FLOWER FOOD TISSUES AS REWARD FOR POLLINATING BIRDS

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Summary: Nectar is the reward regularly offered by flowers to their pollinating birds. Studies on pollination by birds have focused on nectar as a reward while alternative reward systems have been poorly studied. Previous reviews have shown the presence of food tissues that serve as nutritive rewards to different classes of pollinators. However, in a recent revision of plant-bird interactions, the existence of a solid reward for birds has been disregarded. In South America at least three cases of this very particular bird-flower interaction have been recently studied. In this paper we describe the syndrome features (flower morphology, reward properties, position of the pollination unit, flower color display and common visitors), that deviate from the typical ornithophilous syndrome, and its possible origin is discussed.

Key words: Flower, food reward, pollination, birds, syndrome, review.

Resumen: Tejidos alimenticios florales como recompensa para las aves polinizadoras. El néctar es la recompensa típica que las flores ofrecen a las aves polinizadoras. Los estudios sobre ornitofilia se han concentrado en el néctar como recompensa, mientras que otras retribuciones alternativas fueron escasamente analizadas. Revisiones previas han mostrado que la producción de tejidos alimenticios puede servir como recompensa para diferentes polinizadores, y al menos tres casos de esta particular interacción se estudiaron últimamente en América del Sur. Sin embargo, una revisión reciente sobre interacciones planta-ave descarta la presencia de recompensas sólidas. En este trabajo describimos las características del síndrome que lo diferencian del típico síndrome ornitófilo (morfología floral, propiedades de la recompensa, posición de la unidad de polinización, color de la exhibición floral y visitantes más comunes), y también discutimos su posible origen.

Palabras clave: Flor, alimento como recompensa, polinización, aves, síndrome, revisión

INTRODUCTION

Nectar is the reward (primary attractant) regularly offered by flowers to their pollinating birds. In bird-flowers its presence is announced exclusively by color (secondary attractant), which is often vivid and not infrequently scarlet red. Such announcement may enable the birds to locate and individualize particular types of flower among many others.

Flower parts have mechanical functions normally involved either in adaptation to the structure and behavior of the birds or in the deterring of pollinators other than birds. Such is the case of pendant inflorescences (coupled with capillary devices to avoid the dripping of nectar), mechanical deterrents (strong corollas), morphologies adjusted to ensure pollen placement on different parts of the bird's body, etc (Faegri & van der Pijl, 1979). For example,

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the most commonly found tubular, bilabiate or brush-type architectures are related respectively to modes of pollen placement on the back, the front of the head and the ventral body parts (Feinsinger, 1991).

Nectar-feeding birds

Around the world nearly twelve families of birds are known as flower visitors (Armstrong, 1979; Stiles, 1981; Westerkamp, 1990). In the Neotropics, the most notorious bird pollinators are Trochilidae (hummingbirds). This family of 300 species hummingbirds, is considered the largest and most highly specialized group of flower-feeding birds (Stiles, 1981). Passerine pollination has been considered a very common interaction in the Old World (Faegri & van der Pijl, 1979), but in the Neotropics the importance of birds other than hummingbirds as pollinators has been stressed only recently. As an example at least 17 species of the Neotropical *Erythrina* (Fabaceae) show adaptations to pollination by perching birds (Bruneau, 1997; Steiner, 1979). In contrast to the specialization of the hummingbird - flower interactions, those involving New World nectar-feeding passerines are relatively unspecialized

and similar to the interaction between the Old World perching birds and their flowers (Stiles, 1981). The "dogma" that New World bird-flowers are exploited by hovering birds while Old World flowers are generally visited by perching birds (van der Pijl, 1961) has been recently dismissed (Westerkamp, 1990). The presence of the already mentioned passerine perching birds that visit flowers in the New World and the reported cases of hovering visitors in the Old World suggest that neither geographical distribution nor systematic affiliation are direct indication of the kind of flower-bird interactions (Westerkamp. *op. cit.*).

Studies of pollination by birds have focused on nectar as a reward while alternative reward systems have hardly been noticed. In this paper we describe the syndrome features (flower morphology, reward properties, position of the pollination unit, flower color display and common visitors), that deviate from the typical ornithophilous syndrome.

Plant food tissues as reward

Simpson & Neff (1981) reviewed the presence of food tissues that serve as nutritive rewards to different classes of pollinators. Beetles, bats or birds consume different floral or extra-floral parts while pollinating species of *Nymphaea* (Nymphaeaceae), *Bactris* (Arecaceae) or *Freycinetia* (Pandanaceae). These authors confirmed that food tissues are also an alternative reward that flowers offer to birds. However, when reviewing plant-bird interactions Proctor *et al.* (1996), disregarded the importance of solid rewards to this kind of pollinators.

Individual cases of bird pollination with food tissues as reward

In the Old World some observations have been reported: *Osmoxylon* (Araliaceae) from Malaysia attracts birds (pigeons) by means of fruit imitations, which consist on sterile flowers placed between normal ones (Faegri & van der Pijl, 1979).

Freycinetia funicularis (Pandanaceae) from Asia provides fleshy, sugary bracts surrounding the flowers. These are eaten particularly by bulbuls (Pycnonotidae) which act as pollinators, (Proctor & Yeo, 1973). Cox (1983) showed that the bird-pollinated *F. arborea* from Hawaii was originally visited by the endemic, and now almost extinct birds *Psittirostra psittacea*, *Loxiodes kona* and *Corvus tropicus*, and in recent years by *Zosterops japonica*,

the introduced white-eye, and also by rats. *F. reineckei* is visited by flying foxes (Bats, Pteropidae), the starling *Aplonis atrifuscus* and the pigeon *Columba vitiensis* (Cox, 1984).

In South America at least three cases of a very particular bird-flower interaction has been recently studied.

In Scrophulariaceae, the genus *Calceolaria*, which is nectarless throughout, is mainly pollinated by specialized oil-collecting bees (Vogel, 1974; Molau, 1988; Sérsic, 1994). There are about 50 species of the genus, which lack oil-producing glands (elaiophores). As alternative to oil-flowers other pollination strategies are present. In many cases *Calceolaria* species may rely on autogamy or pollination by pollen collecting-bees. But at least in one species, *C. uniflora*, a particular kind of bird pollination with food tissues as reward, has evolved (Sérsic & Cocucci, 1996) (Fig. 1). This species grows within the low vegetation of the patagonian steppe and forms perennial cushions of no more than 10 cm height. The flowers are markedly zygomorphic and two-lipped, the saccate lower lip showing a notorious lap folded to the outside of the flower. This thick and sharply bounded lap is white, and contrasts optically against the yellow and red or brownish red spotted lower lip. This juicy appendage is eaten by the fruit- and seed-eating bird, *Thinocorus rumicivorus*, member of the family Thinocoridae, (Sérsic & Cocucci, 1996). This family does not include flower-birds of any kind, since they don't show specialized morphological adaptations and they forage for food on the ground by walking rapidly across the low vegetation. *Calceolaria fothergillii*, endemic of the Malvinas Islands, is the only species in the genus that shares the striking floral features of *C. uniflora*, suggesting that it could also be similarly bird pollinated (Vogel, 1974; Sérsic & Cocucci, 1996).

In Myrtaceae two cases have been described in two related genera of small trees (Fig. 2). *Acca* (*Feijoa*) *sellowiana* produces flowers with 4 fleshy sweet petals, and numerous stamens. They are visited by pollen foraging insects and by birds, which feed on petals. This case is known since long (Müller, 1886) and has repeatedly appeared in the literature (Popenoe, 1920; Sick, 1986). (Though, van der Pijl, 1961) dismissed the presence of edible petals in this species, Stewart (1986) and Stewart & Craig (1989) showed that birds are more important than insects as pollinators of *Acca* under culture in New Zealand, USA and Japan. A similar syndrome has been hypothesized by Landrum (1986) and Nic Lughadha & Proença (1996) and recently described for *Myrrhinium atropurpureum* (Roitman *et al.*, 1997).
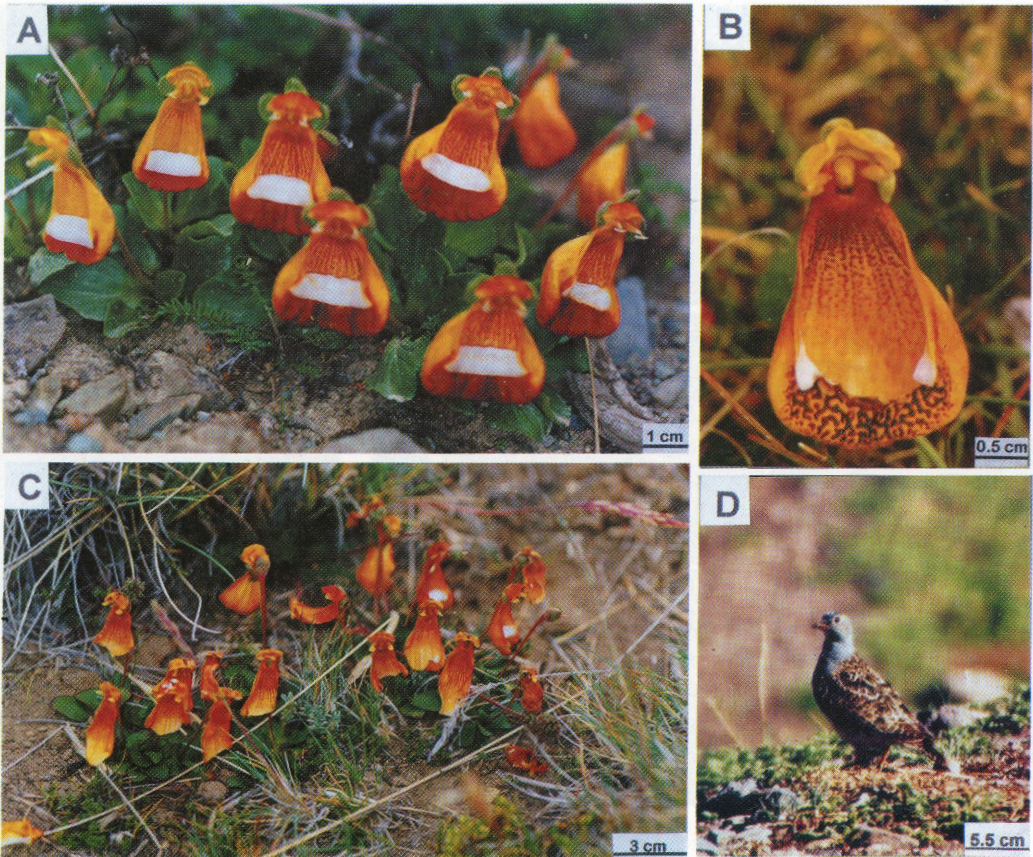
Fig.1: A-C *Calceolaria uniflora.* **A**: cushion of plants with intact flowers. **B**: one flower with the food tissue partially pecked. **C**: cushion of plants where almost all flowers show the appendage completely removed. **D**:*Thinocorus rumicivorus* (female).

The flowers of *Myrrhinium* bear also fleshy petals but the reduction in the number of stamens and consequently in the amount of pollen offered seems a further step towards specialization, because pollen is more efficiently transferred. Fourteen species of fruit- or seed eating birds including Mimidae, Tyrannidae, Turdidae, Thraupidae, Emberizidae, Parulidae, and Icteridae have been observed removing the sweet petals (Roitman *et al.*, 1997).

Syndrome

Some of the features already mentioned for ornithophilous pollination differ or are completely absent in this special category of bird pollination with food tissues as reward. These traits could help to recognize a syndrome by identifying convergences between unrelated taxa. Following are the more salient convergent traits found:

Reward: There's no nectar. Instead, fleshy and sweet parts of a flower or an inflorescence function as reward. Sugar concentration is 14 % in the petals of *Myrrhinium* (Roitman *et al.*, 1997), 2.14 % in the appendage of *Calceolaria* (Sérsic & Cocucci, 1996) and 0.23 % and 1.35 %, respectively in the bracts of the carpellate and staminate inflorescences of *Freycinetia reineckei* (Cox, 1983). These concentration values are coincident with those of generally low food-value fruits or nectar offered by bird-pollinated plants (Moermond & Denslow, 1985; Herrera, 1987; Cox, 1983; Dafni, 1994).

Position of the pollination unit: In all cases known flowers are not pendulous for this ornithophilous category. They are exposed in branches and open in an upright position allowing an access to pollinators from different angles. The two-lipped flowers of *Calceolaria uniflora* make an exception, since flowers are exposed at ground level allowing the access only from one direction.

Visitors: They usually belong to fruit or seed eating groups of birds. Moreover some species belong to families apparently never reported as flower feed-
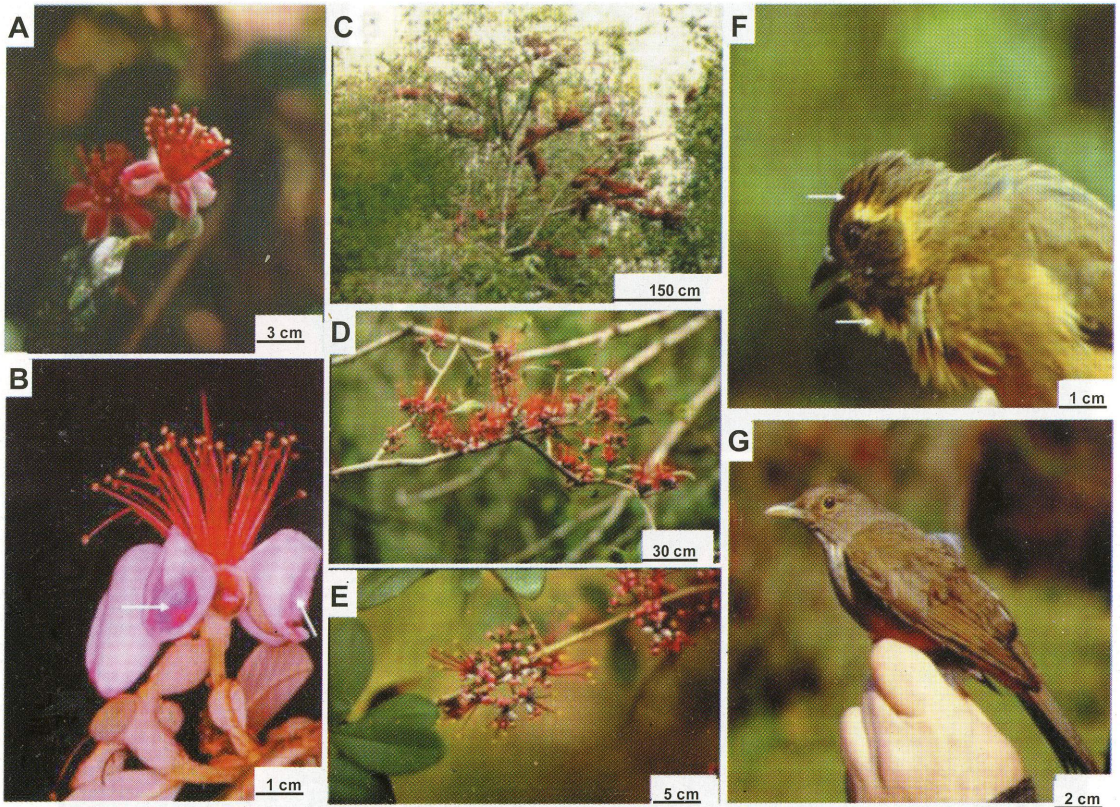
Fig. 2: **A-B** *Acca sellowiana*. **A**: Intact flowers. **B**: flower showing two petals partially removed (arrows). **C-E**: *Myrrhinium atropurpureum*. **C**: aspect of the tree. **D**: flowering branch. **E**: flowers. **F**: *Saltator aurantiirostris*, arrows show the places where pollen were placed. **G**: *Turdus rufiventris* a common visitor to both *Acca* and *Myrrhinium*.

ing birds, like Thinocoridae, Turdidae and Mimidae.

Color: The reward is self-announcing, unlike nectar, the presence of which needs to be revealed by coloration of other flower parts (nectar guides). The food tissue normally resembles a fruit with a vivid and contrasting coloration within the flower. The presence of a contrasting bicolored display, like that occurring both in Myrtaceae and *Calceolaria*, enhances avian visits for fruit removal in *Prunus serotina* and *Phytolacca americana* (Willson & Melampy, 1983).

In *Calceolaria uniflora* the food tissue maintains its white color during the whole anthesis, simulating a juicy fruit. At the site where these plants grow, a variety of fleshy ornithocorous diaspores are also recognizable at ground level, such as those from *Berberis empetrifolia*, *Empetrum rubrum*, *Ephedra frustillata* and *Pernettya mucronata*.

In *Myrrhinium* and *Acca* color changes of the petals are very peculiar. Petals are first dark red (*Myrrhinium*) or pale pink with a dark red center (*Acca*) and turn to gray and completely white respectively (Roitman *et al.*, 1997). One trait that usu-

ally involves animal learning is floral color change (Weiss, 1991). In most cases (ca. 220 genera of 74 families of flowering plants) insects learn to distinguish and visit pre-change flowers (where the reward is available), instead of post-change flowers (rewardless) that only increase the plant attractiveness to pollinators at a distance (Weiss, 1991). In these Myrtaceae the reward is present in the post-change flowers, while pre-change flowers may increase the attractiveness. These features resemble those present in ornithochorous interactions where color signals may be used to indicate which fruits are ripe (post-change) and ready for dispersal (Willson & Melampy, 1983). Since part of the perianth is removed, the attractiveness of the flower diminishes when exploited, thus reducing the probability of successive visits.

Floral construction (architecture): Ornithophilous flowers with food tissues as rewards show the bilabiate and the brush type architectures. Instead, tubular flowers, very widespread in the nectar ornithophilous ones, are not represented.

Origin

Cox (1991) suggested that vertebrate pollination and dioecy are ancestral conditions in Pandanaceae, a primitive group of Liliopsida that may have lacked nectaries "*ab initio*", while anemophily and entomophily are derived in the family.

Although pollination efficiency and effectiveness of bees and birds may vary greatly[4], many cases of ornithophily have demonstrated that they evolved from bee-pollinated groups, see Gottsberger (1993). *Myrrhinium, Acca* and *Calceolaria* seem to be examples of this kind of origin.

The geographic distribution of the oil secreting *Calceolaria* species and their oil bees overlap. About 22 % of the total *Calceolaria* species have developed no elaiophores, the proportion of elaiophoreless species increasing at higher latitudes to the North and South (Sérsic, 1994). There are no collections of oil bees over 43° S, although the range of *Calceolaria* is broader. The harsh patagonian climate at these latitudes, with low temperatures and extremely strong winds, may have limited the distribution of the oil collecting bees, which are normally adapted to more moderate climates.

The absence of the required bees and the natural tendency of some birds to practice flower predation[5] probably promoted the origin of this interaction between birds and *Calceolaria* (Sérsic & Cocucci, 1996). Although members of only one species of birds have been observed visiting the flowers of *Calceolaria*, the possibility that other birds with similar habits also pollinate them is not discarded. Seed-eating birds like the Emberizidae members *Melanodera melanodera* and *M. xanthogramma* and *Turdus falklandii* (Turdidae) are also frequently present in the area and appear as potential pollinators.

The biogeography and the main pollinators of the two ornithophilous Myrtaceae species may give a possible explanation of their evolution from bee pollinated groups. The family Colletidae (Hymenoptera) is considered the most primitive among bees, and Euryglossinae the most primitive subfamily among them. Members of this subfamily are restricted to Australian Myrtaceae on which they principally collect pollen, (Michener, 1965). Australia and South America were never in direct contact but were joined by Antarctica, though the effectiveness as a faunal bridge was limited in early Tertiary to organisms able to tolerate cool temperate climates (Michener, 1979). There are no Euryglossinae out of Australia and, coincidentally, the Myrtaceae are poorly diversified elsewhere, except in South America. In the tropical and subtropical regions of Central and South America, Myrtaceae species are mainly pollinated by Apidae, Anthophoridae and Halictidae (Proença & Gibbs, 1994; Nic Lughadha & Proença, 1996). According to Nic Lughadha & Proença (1996), the presence of nectar in the flowers of the Myrtaceae is basal, while the numerous pollen-flower genera of the Myrtoideae lost their nectary secondarily.

Concluding remarks

The presence of food tissues as reward for birds is rare in the Angiosperms and appeared independently in only few species of three families of the Magnoliopsida and one of the Liliopsida.

This particular pollination strategy evidently has not evolved from true ornithophilous flowers with nectar as reward but probably derived from insect pollinated ancestors. It is noteworthy that most cases mentioned of flowers with food tissues as reward for birds are philogenetically related to nectarless taxa. *Freycinetia* is included in the family Pandanaceae with the anemophilous genus *Pandanus* and the pollen-rewarding beetle pollinated *Sararanga* (Cox, 1990). The closest relatives of the *Myrrhinium-Acca* complex have pollen flowers exploited by bees (Nic Lughadha & Proença, 1996), and finally, *Calceolaria uniflora* is included in a mainly oil-rewarding bee-pollinated genus (Sérsic, 1994). Only few morphological changes were necessary in these flowers or inflorescences to produce profound changes in their pollination strategies. Although the pollination units here involved are well adapted for visitation by birds, there are no evident adaptations of the birds to the plants and they feed opportunistically on food tissues as well as on a variety of fruits. Simpson & Neff (1981) concluded that selection favored the elaboration of a different reward either to capture a segment of the

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[4] For example, bumble bees deposited 10 times more pollen per visit than hummingbirds in *Delphinium nelsonii* flowers, but within a population hummingbird visitation rates are 10 times higher than those of bumble bees Waser & Price (1990).

[5] In fact, *Musisaxicola alpina* (Tyrannidae) was observed eating corollas of the oil-bearing and normally bee-pollinated *Calceolaria brunellifolia* in Mendoza (Argentina); also many passerine birds were observed taking nectar as well as eating the corollas of *Anarthrophyllum desideratum* (Papilionaceae) which occurs together with *C. uniflora* (Sérsic, unpubl.).

pollinator community not used by other plants or to achieve greater pollinator constancy. These changes usually promote a one-to-one relationship and / or a more expensive reward. However, in both *Acca* and *Myrrhinium,* their relationship to birds is still diffuse, since many bird species visit them, and the reward quality has not been increased, in comparison to that of nectar or fruits. Nevertheless, the production of "fruit-like" petals enables these plants to attract a new kind of pollinators (birds) different from those prevalent in most Myrtaceae and *Calceolaria* (bees). The *Acca* and *Myrrhinium* plant-bird interaction seems to be an unspecialized one and it would be the outcome of diffuse coevolution (Janzen, 1980, Jordano, 1987). These characteristics contrast with the highly coevolved oligotropic ornithophilous systems frequently found in the Neotropics, but are similar to the paleotropical allotropic *Freycinetia reineckie*. The latter is pollinated by bats and birds in Samoa in which the reward are fleshy bracts, (Cox, 1990).

The origin and explosive diversification of flowering plants during Cretaceous is often attributed to a simultaneous evolutionary radiation of insects, which served as critical pollen vectors. Vertebrates are thought to have played an insubstantial role in early evolution of angiosperms because the main groups, which are important pollinators of extant plants taxa (birds and bats), originated no earlier than the Eocene, (Kress & Stone, 1993). Insect pollination was probably the precursor of hummingbird pollination, not only because insects were first on scene but also because intermediate processes are visible nowadays (Stiles, 1981).

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