in the three study areas to record variables relevant to the distribution of rodents. Classes of vegetation-soil-rock complexes were derived and evaluated in their utility for predicting relative abundances of rodent prey. Data on the presence and abundance of rodents were collected at each survey point, by counting holes of Murinae rodents and giant molerats, and used to validate the habitat classification. Knowing the spatial location of the samples, these were used as training sites in a supervised classification to generalize the classification of habitats to the whole study area. The classes derived, and their spatial distribution, closely matched the micro-habitats defined by previous studies in Bale, reflecting rodent distributional patterns in relation to terrain forms and associated soil depth and soil moisture regimes (reviewed in Chapter 2).

Field surveys

A total of 179 point-samples representative of the range of vegetation types and land systems were surveyed. At each site, variables relevant to rodent distributions were measured, including the percentage cover of vegetation (grasses, flowering plants and mosses) and physical variables (bare ground, stone). Soil and rocks can form a significant portion of the landscape and these variables are also likely to be captured by image reflectance (Lewis, 1998). Other environmental variables were also recorded to represent the landscape in which the sample was found (e.g. land-form and slope).

The point samples were located every 200m along line-transects running across the study areas (four in Web, five in Sanetti, two in Tullu Deemtu). A systematic sampling strategy was chosen in preference to either a random strategy, which would have been impractical due to the size of the study area, or a stratified strategy that would have required a subjective definition of habitat types. By using line-transects, the range of vegetation variation was more efficiently covered and the data remain adequate for objective classification of the vegetation. It is very unlikely that the distribution of sites along transects - with lengths of between 2.2 and 4km- overlaid environmental gradients because vegetation patterns in Bale follow small-scale landforms within an otherwise relatively homogeneous area. On the same bases, it was assumed that the distances between transects (2,000m) and sample points (200m) were large enough to avoid spatial auto-correlation and ensure independence.

The percentage cover of bare ground, stone, and plants were visually assessed on a circular area of 5m radius, referred to as a ‘quadrat’. The choice of quadrat size was influenced by considerations of the fine scale at which variations in plant communities occur, and of previous studies that used this method to investigate relationships between counts of rodent signs and habitat types. Cover was measured following Braun-Blanquet’s scale: **1**= <5%; **2**= 5-25%; **3**= 25-50%; **4**= 50-75%; **5**= >75%**.** For additional information on the structure of vegetation, the cover by vegetation layer was also recorded, using the three layer model that typically describe the structure of Afroalpine-type vegetation, with few and low strata: modal height <5 cm *ground level*; 5-30cm *herbaceous level*, and >20cm *shrub level*. The abundance of small plants on the ground level layer were measured within a concentric 80cm radius-circle or “small quadrat”. This was used to characterize the ground-level component at each sample point (there was a close correlation between the cover of each vegetation layer in the two quadrats, e.g. r=0.74 between ground-level vegetation cover in the large and small quadrat).

Most flowering plants were identified at the species level - some at the genus level - with the support of identifications of specimens collected during the survey at the National Herbarium in Addis Ababa. Grasses were considered as one category because approximations to species-level identifications in the field require a high level of expertise and are particularly difficult during the dry season. Grass cover was recorded as ‘short grass’ or ‘tall grass’ where they belonged to the ground or herbaceous layer respectively.

Landscape environmental variables included: the presence or absence of mima mounds (completely or partially included in the quadrat); four categories of slope: flat, gentle, moderate and steep; and terrain forms: swamp, plateau, valley bottom, *mesa* top, low ridge, hill slope, and mountain slope. Valley bottom included accumulation plains in valley floors, small valleys, depressions and drainage lines; low ridges were short and mainly rocky slopes including *mesa* slopes, banks and cliffs.

Vegetation classification

The first step in defining habitat types was the identification of plant communities or vegetation classes. For this, cluster analysis was used to summarize the vegetation and physical data (soil and stone cover), a method especially useful for defining mapping units (Jongman, 1987). This type of classification is based on the idea that community types exist, and that each can be described by characteristic species combinations. Specifically, the two-way indicator species analysis (TWINSPAN) was chosen, using the Community Analysis Package (Henderson & Seaby 2002). This method, one of the most widely used in community ecology, characterizes groups by a set of differential species that prevail in one side of a dichotomy, produced by ordinating the samples in an iterative process (Tabachnick & Fidell 1989). The indicator species are the set of most highly preferential species that reproduce as good a refined ordination as possible. TWINSPAN incorporates quantitative data, percentage cover in this case, by defining a qualitative equivalent of species abundance, the ‘pseudo-species’. Each species' abundance is replaced by the presence of one or more pseudo-species, defined by the minimum abundance of the correspondent species or 'cut level' (e.g. *Achemilla abyssinica* 1, *A. abyssinica* 2, etc). As a divisive method, TWINSPAN starts with all quadrats as a group and divides it into two smaller groups, and so on. In this way of clustering, large differences prevail over the less important smaller differences.

Rodent abundance

Measurements of rodent abundance, using counts of holes in each quadrat, were used to assess the utility of vegetation classes in predicting prey abundance and distribution. Counts of rodent signs were assumed to be an appropriate measure of prey availability to wolves because, applying similar methods, they were found to correlate positively with wolf abundance in Bale (Sillero-Zubiri *et al.* 1995a,b; reviewed in Chapter 2); a giant molerat index based on their signs closely correlated with their abundance as determined by actual animal counts (Sillero-Zubiri *et al.* 1995b); and estimations of rat abundances based both on hole counts and trapping evidenced the same positive relationship with wolf densities.

Numbers of burrow holes of Murinae rats and Rhizomyinae molerats were measured in each 5m-radius quadrat. The burrows of these two groups are sufficiently different to be visually discriminated. Counts excluded old unused rat holes, distinguished by plant growth around the entrance. Molerat signs included open and plugged holes and earth mounds.

Tests were used to confirm statistically significant differences among vegetation classes on the number of rodent signs per quadrat. One-way ANOVA and the post-hoc Tukey test were used to test for differences in mean rat abundance between habitat types using the log-transformed data (the null hypothesis of heterogeneity of variances could not be rejected: Levin's statistic 1.541, df 7, P=0.157). The Kruskal-Wallis H test, a non-parametric analogue of the one-way ANOVA, was applied to comparisons of giant molerats sign counts, which presented a more skewed distribution. Chi-square tests were used to test for significant differences in giant molerat presence-absence among habitat types.

Habitat mapping

Habitat mapping was used to generalize the classified vegetation data so that they could be depicted on a map, using remotely sensed data. Stability in the spatial distribution of vegetation types was assumed for the study period (1988-2000), because the topographic features that are the main determinants of vegetation are unlikely to change at this time scale. Past vegetation patterns as depicted on field maps of the Web Valley from 1988-1992 (D. Gottelli & C. Sillero-Zubiri, unpublished) also matched closely with the distribution patterns obtained from this recent image of the study area. The fact that, 10 years later, similar numbers of wolves and packs occupied the same study area when they recovered from epizootics in Web and Sanetti (Chapter 6) further supports the assumption of stability in vegetation patterns and rodent abundances.

A Landsat Thematic Mapper Plus (U.S. Geological Survey) of the dry season landscape was the source of the remote sensed data. At this time of year vegetation types contrast most (dry grasses were expected to contrast with the evergreen *Alchemilla* spp. herbs). The size of the pixel (28.5m) provided the resolution required for the scale of vegetation variation at which rodent preferences occur. Field surveys were conducted during the 1999 dry season (mostly in January) but a clear image of the dry season was available only for January 2001.

The image used provides geometric accuracy within 250m for low-relief areas at sea level (Landsat 7 TM+, Level 1G product, systematically corrected, radiometrically and geometrically). Twenty control points spread across the study areas were used to georeference the data with sufficient accuracy. These were obtained from 1:50,000 cartographic maps and GPS measurements and their locations converted from the ADINDAN datum (specific for Ethiopia) to that of the image. A consistent longitudinal drift of around 300m westwards (299 ± 49m) was detected, while no apparent drift existed along the latitudinal axis (differences on the y coordinate averaged -10± 37m). In order to locate the quadrats on the image, their GPS positions measured in the field were modified accordingly (adding 300m to the East-West coordinate value). Considering GPS location errors up to 100m (Janeau *et al.* 2001) some uncertainty existed on the exact location of the sites. For this reason, the sites used for the development of training areas in a supervised classification were those located within relatively homogenous areas of pixel.

All six visible, near and middle infra-red bands of data were used in a supervised classification of the image. In general, classification accuracy increases as a function of the number of spectral bands used, because some bands are particularly helpful in identifying rock types, soil or moisture contest, all features relevant for the classification of habitat types in this study. The maximum likelihood procedure provided by IDRISI software (Clark Labs, Clark University, Worcester, USA) was used for a supervised classification of the image. The procedure is based on Bayesian probability theory; it uses the information from a set of training sites to calculate the mean and variance-covariance data of the spectral signatures to estimate the posterior probability that a pixel belongs to each class.

8.3.2 Pack size, territory size and habitat composition

Pack and territory sizes were measured over the monitoring period 1988-2000, with an interruption between 1992 and 1997, corresponding to the years after epizootics in Web and Sanetti (see Chapter 6 for more details); data from Tullu Deemtu were recorded for 1989-1991. The range of variation in group and territory sizes in Web and Sanetti includes that analyzed by Gottelli & Sillero-Zubiri for the period 1988-1992 and new data collected by Ethiopian Wolf Conservation Programme (1997-2000).

The data come from four packs in Tullu Deemtu, three packs in Sanetti; and ten packs in Web, including the new packs that formed after the epizootics (Chapter 7). The data from years marked by disease outbreaks (1990 in Sanetti, 1991-92 in Web) were excluded, because of the uncertainty on defining the size of the group and the home range used during this period of rapid changes. Data after the epizootic are from several years after the disruption; this gap reduced the chances that study packs were still affected by the immediate consequences of high mortality.

Pack size is the number of adult and subadult wolves present during the reproductive season (November to March) (see Chapters 6 and 7 for the methodological details). Pack home ranges were estimated by restricted minimum convex polygons (i.e. 5%

outlier locations removed, ArcView's Animal Movement programme, Hooge & Eichenlaub 2000) to minimize the effect of outliers and unused areas in the habitat composition analysis. Sillero-Zubiri & Gottelli (1995b) showed that individual home range sizes were not related to the number of locations (range 17-315) used to determine them and that the home ranges varied little between members of the same pack. Therefore, all packs with at least 40 locations for a given year were included in the analysis and pack home ranges were calculated by pooling the locations of independent sightings of all wolves - adult and subadults - in a pack in the dry season (November and March), which matches the biological breeding-through-independence period.

Two measures of prey availability within territories were derived from the habitat map by overlying home range polygons:

a) the extent of each habitat type within the home range, to estimate the abundance of prey resources; and .
b) their proportion within the home range, to provide a measurement of heterogeneity in the availability of prey resources.

Pack size, territory size and measurements of habitat composition were statistically compared between study areas of contrasting prey quality (Tullu Deemtu versus Web and Sanetti), and within the more productive areas (Web-Sanetti) to account for the effect of expansionism in the simultaneous regulation of group size and territory size in these populations. Variables were averaged per each pack across the study period, to control for lack of independence between subsequent points for any given pack.

8.4 Results

8.4.1 Habitat quality types

Rodent-habitat associations

A lack of association between counts of signs of Murinae rats and giant molerats indicated that the two types of prey had independent spatial distributions (both at the level of the whole sample (Spearman R= –0.066 P>0.1) or within study areas (Web Valley R= 0.016, P>0.1, Sanetti R= -0.069, P>0.1)). Pairwise comparisons detected associations between single environmental variables and rodent abundance, but these varied with prey type and study area. Similarly, correlations between counts of rodent signs and the two first axes of a Principal Component Analysis (PCA) showed that vegetation-soil-rock complexes co-varied with rodent abundance, but signs of each prey type correlated more closely with one or the other axis. Correlations were also strongest when sites were ordinated separately for each study area. This preliminary analysis evidenced that the two prey types were distributed independently in relation to their associated environmental variables. Accordingly, the classification of vegetation was conducted separately for each study area, and the dividing environmental variables were also those identified as good predictors of rodent abundance in preliminary analyses (see below).

Vegetation classes

TWINSPAN clusters representing four vegetation classes in Web Valley, and four in the Sanetti Plateau (including *Sanetti* and *Tullu Deemtu*) (Fig. 8.1) resulted in better predictors of prey abundances than the classes derived from a classification of all sites. Variables that correlated individually with rodent type abundances appeared as indicator species at the TWINSPAN divisions. Of these, short grasses and *A. abyssinica* were frequently found in most classes, while *H. splendidum* was frequent in some (e.g. class 1 and 2) but absent or rare in others (Table 8.1). In summary, most classes differed mainly on the relative proportions of soil, stone, short grass, *A. abyssinica* or *Helichrysum* spp., whereas the herb *A. pedata* characterized class 5 (in association with other plants typical of waterlogged and seasonally flooded environment) and *Artemesia* and *Kniphofia* shrubs dominated class 7 (Fig. 8.2).

Vegetation classes were also associated, in the way expected, with landform types, the steepness of the ground, and the presence of mima mounds. Figure 8.2 combines these sources of information providing a synoptic description of each vegetation class. Two vegetation classes, 'Sedge swamp' and '*Alchemilla haumanii* heath' differed markedly from all other clusters and were represented by few sites (n=4 and n=8 respectively). Swamps with *Carex* spp. sedges occupy permanently flooded depressions and have no value for wolves in terms of prey availability (Sillero-Zubiri *et al.* 1995a). *A. haumanii* heath occupied a restricted area within the range of the packs in Sanetti. Both were used for Landsat image classification but more detailed analysis concentrated on the more common habitat types.

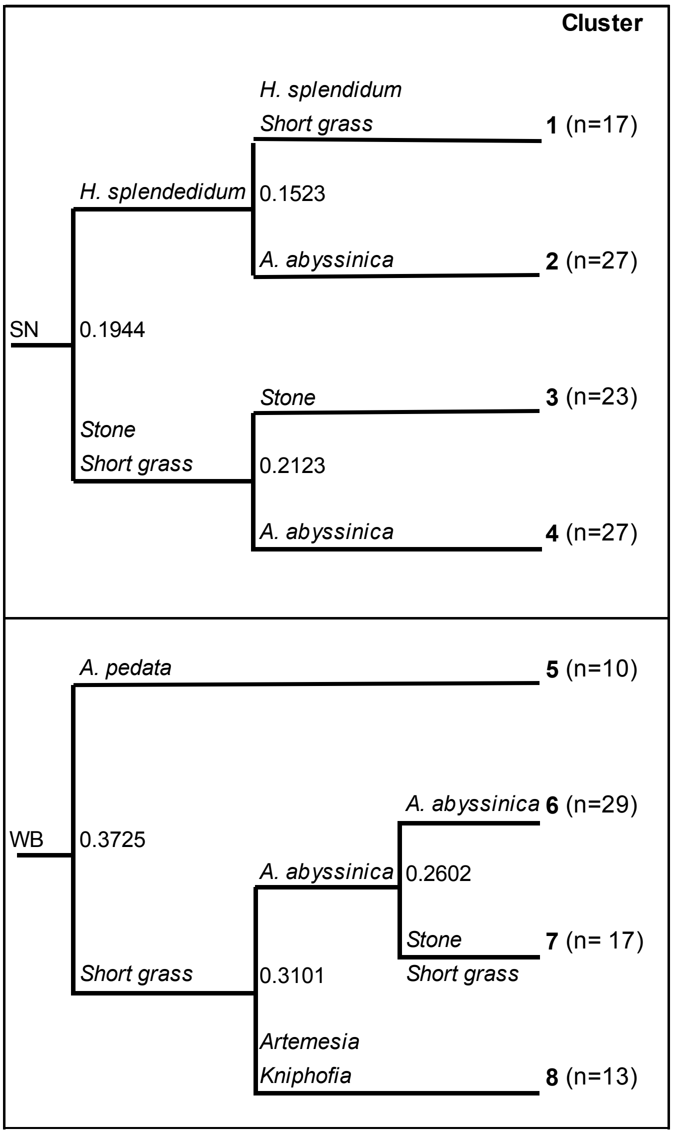
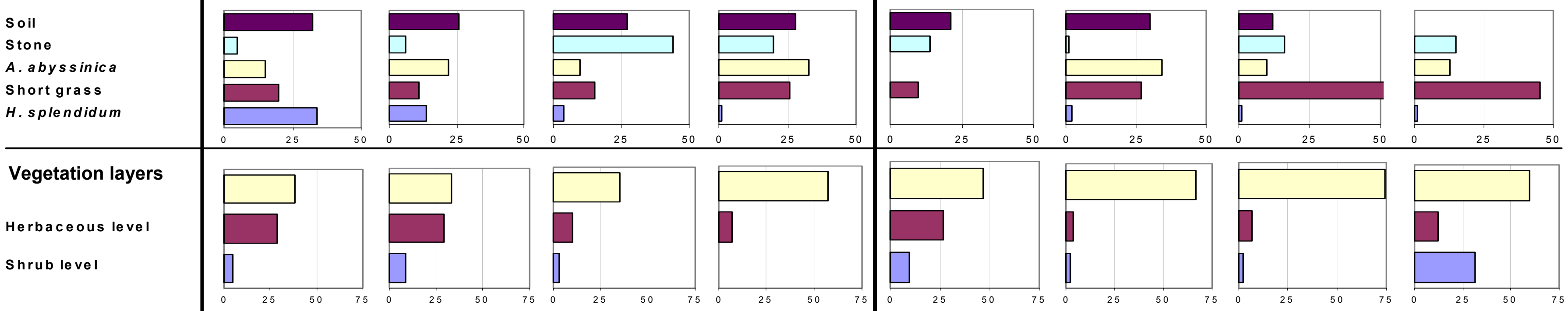


Figure 8.1 Dendrogram showing vegetation classes (clusters), the eigenvalue for each division, and the indicator species associated to each side of the division. N= number of quadrats per division

	Sanetti				Web			
	1	2	3	4	5	6	7	8
soil	V	V	V	V	IV	V	V	
stone	IV	V	V	IV	III	II	IV	IV
short grass	V	V	V	V	III	V	V	V
Alchemilla abyssinica	V	V	IV	V		V	IV	V
H. splendidum	V	V	II	I		II	I	II
Thymus schimpery	III	IV	I	I		I		IV
Erigeron alpinus	IV	III	II	I		I		I
Tall grass	V	III	II	I	III	I	I	I
H. cymosum	III	III	II	II		I		II
Euryops postratus	II	I	I	I				
Dichrocephala spp	II	I	I	II		II	I	I
Wahlenbergia pusilla	II	I	II	I				
H. citrispinum	I	III	III	I		II	I	III
Sagina afroalpina		II	I	I		II	III	IV
Veronica spp		II	II	I				
H. gofense		IV	III	I				
Sagina abyssinica	I	I	III	I				
Geranium arabicum	II	I	I	II		I		
Galium aparinodies			I	II				
Anthemis tigreensis	II	I	I	II				
Alchemilla microbetula		I	I	II	I			
Haplocarpa spp		I	I	I	I		I	
Alchemilla pedata					IV	I	II	
Carex monostachya		I			III			
Cyperacea		I	I		II		I	
Mosses	I	I	II	II	I	II	I	I
Salvia merjamie						IV	I	
Carduus chamaecephalus						II		
Polygala spp						II		I
Senecio spp	I	I	I	I			II	
Trifolium spp	I		I	II	II	I	II	IV
Kniphofia isoetifolia					I	II	I	IV
Artemesia afra						I	I	IV
Erica spp								III
Hebenstretia dentata						I		II
Crepis carbonaria						I		II

Table 8.1 Frequency of occurrence of species and physical variables. Presence classes I to V represent within cluster frequencies (respectively 0-20%, 20-40%, 40-60%, 60-80%, 80-100%). The commonest species are highlighted in grey shading and squares mark the most frequent bush life-form species.



		SANETTI PLATEAU				WEB VALEY			
Cluster		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Dominant cover components		1 *H. splendidum* 2 Soil 3 Short grass	1 Soil *2 A.abyssinica* *3 H. splend. & H cittrispinun (14%)*	1 Stone 2 Soil 3 Short grass (*H cit.* 6%)	1 *A. abyssinica* 2 Soil 3 Short grass	1 *A. pedata* 2 Soil 3 Stone & tall grasses (14%)	1 *A. abyssinica* 2 Soil 3. Short grass	1 Short grass (61%) 2. Stone	1 Short grass 2 *Artemesia* 3 Stone *(Kniphofia* 11%)
Mima mounds		12 %	30%	30%	**52%**	20%	**59%**	29%	0%
Terrain		Plateau 82% Hill slope 12%	Hill slope 56 % Plateau 22% Ridges 19%	Plateau 52% Ridges 22% Hill slope 13%	Plateau 52% Valley bott.30%	Plateau 50% Valley bott.40%	Plateau 48% Valley bott.34%	Plateau 41% Mesa top 29%	Hill slope 54% Ridges 23% Mesa top 15%
Slope	0	* * *	* *	* * *	* * * * * * * *	** * * * * * * *	* * * * *	* * * * * * *	* *
	1	* * * * * * *	* * * * *	* * * * * *	* *	*	* * * *	* *	*
	2	*	* *	* *	*		*	* *	* * * *
	3		*	*					* * *
Vegetation classes and rodents		**HELICHRYSUM HEATH**	**OPEN HELICH. HEATH**	**ROCKY GRASSLANDS**	**ALCHEMILLA**	**BOGS**	**ALCHEMILLA**	**SHORT GRASSLAND**	**ARTEMESIA-GRASSLAND**
		RAT 1	**RAT 3**	**RAT 3**	**RAT 2**	**RAT 2**	**RAT 2**	**RAT 2**	**RAT 1**
		GMR 0	**GMR 1**	**GMR 2**	**GMR 2**	**GMR 2**	**GMR 2**	**GMR1**	**GMR 0**

Figure 8.2 Vegetation clusters and environmental associations. Each cluster was associated to a prey category (RAT 1 to 3 and GIANT MOLERAT 0 to 2) and combined into three main habitat quality types (shown on a gradients of grey).

Validation of vegetation classes

Rat holes were present in between 60 to 100% of the quadrats across vegetation classes, and the mean number of rat holes varied from around 3 in '*Artemesia*-grassland' to 22 in 'open *Helichrysum* heath' (Fig. 8.3). Differences among classes were statistically significant (log+1 ANOVA: F $_{(7,155)}$= 8.779, P=0.000) and explained over 50% of the variability in the counts (Eta: 0.5333). Three categories of rat abundance were derived from multiple comparisons between vegetation classes: *Rat 1*(range 3 to 6 holes per quadrat on average); *Rat 2* (9 to 13); *Rat 3* (20 to 22) (marked in shade in post-hoc test results, Table 8.2). Although not all classes within each group were significantly different from all other classes in the other groups, this division represented well the observed range of variation (see Figure 8.3), perhaps with the exception of 'bogs', in turn the class with the larger variation in rat sign counts.

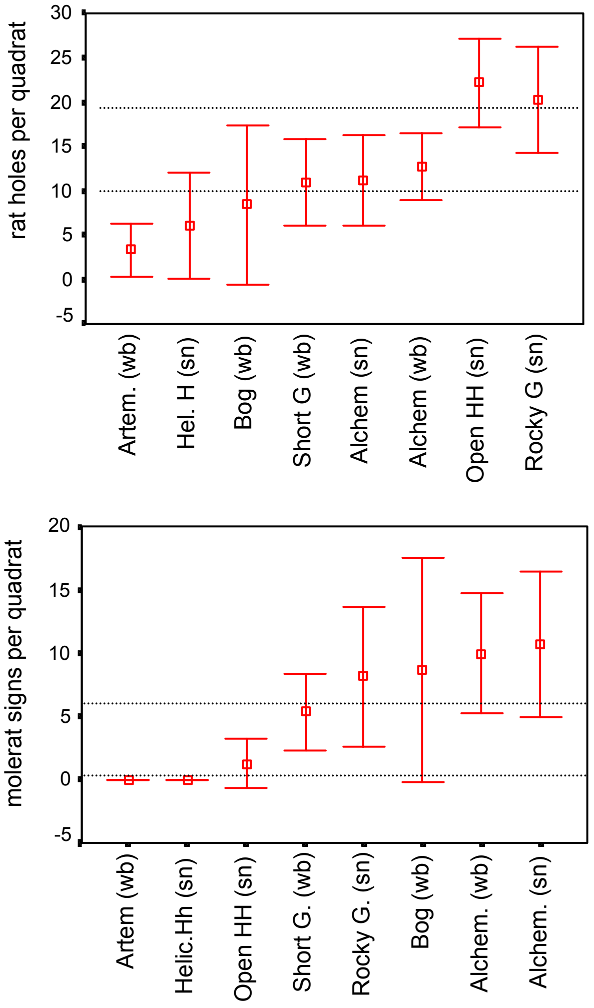


Figure 8.3 Mean and 95% confidence interval for the average number of rat (a) or giant molerat (b) signs in quadrats by vegetation class. SN=Sanetti, WB=Web Valley sites. Horizontal lines indicate the three classes of rodent abundance.

	RAT holes (log+1) Tukey test			% quadrats with holes
	1	2	3	
Artemesia-grassland	0.97			61
Helichrysum heath	1.11			58
Bogs	1.55	1.55		70
Alchemilla meadow (SN)	1.88	1.88	1.88	77
Alchemilla meadow (WB)		2.17	2.17	100
Short grassland		2.36	2.36	100
Rocky grassland			2.73	100
Open Helichrysum Heath			2.93	96
Significance	0.16	0.28	0.05	

Table 8.2 Comparisons among vegetation classes of the mean (log+1) number of rat holes and the percentage of quadrats with rat signs. In shade are shown the groupings used to define habitat quality types.

Giant molerats presented a more clumped distribution than rats. No signs were found in '*Helichrysum* heath' and '*Artemesia*-grassland', rare in 'open *Helichrysum* heath' (found in 4 out of 27 quadrats, or 15%), but were otherwise present in between 52 to 70% of the quadrats. Vegetation classes differed on the average number of molerat signs (Fig. 8.3; Kruskal Wallis test: Chi-square=37.454, df 7, P<0.001). This difference was still significant when the two classes with no giant molerats were excluded (Kruskal Wallis test: Chi-square=37.454, df 7, P=0.000), but not when 'short grasslands' were removed from the comparison (Fig. 8.3). Therefore, three quality classes were defined: *Giant molerat 0* =absent, *Giant molerat 1* = fewer than 6 holes on average, *Giant molerat 2*=between 8 and 13 holes on average.

Habitat quality types

To enable comparisons among the different areas, the independent distribution of prey types and their abundances were combined into three main habitat quality types, which summarized resource availability as depicted by the different vegetation classes.

HQ1: *Habitat quality 1 = high abundance of rats and giant molerats (RAT 2 or 3 - GMR 2).*

- **'*Alchemilla* meadows'** = short afroalpine vegetation in plateaux and valley bottoms with mima mounds in Web and Sanetti;
- **'rocky grasslands'** = with high percentage of bare ground and pebbles, occupying many flat areas of Sanetti;
- **'bogs'=** dominated by bare soil and *Alchemilla pedata* –with other semi-aquatic

plants- in depressions that were waterlogged or seasonally flooded, in Web's flat areas and valley bottoms.

HQ2: *Habitat quality 2 = high rat abundance (RAT 2 or 3) and few giant molerats (GMR 1)*

- **'open *Helichrysum* heaths'** = the vegetation with more complex structure, including sparse bushes of *H. splendidum* and *H. citrispinum,* tall grasses, and various herbs; found in hills with moderate slopes, ridges and some flat areas in Sanetti;
- **'short grasslands' =** dominated by short Afroalpine tussocks and some herbs, occupying the thin-soiled habitats such as the *mesas* of Web .

HQ3: *Habitat quality 3 = few rats (RAT 1) and no giant molerats (GMR 0)*

- ***'Helichrysum*** **heaths'=** important shrub level component -mainly by *H. splendidum*- and tall grasses; represented mostly in quadrats from the rain shadow of the Tullu Deemtu peak, also on hill slopes in Sanetti;
- **'*Artemesia*-grasslands'=** vegetation with an important cover of *Artemesia* and *Kniphofia* shrubs, and bushes of *Erica* and *H. citrispinum;* found in moderate to steep slopes in hills and rocky ridges in Web.

The maps in Figure 8.4a, b and c show the distribution of habitat quality types in the study areas, and the location of home ranges in a given year. On the bases of these maps, the areas of each habitat type within territories were calculated. These were used on the following section to tests the predictions initially stated.

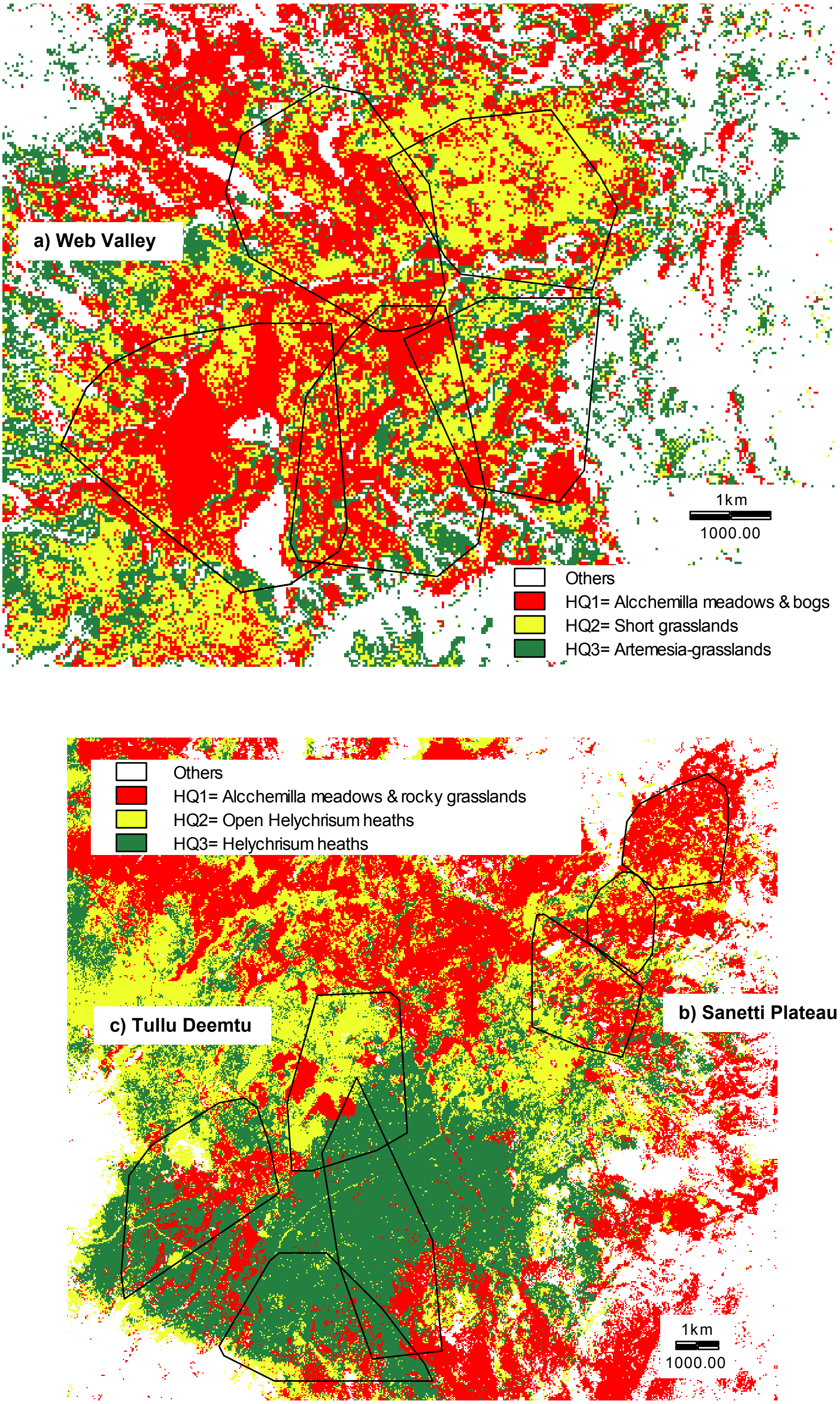


Figure 8.4 Maps with the distribution of pack home ranges in 1989 and the habitat quality types: a) Web Valley, b) Sanetti and c) Tullu Deemtu.

8.4.2 Habitat composition analysis

Variations in pack size and territory size

The average pack size in Tullu Deemtu was markedly lower than in Web or Sanetti (adult and subadult wolves 2.4 ± 0.5, 6.0 ± 1.9 and 6.8 ± 1.5 respectively) whereas the average territory size was twice as large as that in other areas (10.6 ± 1.1 km^2, 4.3 ± 2.7 km^2 and 4.6 ± 1.8 km^2 respectively) (Table 8.3 and Figure 8.5). Differences in home range and group size were statistically significant (ANOVA F (1,15) =22.602, P<0.001; F (1,15) =13.64, P=0.002). This result expanded the range of population densities for which this basic relationship -previously described by Sillero-Zubiri and Gottelli (1995b)- was maintained.

			Group size		Home range size		
	Pack	Years	AV	SD	AV	SD	AV nb locations
Web Valley	Kotera*	*7*	8.6	2.6	8.8	1.9	*145 (min 42)*
	Sodota	*4*	7.5	2.6	4.9	1.6	*188 (min74)*
	Terapesa	*1*	4.0		1.8		*195*
	Fincha	*2*	7.0	2.8	4.8	0.8	*113 (min 52)*
	Mulamu*	*4*	8.3	1.0	9.4	2.7	*113 (min 100)*
	Wolla	*4*	6.5	1.3	3.7	0.7	*158 (min 126)*
	New Fincha**	*1*	3.0		2.0		*45*
	New Sodota**	*1*	4.0		2.0		*87*
	Darkeena**	*1*	5.0		2.6		*61*
	Megity**	*1*	4.0		3.4		*100*
Sanetti	BBC*	*4*	8.5	3.1	5.3	2.4	*107 (min 40)*
	Crane	*2*	5.5	0.7	2.6	0.2	*157 (min 150)*
	Nyala*	*3*	6.3	0.6	5.9	2.4	*70 (min 43)*
Tullu Deemtu	T-Deemtu 1	*1*	2.0		10.0		*111*
	T-Deemtu 3	*2*	2.5	0.7	11.9	3.1	*95 (min 73)*
	T-Deemtu 5	*1*	3.0		9.4		*100*
	T-Deemtu 9	*1*	2.0		10.9		*64*

Table 8.3 Home range and group sizes of wolf packs averaged across years. *Packs that persisted through an epizootic in Web and Sanetti populations in the early 1990s. ** New packs formed in Web after the population decline.

The size of home ranges in Tullu Deemtu showed little variation (CV=0.1) in comparison with Web and Sanetti (CV=0.5) (Table 8.4 and Figure 8.5). In Web and Sanetti average group size correlated closely with average home range size (Spearman's r 0.72, P=0.002), indicating that wolves behaved as expansionists throughout the study period (Fig. 8.5.), in spite of the effect of the epizootic.

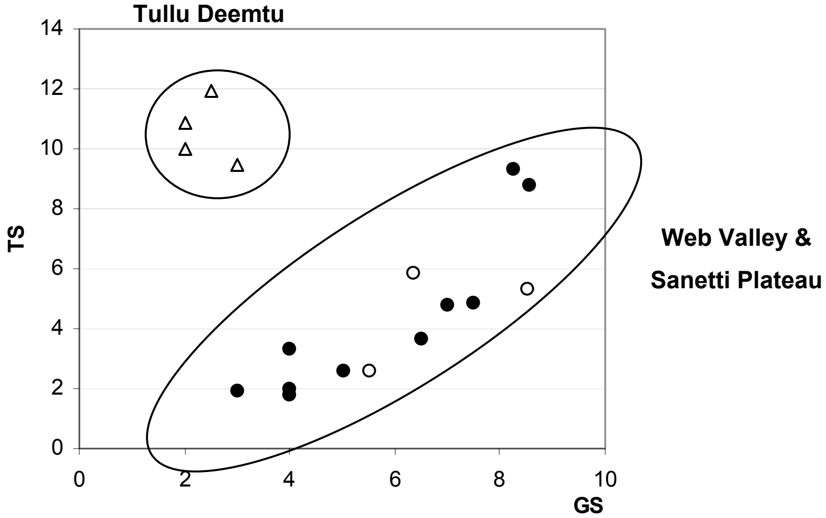


Figure 8.5 Relationship between group size and home range size. The comparison includes 13 packs from Web (black circles) and Sanetti (empty circles) and four packs from Tullu Deemtu (triangles). GS= group size (adults and subadults); TS= territory size (km^2).

Comparisons between contrasting areas

Pack home ranges contained similar amounts of the two richest habitats (HQ1 and HQ2, shown in red and yellow in Fig. 8.4), irrespectively of the extent of poor habitat (HQ3, shown in green in Fig. 8.4) (see Fig 8.6a and statistical tests on Table 8.4).

The area of the less-productive habitat was the most variable (Table 8.5 and Fig. 8.6) It was the area of HQ1, and the combined amounts of HQ1 and HQ2, that showed the lowest coefficient of variation between home ranges (Table 8.5). In Web and Sanetti, the two richest habitats combined (HQ1 + HQ2) occupied between 63 and 90% of the packs' average home range. In Tullu Deemtu, the rodent-poor *Helychrisum* heaths (HQ3) occupied on average 60% of the home range, compared with 6 to 20% in Web and Sanetti (a percentage significantly lower: ANOVA: F (2,14) 17.957, P<0.001) (Figure 8.6b).

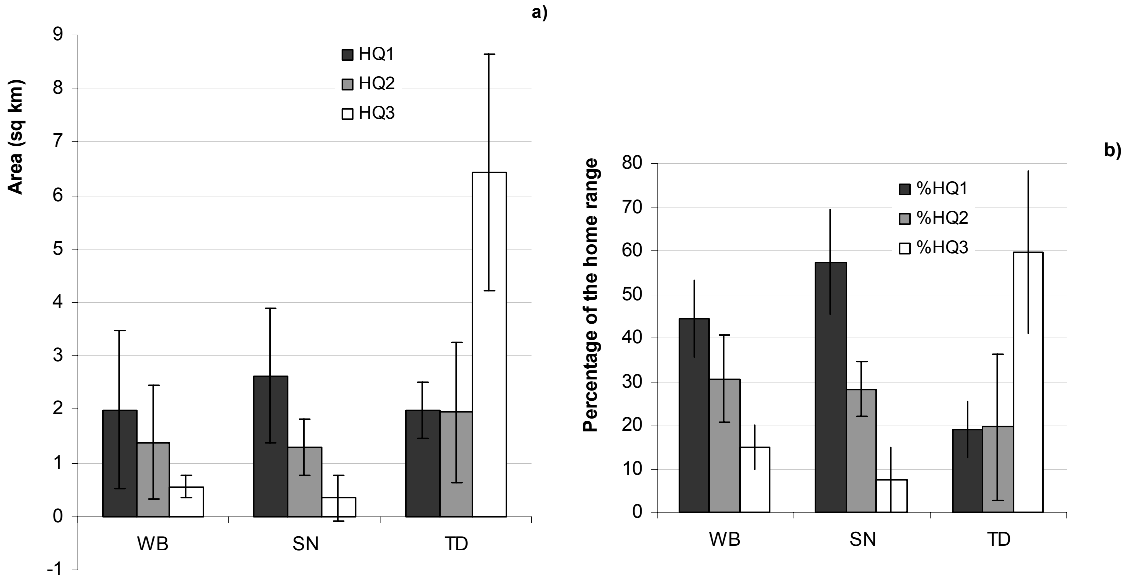


Figure 8.6 Home range composition: a) average area of each habitat quality type (1 richest to 3 poorest) and b) percentage occupied by each habitat, in Web (WB), Sanetti (SN) and Tullu Deemtu (TD). Error bars are standard deviations

One-Way ANOVA

	df	F	Significance
HQ1	2,14	0.28	0.757
HQ2	2,14	0.41	0.674
HQ3	2,14	37.17	** P<0.001)
(HQ1+HQ2)	2,14	0.13	0.876

		Tukey test	
HQ3	n	1	2
Sanetti	3	0.34	
Web	10	0.56	
T-Deemtu	4		6.44
Significance		0.962	

Table 8.4 Statistical comparison of the area of habitat types within home ranges across study areas

In particular, the amounts of HQ1 within home ranges in Tullu Deemtu were the least variable (Table 8.5). The small variation observed in the size of home ranges in Tullu Deemtu was mostly explained by differences in the area of HQ3 (the habitat most strongly correlated with variations in home range size, Table 8.6). In Web-Sanetti, home range size was highly and positively correlated with the area of HQ1 and HQ2, alone or combined, but not with HQ3 (which occupied a small proportion of the home ranges) (Table 8.6).

			Habitat quality types (sq/km)			
		Home range	**HQ1**	**HQ2**	**H1+ H2**	**HQ3**
ALL PACKS (n=17)	Mean	5.8	2.1	1.5	3.6	1.9
	CV	*0.6*	*0.6*	*0.7*	*0.6*	*1.5*
WEB-SANETTI (n=13)	Mean	4.4	2.1	1.4	3.5	0.5
	CV	*0.6*	*0.7*	*0.7*	*0.6*	*0.5*
MINIMUM TERRITORY						
New pack (group size 3)- Web		2.0	0.7	0.7	1.4	0.4
Pre-epizootic (group size 4) - Web		1.8	0.8	0.6	1.4	0.3
Pre-epizootic (group size 5) - Sanetti		2.4	1.4	0.7	2.1	0.2
TULLU DEEMTU (n=4)	Mean	10.6	2.0	1.9	3.9	6.4
	CV	*0.1*	*0.3*	*0.8*	*0.4*	*0.4*
MINIMUM TERRITORY						
Pair of wolves		9.7	1.5	1.2	2.7	6.8

Table 8.5 Home range habitat composition and description of minimum territories. In grey is highlighted the constant composition of habitats within the smallest territories.

		Habitat quality types			
		HQ1	**HQ2**	**HQ1+ HQ2**	**HQ3**
All packs (n=17)	Spearman's r	0.67	0.58	0.73	0.80
	P=	0.003	0.014	0.001	<0.001
Web-Sanetti (n=13)	Spearman's r	0.92	0.88	0.96	0.55
	P=	<0.001	<0.001	<0.001	>0.05
Tullu Deemtu (n=4)	Spearman's r	0.20	-0.80	-0.80	1.00
	P=	>0.05	>0.05	>0.05	<0.001

Table 8.6 Correlations between home range size and the area of each habitat type.

Home ranges in Tullu Deemtu appeared configured in a way that embraced 'patches' of the richest habitat type (HQ1, in red in map Fig 8.4). This was in accordance with the expectation of key habitats (that with high abundance of giant molerats and rats) being paramount in the configuration of territories.

On the other hand, the smallest home range used by pairs of wolves in Tullu Deemtu (9.7 km^2) contained more area of the rich habitat type (HQ1 and HQ2 alone or combined) than the two smallest home ranges in Web-Sanetti (1.8 and 2.0 km^2) -the territories of three wolves before the epizootic in Web and of four wolves forming a new pack during the recovery (Table 8.5). These minimal territories in Web-Sanneti contained almost identical amounts of each habitat type, with an absolute area of HQ1 (or HQ1+HQ2) eight times lower than that included in the largest home range recorded in this area (11.75 km^2, used by eight wolves).

Comparisons within rodent-rich areas

The comparison among pack home ranges from Web and Sanetti took into account variations in home range size due to the tendency for larger packs to defend larger territories (Fig. 8.5), previously hidden on the average values when comparing across areas.

Increments in home range size were accompanied by linear increments in the areas of HQ1 and HQ2 (territory size=1.25+1.644 HQ1, R= sq=0.88, F=80.49, $P<0.001$; territory size=1.26+2.28 HQ2, R sq=0.77, $P<0.001$) (Fig. 8.7a), or a combination of both. The area of poorer habitat (*Artemesia* grasslands and *Helicrhysum* heaths) occupied a small proportion. This correlated positively with home range size (Pearson's correlation coefficient r 0.671, P=0.012) but not consistently. Overall, the proportional representation of habitat types did not vary with the size of territories (Pearson's correlation coefficient, percentage of HQ1 r=0.26, P=0.386, percentage of HQ2 r=0.13, P=0.666).

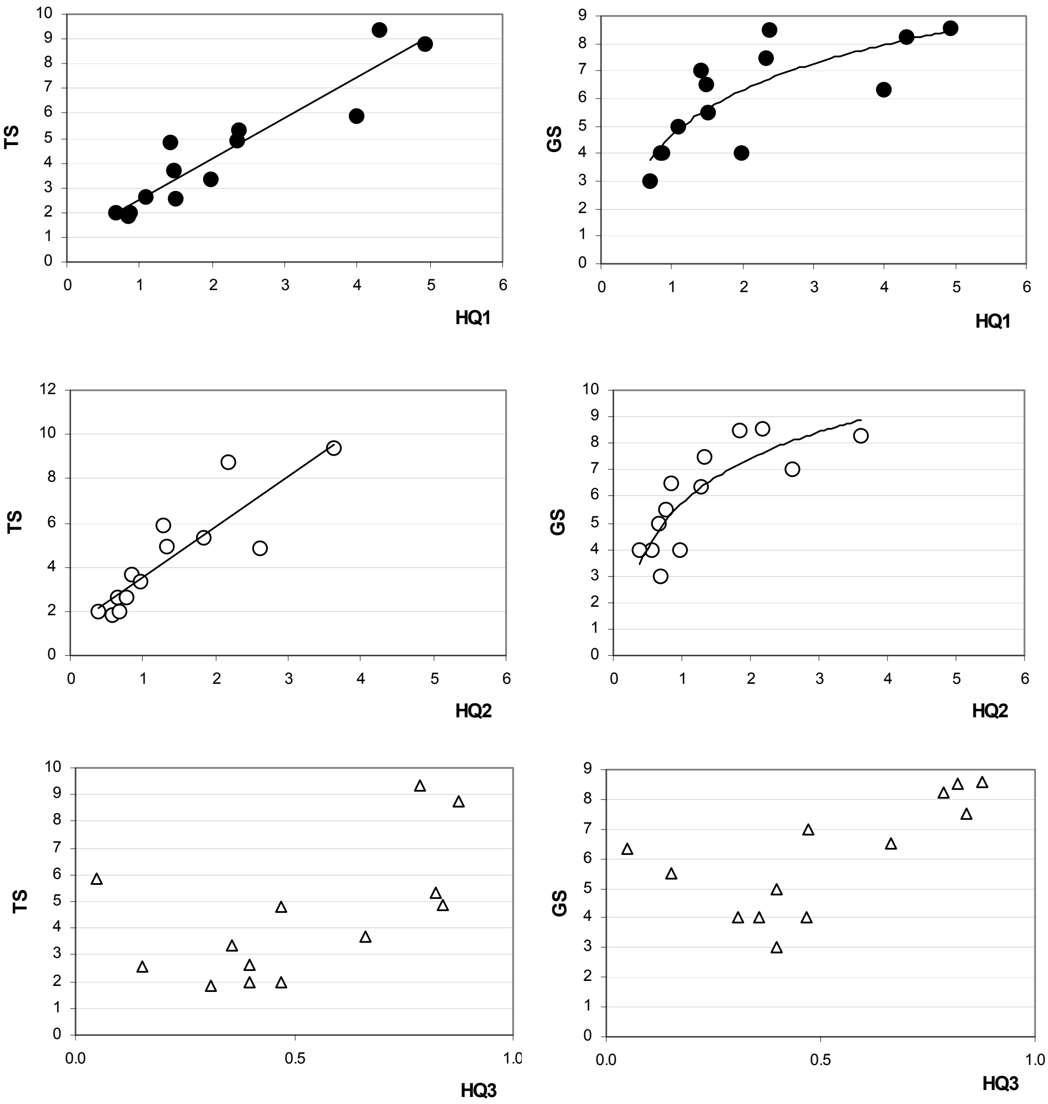


Figure 8.7 a) Relationships between the area of each habitat type (HQ1, HQ2 and HQ3) and group size (GS) or territory size (TS) in Web-Sanetti. GS and TS are averages per pack across the study period.

Group size increased less rapidly with the increasing area of HQ1 and HQ2 -did so particularly above a threshold area of ca 2km^2 of HQ1 and 2km^2 of HQ2 (Fig. 8.7b). The function that explained better the simultaneous variation in the size of groups and home ranges was a linear regression of the log-transformed values of territory size on group size (log group size = - 1.51 + 0.548 log home range size; R-sq 76.9%; ANOVA F (1,11)=36.66 P<0.001). The slope significantly less than one (one-sample T test, $t_{(11)}$=4.9982 <0.9998) signified that larger territories contained larger areas per wolf. The tendency for larger territories to contain more space per wolf was apparent across all packs (Fig. 8.8), and the data showed that this was not explained by larger packs containing less of high quality habitats (Fig. 8.7.a).

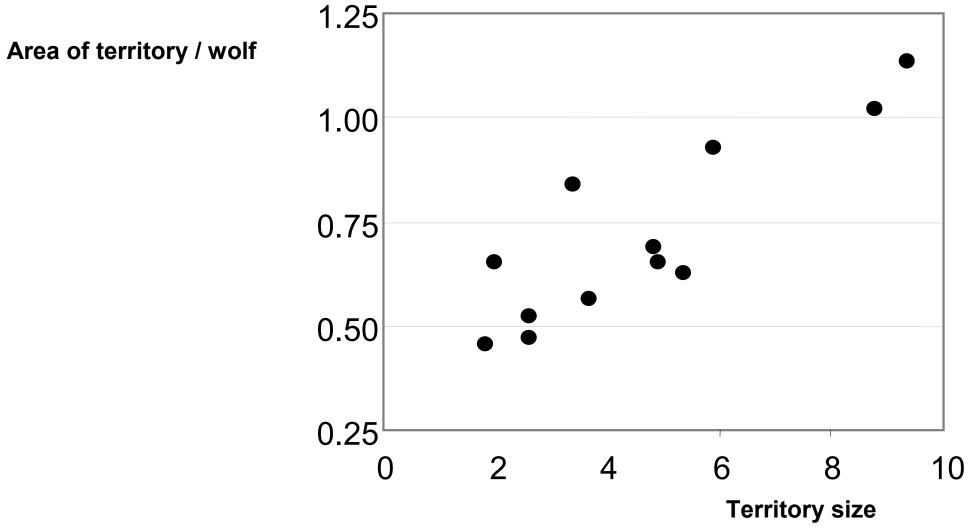


Figure 8.8 Relationship between the average area per wolf within territories and the size of the territories.

8.5 Discussion

In spite of marked variations in home range size, this study found that Ethiopian wolves defend territories containing similar amounts of key habitats -the two rodent-richest types in variable proportions- irrespectively of the area of poor habitat. The larger territories of Tullu Deemtu appeared delimited to enclose patches of high giant molerat abundance (in amounts that were also the less variable among packs), dispersed within a matrix of poor habitat -in the more productive areas the low-quality habitat was poorly represented within home ranges. It became therefore apparent that these 'key' habitats were influential in the configuration of territories, more specifically that with high abundance of the preferred prey, the giant molerat.

Similar patterns have been shown to link territory size and shape with the area and dispersion of key habitats for several carnivores (e.g. Arctic foxes *Alopex lagopus*, Hersteinsson & Macdonald 1996; Blanford's foxes *Vulpes cana*, Geffen *et al.* 1992; Eurasian badgers *Meles meles*, Kruuk & Parish 1982; white-nosed coatis *Nasua narica*, Valenzuela & Macdonald 2002). In agreement with the RDH (Macdonald 1983; Carr & Macdonald 1986), larger wolf territories in Bale existed in areas where key resources were more dispersed ('patches' within a poor 'matrix' in Tullu Deemtu). In turn, small territories occurred where rich habitats are highly aggregated, in an almost continuous fashion (Web-Sanetti).

Wolves in the large territories of Tullu Deemtu lived in pairs or small groups, while in Web and Sanetti large groups used small territories, but on average territories contained similar amounts of the rodent-rich habitat. This contradicts the RDH, which predicts group size to be determined mainly, and independently of territory size, by the total abundance of resources, or a key resource. A straightforward explanation would be that the prey abundance index is not consistent across study areas (the validation dataset indeed contained few samples of the rich habitat from Tullu Deemtu, because of its more restricted distribution there). An alternative explanation is that the pattern of dispersion of habitats types is actually affecting the wolves' foraging efficiency and energetic requirements. Wolves in Tullu Deemtu defend large territories and probably travel further between foraging grounds (the rodent-rich 'pacthes'). Detailed studies of foraging behaviour in areas of contrasting prey distribution are needed to explore these or alternative explanations. In particular, and independently of the advantages, if any, of sociality and cooperation, the RDH postulates that lower conspecific competition when the food resource if very rich (e.g. like in Web and Sanetti) facilitates the formation of 'spatial groups' (Macdonald 1983).

Returning to our original question, a complementary approach would be to consider the costs and benefits of group living under the different patterns of prey availability. This study would indicate that expansionism was favoured by the extreme aggregation of rodent-rich habitats in Web and Sanetti, because territorial expansion was concomitant with a proportional acquisition of rich habitat area. In Tullu Deemtu, instead, an increment in territory size will clearly not ensure the same rate of acquisition of key resources. To include more of high-quality habitat a pair or small groups may need to expand an already large territory to a size that is not economically defensible.

Additionally, wolves in larger groups in the more productive areas benefited from expansionisms by acquiring a greater area of territory by wolf than was available to wolves in smaller groups. It becomes clear that, whenever possible, packs would expand first looking to future augmentation, a finding that contribute to disentangle whether territorial expansion or group augmentation come first in expansionism.

In Kruuk and Macdonald’s view (1985), variations in group and territory size can be viewed as animals adopting one of two main alternative strategies in exploiting a limited resource:’ expansionists’ tend to increase the size of the territories -thus larger group inhabit larger areas- and ‘contractors’ maintain the smallest economically defensible area, living in larger groups if resources within this area allow. Even in the less productive Tullu Deemtu area, pairs of wolves used territories with more area of key habitat than the minimum used by packs in the more productive areas. This would suggest that wolves are always expansionists, but in Tullu Deemtu group formation appeared constrained by the pattern of prey distribution, most importantly giant molerats. On the other hand, expansionist wolves in Web and Sanetti lived in groups with a larger membership than that sustained by the minimum territory (by proxy, those which encompassed the minimum amount of key habitats), so that the extra costs of territorial defence appeared outweighed by the advantages of a larger group size (Kruuk & Macdonald 1985)

The relic distribution of Afroalpine habitats, and the competition for localized areas of high prey quality, possibly favoured the formation of larger groups that could defend an area from expanding neighbours -pre-empting a contractor strategy or territories used by wolf pairs. As discussed in Chapter 7, the benefits of long-term food security appear as the crucial selective pressure for group living in Ethiopian wolves (Sillero-Zubiri 1994). By tolerating conspecifics, the dominant animals ensure their offspring a territory to breed or inherit (Sillero-Zubiri *et al.* 1996a), whereas in population of pair-dominated territories, the only option at saturation would be long distance dispersal.

The apparent benefits of expansionism for the acquisition of critical resources is a good starting point to explain why wolves in Web and Sanetti do not live in pairs or small groups in smaller territories, while maintaining the per-capita intake rate (Kruuk & Macdonald 1985). Or why packs in Tullu Deemtu do not grow larger as allowed by the resources contained within territories. Some possible foraging constraints to sharing the more dispersed food resources in Tullu Deemtu have been already mentioned. A more comprehensive explanation will require due consideration of the costs and benefits involved in territorial defence and group living, including those affecting processes at longer time scales, such as life-time reproduction. This study identified some ecological conditions favoring group augmentation in Ethiopian wolves and postulated the benefits of expansionists may decline when resources are more dispersed.

CHAPTER IX

Summary discussion

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9.1 The multi-level approach

In this study I investigated aspects of a species' biology (the Ethiopian wolf) spanning across spatial and temporal scales, within a hierarchy of patchiness and heterogeneity in its environment. To do so I applied existing ideas of the ways individuals respond to their environments and, ultimately, queried the adaptive value of behavioural strategies. This approach subscribes to that proposed by Wiens (1992), who argues for the development of more specific, mechanistic based theories to advance understanding of ecological relationships. He noted that ecological studies have been largely phenomenological: a pattern is observed and matches with the prediction of a theory that postulates a certain linkage between pattern and process (Wiens 1992); but while the pattern can be empirically determined, the underlying process is still largely inferential. Under Wiens's 'mechanistic ecology', observed phenomena should be considered in terms of their underlying causes or mechanisms. Resources are the foundation of ecological processes and, as such, are the basic mechanistic element in biology. In accordance with Wiens' views, this study assumes simplicity, searching for the underlying, critical factors (resources) driving fitness and the constraints on their use.

Stephens and Krebs (1986) recommended that we must first clearly elucidate and separate resources and constraints. Then, if the interest is in constraints, we should study systems in which the resources are well known. It is in this regard that the specialized nature of Ethiopian wolves made a more rigorous understanding of their ecology possible. Wolves are pre-eminent hunters of Afroalpine rodents and the biological system under study is simple and clearly defined: a specialized top predator of the Afroalpine ecosystem. In such a case, we can learn a lot about the animal's behaviour along a 'single resource axis' (i.e. the Afroalpine rodent prey), as in MacArthur's (1968) concept of niche. His description of 'niche' plots utilization against some quantifiable resource variable -the resource utilization function. Conceptually, this function describes the choice of resources by animals; choices that can be constrained by predators, competitors, and various other factors, all of which can be tested. Ideally, the resource currency must have relevance for the fitness of the animal and be within their perceptive abilities (Abram 1988).

Following from this rationale, I focused on the food resource axis of the Ethiopian wolf niche and studied constraints as imposed by its relict distribution, fragmentation and heterogeneity. Whenever possible, I defined and measured resources and tested the assumption of resource limitation, concentrating on expressing patterns in terms of wolf behaviour and life-history traits, with a focus on aspects related to density effects and habitat selection.

In the following sections I interpret the results of the various studies in this thesis and generalize from them within the appropriate domain of spatial and temporal scales for the phenomenon investigated. At each level, I discuss the evidence of ecological conditions imposing constraints on processes occurring at lower levels of biological organization, and contrast the results with ecological theories relevant to the questions asked. Several aspects with important implications for the species' conservation are discussed in a final section.

9.2 Spatial ecological patterns in the Ethiopian wolf

9.2.1 Biogeography, evolution and specialization

The Ethiopian dome is an island within Africa. Its unique environment and isolation provided a potent millieu for speciation, particularly among the species that colonized the mountains with extreme climatic conditions (Kingdon 1990). *Canis simensis* is one of a handful of Ethiopian endemics of Palearctic origin believed to have invaded the Ethiopian dome from Eurasia in the last glacial age via land bridges. The time elapsed since the origin of the Ethiopian wolf, estimated at around 100,000 years (Chapter 5), further supports the hypothesis of its recent immigration to Africa (Kingdon 1990; Gottelli *et al.* 1994; Sillero-Zubiri 1994). This took place well within the Pleistocene, when Afroalpine habitats occupied vast areas of the country. Mitochondrial DNA phylogeography indicated a single colonization event and rapid expansion, followed by isolation and divergence of populations, as expected from the fragmentation of the high altitude habitats during the late Pleistocene.

Surprisingly, the genetic data also indicated that the Ethiopian wolf genome is still a relict of this late Pleistocene expansion. While fragmentation and genetic drift over the last 10,000 years resulted in local loss of genetic variability, the species as a whole conserved its variability. Random fixations of alleles within isolated populations -as wolves disappeared from intermediate lower areas pushed away by expanding forests- was deduced as the most parsimonious explanation for the genetic structuring of the mitochondrial DNA. Populations genetically closer were also geographically proximal and these were grouped in accordance with the pattern of Afroalpine fragmentation, reconstructed on the bases of shifting vegetation belts following the warming up of the late Pleistocene. The Ethiopian wolf genome gives evidence for limited dispersal among the fragmented populations -for example North and South of the dividing Rift Valley- and all seems to indicate that the species habitat specificity appeared early in its short evolutionary history.

The driving forces behind this specialization are ground for speculation. Most likely it was the combined result of various factors known to lead to ecological specialization (Futuyma & Moreno 1988), namely: the environmental constancy of Afroalpine ecosystems, an empty niche (the emerging Afroalpine habitats), conditions for rapid speciation in the extreme climate of the highlands (discussed in Kingdon 1990), the Palearctic ancestors' pre-adaptation to a cold climate, and competitive exclusion from alternative habitats by jackals, spotted hyaenas (*Crocuta crocuta*), African wild dogs (*Lycaon pictus*), lions (*Panthera leo*) and other large predators living in lower areas. Equally, in Afroalpine ranges where Ethiopian wolves became locally extinct, we observed golden jackals (*Canis aureus*) foraging in daytime (e.g. Mt. Choke, Gosh Meda) suggesting that the reverse exclusion competition scenario could also be true. Indeed, the cranio-morphological adaptations that make wolves so well equipped to catch Muridae rats may have determined that wolves out-competed jackals in exploiting the abundant rodent resource.

9.2.2 Habitat loss, fragmentation and metapopulation dynamics

Relatively slow processes of specialization and climatic change shaped the restricted distribution of Ethiopian wolves within Ethiopia. More recently however, habitat loss and fragmentation accelerated with the rapid expansion of humans into the highlands. This study identified that today seven extant wolf populations are restricted to the highest mountains of Ethiopia, in virtual isolation from one another, some internally subdivided (Chapter 3). Wolves were not seen, or any sightings reported, in cultivated land outside these Afroalpine remnants, or in relicts of natural montane forests below the Afroalpine belt (e.g. Bale's Harenna forest in Bale). Additionally, a diet study

(Chapter 4) confirmed that Ethiopian wolves are indeed highly specialized all across their distributional range, consuming chiefly diurnal Muridae rodents. Still, climate-induced variations in primary productivity apparently affect the availability of rodent prey types across populations, as a certain degree of dietary variation was evidenced from geographic changes in diet composition.

A highly specialized diet and an apparent lack of flexibility closely tie up the fate of Ethiopian wolves to the persistence of Afroalpine habitats. Suitable wolf habitats remain today only in 40% of the area potentially available under current climatic conditions (ca. 3,000km² of 7,000km² of land above 3,200m) (Chapter 3). In many parts of Ethiopia the upper limit of subsistence agriculture reaches as high as 3,900m, imposing a higher low-level boundary to wolf ranges than that biologically possible. As population sizes are determined by the extent of Afroalpine habitats, all extant wolf populations are very small. In Mt. Guna for instance, a mere 10 adult wolves live in an area of $50km^2$. Most other populations consist of fewer than 50 individuals; and only Bale contains a population in the low 100s, accounting for half of the global population.

Theory would predict high rates of extinction in such small populations due to stochastic processes alone (Soulé 1987). However, only one Ethiopian mountain range with suitable wolf habitat was found vacated (Mt. Choke – where wolves reportedly disappeared as long as 100 years ago). In more recent times, two other local extinctions occurred where Afroalpine patches shrunk to around $20km^2$. These results contradict expectations that a once-widespread species would collapse rather suddenly due to regional extinction when too few fragments of habitat remain, or when the flow of dispersers among them is disrupted (Hanski 1999). Instead, these findings highlight the species' resilience to small population sizes and isolation, and further substantiate the notion of stable prey populations in a stable tropical alpine environment.

Unfortunately, current trends of habitat loss are bound to lead to further extinctions. In particular, populations inhabiting small Afroalpine ranges in the northern highlands are the most vulnerable. In this regard, Ethiopian wolves seem to subscribe to the model of 'non-equilibrium metapopulation', characterized by isolated populations with low rates of colonization, which predicts regional extinctions rather than compensatory mechanisms of extinction and colonization, as in the classical metapopulation theory. This study found no proof of metapopulation-type dynamics along the past history of the species either. Our interpretation of the genetic data does not support extinction-colonization processes or bottlenecks as possible explanations low diversity and structure of the species genome. Indeed, for the more recent times, the evidence supports panmixia on a local scale.

9.2.3 Local population dynamics

The spatial structure of Ethiopian wolf populations we observe today is the result of the loss of Afroalpine habitat to agriculture over the last few centuries. Under these constraints, local processes of population regulation - rather than complex metapopulation dynamics- would likely decide the ultimate fate of small island-populations. By studying the dynamics of local populations in the Bale Mountains I have attained a better understanding of the demographic mechanisms that enable Ethiopian wolf populations to remain viable in spite of their small size and isolation.

Long-term trends analysis showed that, in the absence of disease, wolf populations in Bale were relatively stable, occurring at densities primarily defined by the local abundance of prey (Gottelli & Sillero-Zubiri 1992, 1995b; Sillero-Zubiri *et al.* 1995a,b). A population viability model developed by Haydon *et al.* (2002) also substantiates the notion of population stability favouring the long-term persistence of wolves in Afroalpine islands. The causal implication is that environments are stable and, by extension, prey populations are too. The Bale study case also indicate that populations appear insensitive to potential agents of decline other than disease, such as livestock grazing –believed to affect rodent abundance through reductions in plant biomass- or direct human interference. This assertion however may not be equally true for all extant populations, as ecological conditions vary across regions with climatic-induced gradients of productivity and the concentration of people. Still, probably with the exception of Mt. Choke, all recent extinctions have been driven mainly by loss of suitable habitat.

Still, wolf populations need to be resilient to demographic stochasticity to avoid numeric decline to unsustainable levels by chance alone. High survivorship after the first year of life certainly contributes to the resilience of populations. High survivorship results in the production of surplus animals that either disperse or remain in their natal packs, even if reproductively suppressed (Sillero-Zubiri *et al.* 1996a). This has two important implications for the dynamics of local populations (Chapters 6 & 7). Firstly, wolf populations can cope with years of poor reproduction or recruitment, because a large proportion of the population is composed by adult wolves with the potential to live for several years (oldest individual recorded 13 years – Sillero-Zubiri & Marino in press). Secondly, it was the capacity of these additional members to colonize and reproduce in newly established territories that contributed to the eventual recovery of wolf numbers after epizootics in Bale.

If population densities drop to low levels, however, social and territorial behaviours can forestall the speed of population recovery. It is the severity of habitat shortage within virtual Afroalpine 'islands' that underlies Ethiopian wolves' behavioural strategies (Sillero-Zubiri 1994; Sillero-Zubiri & Gottelli 1995b; Sillero-Zubiri & Macdonald 1998). It was in fact at the scale of territories and groups that regulatory mechanism became more evident, and in some ways wolf populations deviated from the predictions of classical population models.

9.2.4 Intrinsic regulation at the social group-local population interphase

Local wolf populations in the Bale Mountains were regulated by density dependent changes in the rate of population growth at high densities (Chapter 6). In the classical view of population ecology, two common biotic processes are density dependent factors that act as negative feedbacks, imparting stability to a population (reviewed in Caughley & Sinclair 1994): predation (that can be safely discarded in the Ethiopian wolf case) and intra-specific competition for food.

In accordance, at the local population level, survival rates -but not reproduction- changed consistently with increasing densities. Whether these factors limited population growth before resources were exhausted, or other factors were involved, was still equivocal. For example, most packs fluctuated in size while population numbers remained relatively constant at high density. The species' expansionist strategy (*sensu* Kruuk & Macdonald 1985) is the possible mechanism linking these changes in pack size; packs shrinking in size during a bad year will be 'pushed' into smaller territories by larger neighbouring packs, which can then accommodate new members within the expanded territory. In addition, crowded territories were associated with pack reproductive failures, possibly due to physiological causes and/or social tension among females. Thus, in this 'dynamic equilibrium', population regulation was mostly the result of intrinsic mechanisms -although long distance dispersal and the recruitment of young may ultimately depend on competition for food.

In carnivores such as grey wolves (*Canis lupus*), coyotes (*C. latrans*), red foxes (*Vulpes vulpes*) or African wild dogs, the distribution and abundance of resources apparently determines foraging efficiency which, in turn, determines optimal territory size and the number of breeding territories available within a given area (Wolff 1997)). In general, Wolff (1997) predicted that in social species self-regulation, if present, would be mediated through territoriality and reproductive suppression, which limits the number of breeding females in a population. In the Ethiopian wolf, territoriality and reproductive suppression eventually lead to inverse density dependence in the rate of population growth at reduced densities (Chapter 7).

In the Bale Mountains, constrains to the formation of new breeding units limited reproduction after epizootics. A combination of territorial expansion, delay dispersal and reproductive suppression determined the production of relatively few pups at low population densities. Reproduction only increased as the population grew and the conditions for dispersal and successful colonization appeared to be given. This process, rather than the alternative Allee effect, was the explanation for the inverse-density dependence observed at the population level.

9.2.5 Selective pressures favouring sociality

The fact that expansionism was favoured at relaxed levels of competition and space constraints was somehow surprising, and provided an interesting opportunity to explore the selective forces behind sociality in Ethiopian wolves. The 'natural experiment' provided the fall and rise of wolves in Bale indicated that habitat saturation was not necessary to promote delayed dispersal. The possible gains of independent reproduction in populations reduced by disease appeared outbalanced by the pressures of habitat shortage, food security, and the gains of inheriting a breeding space.

Because female wolves are the least benefited by philopatry among Ethiopian wolves (Sillero-Zubiri *et al.* 1996a), it is likely that their decision to disperse was crucial for the process of pack formation. In this regard, and as postulated by Macdonald and Carr (1989), my study indicated that the number of subordinate females 'in line' to inherit the reproductive position within the pack, was more determinant than the prevailing conditions at the population level.

By staying and waiting, subordinates capitalized on their chances to disperse and colonize a known area of high quality near or in the periphery of their natal territory, although some immigration was also involved. Such an expansionist strategy will be perpetuated in a population because all pack members may benefit from securing the long-term access to a highly restricted food resource and in doing so they enhance their lifetime reproduction. Moreover, when staying was no longer advantageous, individuals from these packs were likely to form new breeding units in populations under the level of habitat unsaturated.

These findings give support to the thesis that group-living in this species is directly related to the benefits of group augmentation, using strength of numbers in the acquisition and retention of resources (Sillero-Zubiri & Macdonald 1998), whereas the benefits of cooperative breeding still remain elusive (Sillero-Zubiri 1994; Chapters 7). In this respect, Clutton-Brock (2002) argues in his recent review of cooperative societies that if group members automatically shared benefits derived from increased group size, cooperative behaviour can be maintained by group augmentation alone. He observes that, in combination with kin selection, group augmentation can produce elevated levels of cooperative behaviour, and cheating may not be favoured unless the costs of helping are high. Indeed, helpers in some facultative cooperative breeders do not appear to increase the growth or survival of the young they are rearing, as it seems to be the case in Ethiopian wolves (Sillero-Zubiri *et al.* in press). In such cases, helping may reduce the chance that helpers will be ejected from their original group by dominants (Gaston 1978), although there is little empirical evidence to show that this is indeed the case.

9.2.6 Resource-based explanations of sociality

Creel and Macdonald (1995) summarised five types of selective pressure that may select for sociality in carnivores. Of the three selective pressures that may increase the benefits of tolerating group members through behavioural mechanisms, 'better resource acquisition', as discussed above, seems to best apply to Ethiopian wolves (wolf groups use strength of numbers in the acquisition and retention of resources, as larger packs fare better in territorial defence).

In addition, the balance of two essentially ecological factors may facilitate group formation by reducing the costs of tolerating conspecific group members. These are 'high dispersal costs' (e.g. constraints on dispersal opportunities such as lack of suitable habitat may encourage young to stay within their natal group past the age of maturity) and 'resource dispersion' (most obviously, abundant prey, rich or variable prey patches, or rapid prey renewal, may all lead to lower costs of tolerating conspecifics).

Previous studies in Bale showed that local resource abundance lead to different types of society; wolf packs in areas with low rodent density existed mostly as pairs, rarely accompanied by older offspring (Sillero-Zubiri & Gottelli 1995b), and their territories were also at least twice as large as those from larger packs in rodent-rich habitats. Quantification of relative prey abundances within territories -using habitat types as a reliable surrogate- showed that while in the two contrasting habitats total prey abundance seemed to be similar, packs in one area needed larger territories to encompass what appeared as the minimum area of the richest habitat types required to sustain a pair of wolves. This result was consistent with the Resource Dispersion Hypothesis (Macdonald 1983) in that it predicts larger territories where resources are more dispersed. Larger territories were configured such as to contain areas of rich-rodent habitats within a matrix of poor habitat, whereas the smaller territories were composed almost entirely of continuous areas of high prey density.

On the other hand, the large territories of small packs or pairs contained similar amounts of the key habitats to those found in the smaller territories of large packs. These results contradicted the expectation that resource availability will determine the size of groups, independently of their territory size. It could be argued that the measurement of resource abundance chosen by this study was a poor proxy for availability when comparing areas with contrasting patterns of habitat dispersion. It is likely, however, that the pattern of food dispersion itself is affecting individual's foraging efficiency. For example, the costs of travelling between foraging grounds and of defending a large territory may determine higher energetic demands for wolves in the rodent-poor in comparison with the more productive area.

Detailed studies of foraging ecology are needed to test this or alternative explanations. Such studies could more fully resolve the question of why wolves living in rodent-rich areas do not live as pairs in territories of the smallest size observed, or why -with the same amount of key resources- wolves in larger territories do not tolerate more conspecifics. What appeared more manifest from the present study is that the immediate benefit of resource acquisition via group augmentation outweighed the costs of the defence of an enlarged territory (Chapter 8). This occurred in the Web Valley and Sanetti Plateau, where the high aggregation of food resources determined proportional increments in the area of prey-rich habitats with increasing territory size. The same may not apply for packs in the low rodent density area of Tullu Deemtu, where the advantages of 'better resource acquisition' may imply high costs of defence and the expansion of an already large territory to incorporate more patches of the key habitat. For this argument to suffice in explaining group size differences -assuming similar resource availability within territories- any additional benefit of cooperation for territory owners in the poor-rodent habitat needs to be minimal or null, as well as the costs of evicting conspecifics (Macdonald 1983).

Social systems are the product of evolutionary cost-benefit analysis that balance the behaviours that allow individuals both to eat and avoid being eaten themselves, reproducing as successfully as possible along the way. Lifetime reproduction is the ultimate bottom line, and social organisations represent the most cost-effective behavioural solution for individuals of a particular species or population, given their morphology, ecology, and evolutionary history. Where rodent prey is very rich, reduced feeding competition may have permitted overlapping home ranges and the consequent formation of 'spatial groups' in the Ethiopian wolf. Cooperation may have then evolved and been maintained under these ecological conditions (Kruuk & Parish 1982, Macdonald 1983, Wrangham 1993, Creel & Macdonald 1995). This Resource

Dispersion Hypothesis has been invoked as the most parsimonious explanation for sociality in species that are (at least sometimes) group-living but apparently non-cooperative, such as red foxes (Macdonald 1981), Blanford's foxes *Vulpes cana* (Geffen *et al.* 1992), Arctic foxes *Alopex lagopus* (Hersteinsson & Macdonald 1982), Eurasian badgers *Meles meles* (Kruuk 1978) and brown hyaenas *Hyaena brunnea* (Mills 1982). A flexible social organization, however, suggests that Ethiopian wolf pairs could have been as successful in exploiting the rodent resource in areas with lower abundance and/or more dispersed distribution.

9.3 Conservation implications

The survival of several populations in isolation is a good omen for the long-term conservation of Ethiopian wolves, but because of their small size all extant populations are intrinsically vulnerable to extinction (Marino 2003). The wolves' habitat specificity and narrow diet means that the fate of these populations is closely linked to the persistence of suitable habitats. It is an accepted dogma that Afroalpine habitat conservation should be central to conservation strategy (Sillero-Zubiri & Macdonald 1997); this study confirmed that the northern populations, particularly those in lower lying ranges such as Delanta, are the ones at higher risk of extinction in the face of further habitat loss to subsistence agriculture. It became clear that this and other threats vary among regions and thus conservation priorities need to be adapted to local conditions. Moreover, patches of high-quality habitat are in themselves restricted within suitable areas; and those patches should be a particular focus of conservation efforts. It thus follows that conservation actions should be adapted to the problems at various organizational scales, for which this study provides several indications that should be taken into consideration.

Genetic concerns are part of the reason for the increasing interest in metapopulations in conservation, as theory predicts that metapopulation structure may have profound effects on total genetic variation (Hastings & Harrison 1994). Fragmentation can lead to increasing rates of local extinctions and decreasing rates of colonization, and ultimately cause the genetic variation both within and between subpopulations to be lost. Additional destructive feedbacks may generate inbreeding (Gilpin & Soulé 1986), but there is a general lack of evidence for this, and it has not been substantiated for Ethiopian wolves either (Gottelli *et al.* 1994; Wayne & Gottelli 1997). The lack of mitochondrial DNA variability in Ethiopian wolves contrasts with other species of wolf-like canids (Gottelli *et al.* 1994) and is amongst the lowest reported for carnivores that have relatively low variation (e.g. African wild dogs, Girman *et al.* 2001; cheetahs A*cinonyx jubatus*, Menotti-Raymond and O'Brien 1993; giant pandas *Ailuropoda melanoleuca*, Lu *et al.* 2001; pumas *Puma concolor*, O'Brien *et al.* 1990). The progressive decline in Ethiopian wolf numbers has not yet caused a substantial reduction in diversity at the species level, but local losses have resulted in variability being spread across populations. There is a need for protecting the northern populations identified as the main reservoir of genetic variability -largely exceeding the largest population in Bale. Particularly in the North, the impact of human disturbance further aggravate isolation and reduce population sizes, increasing the likelihood of local fixation of haplotypes, and the overall loss of haplotypes (this was exemplified by the comparison of historic and recent wolf samples from the Arsi population).

The metapopulation paradigm in conservation biology stresses the maintenance of an extinction-colonization balance (Caughley 1994). A successful strategy requires conserving numerous habitat patches and the potential for dispersal between them (e.g. systems of multiple reserves connected by corridors). However, in many species including the Ethiopian wolf, both natural patchiness and fragmentation are likely to create mainland-island or non-equilibrium metapopulations, rather than sets of populations in a delicate balance of extinction and colonization. Taken too literally the metapopulation concept could lead to the 'principle' that single, isolated population are always doomed, or that costly strategies involving multiple connected reserves are always necessary. In Ethiopian wolves, management to restore or maintain variation in genetically-at-risk populations (Sillero-Zubiri & Macdonald 1997) could be effective while still maintaining genetic patterns by means of translocations among groups of closely related populations. The most likely genetic partitioning corresponds to three mountain groups, namely Arsi/Bale, Wollo/Shoa, and Simien/Mt.Guna. On the other hand, surplus animals from high-density local populations in Bale may be the most practical and safe source of individuals for reintroductions or translocations. Considering too the lack of evidence of inbreeding depression and the short evolutionary lapse for population-specific adaptations, this possibility should be strongly considered.

In assessing the importance of metapopulation processes in conservation, a possible way forward is to ask in each specific case what is the relative importance of among-population processes versus within-population processes in the viability and conservation of a species. This study provided ample evidence that the fate of populations will depend on local dynamics and that, while inherent population stability will favour long-term persistence, this is jeopardized by current habitat reduction trends. It is a sad reality that habitat protection may not be feasible in most cases; politics, the economic situation and land pressure in Ethiopia place conservation of Afroalpine ecosystem low in the priority list. There are however examples of successful initiatives, such as the traditional community management of Afroalpine resources in Menz (Ashenafi 2001) and the regional protection of *Erica* forests in Denkoro (Marino 2003) which indirectly protect wolf populations in areas that would have otherwise been overtaken by agriculture (as it was the case of Gosh Meda near Menz). The key to Afroalpine conservation in Menz is the rational exploitation of the *guassa* grass (*Festuca richardii*), used to manufacture ropes, basket weaving and thatching and also a cash crop sold in local markets (Ashenafi 2001). Cultivation of *guassa* was observed at small scales near households elsewhere in northern Ethiopia. The possibility of a sustainable use and cultivation of this plant has some potential for Afroalpine conservation, and indirectly for the protection of wolves.

The relatively recent expansion of humans and their agricultural activities invariably result in the reduction of habitat available to many species that are not necessarily adapted to space constraints. In the field of conservation biology spatial ecology dominates analysis of the shape, size and connectivity among conservation areas to ensure the persistence of populations and the maintenance of diversity (Woodroffe 1998). However, it is vital that conservation actions be based upon a realistic understanding of the causes of decline. For example, no amount of captive breeding can bring about the recovery of wild populations of Ethiopian wolves if they have declined as a result of habitat destruction. Management can only halt a decline if it is aimed at the causes of that decline – and this demands knowledge of what those causes are (Caughley 1994). Habitat loss has driven local wolf populations to extinction, but other factors of decline also exist that may be easier to tackle and their control can ensure the persistence of the larger populations inhabiting more extensive mountain blocks. Although there are multiple examples highlighting the effect of people, larger predators, and landscape features on carnivore distribution, the abundance of food is often the major natural force influencing carnivore population density and viability (reviewed by Fuller & Sievert 2001). Mortality induced by rabies and human persecution is certainly an important component of density changes in the Ethiopian wolf, but the potential densities that populations reached were more generally understood to be a reflection of prey abundance. The utilization of Afroalpine pastures for livestock grazing in Ethiopia is an increasingly worrying problem; while current stock densities have not yet apparently affected wolf abundances in Bale, intensive grazing in the less productive northern highlands are bound to have affected negatively the abundance of the rodent prey. People traditionally keep livestock as a capital to overcome periods of difficulty, for example when crops fail during droughts. Because livestock is not necessarily a food source, targeted initiatives aimed at reducing family stocks may be possible, given an adequate scheme of compensation.

Reducing livestock numbers across the Afroalpine poses an insurmountable task, but a compromise would be to prioritize protection of localized areas where prey communities are more productive, or where the larger molerats (*Tachyoryctes macrocephalus*) are present, and thus highest wolf densities can be attained. The study of dietary variations along climatic gradients of resource distribution indicated where those areas might be found, but field measurement of actual prey abundance in all wolf populations is urgently needed.

The need to protect the small wolf populations at higher risk of extinction is clearly urgent. However, pragmatically it is the largest population of Bale that provides the better chances for long-term persistence. At the time of writing this conclusion, a wolf subpopulation in western Bale is succumbing to rabies and the EWCP is urgently inoculating the wolves. This study highlighted the vulnerability of localized, high-density populations to infectious diseases in Bale. Targeted vaccination efforts, particularly when densities reach high levels, may be the most effective way in controlling infectious diseases. The implementation of practical conservation actions by EWCP and scientific advances in our understanding of Ethiopian wolf ecology will continue to help the survival of the precious remaining wolves and by extension, the protection of an ecosystem crucial for highland biodiversity and the livelihoods of many people in the overpopulated highlands of Ethiopia.

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