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Effect of nectar-robbing birds on fruit set of *Fuchsia magellanica* in Tierra Del Fuego: a disrupted mutualism

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Summary

1. This paper investigates spatial habitat variation in flower visitation by avian pollinators (mainly Hummingbirds) and nectar robbers to *Fuchsia magellanica* at the southern limit of its range, Tierra del Fuego, and their effects on plant reproductive success.

2. The plant-pollination mutualism appears to be disrupted as Hummingbirds (*Sephanoides galeritus*) are rare at this high latitude and the frequencies of a nectar-robbing bird (*Phrygilus patagonicus*) are high, especially in open areas where *F. magellanica* is most abundant.

3. Nectar robbery by *P. patagonicus* reduced fruit set about 20%, mainly because this fringillid can damage the ovary when piercing a flower. This bird was more abundant in open areas than inside the forest and, as expected, flower piercing was also more frequent in the former habitat.

4. Spatial variation was also found in the frequency of flower visitation by Hummingbirds; these birds foraged chiefly in the forest presumably because of the greater probability of finding intact (non-robbed) flowers there. This suggests that cross-pollinations in this self-compatible plant are more likely to occur in the forest. Nectar robbers therefore may influence not only the quantity of seeds produced but also, indirectly, their quality.

5. *Fuchsia magellanica* is polymorphic in flower colour. Robbery was significantly lower in the pale than in the normal (red) morph, although fruit set was similar between morphs.

Key-words: Hummingbird, marginality, *Phrygilus patagonicus*, plant reproductive success, pollination, *Sephanoides galeritus*

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Introduction

All mutualistic interactions run the risk of being 'parasitized' by species that obtain benefits (gathering the rewards offered by one of the interactors) from the relation without paying anything for it. This appears to be quite common in the particular case of plant–pollinator sytems, where some species rob or thieve (see distinction in Inouye 1980) either pollen or nectar from the flowers without performing any pollination. This cheating behaviour, usually performed by insects or birds, may not always have a detrimental effect on plant reproductive success (Arizmendi, Domínguez & Dirzo 1996; Morris 1996), but has been shown to decrease pollinator visitation rates and/or seed set in many other cases (e.g. McDade & Kinsman 1980; Wyatt 1980; Fritz & Morse 1981; Gill, Mack & Ray 1982; Roubik 1982; Galen 1983; Roubik, Holbrook & Parra 1985; Zimmerman & Cook 1985; Askins, Ercolino & Waller 1987; Norment 1988). Such 'parasites' of the mutualism may have a greater negative effect on the plant when the population of effective pollinators is low owing to, for example, habitat destruction or for being rare at the extreme of their range distribution.

Cases in which the distributional range of one member of a mutualistic interactor extends beyond that of its partner(s) have been reported for both pollination and seed-dispersal systems (e.g. Galen 1989; Eckhart 1992; Jordano 1993; Thompson 1994). This 'uncoupling' implies geographic variation in the interaction and may lead to differences among conspecific populations in patterns and intensities of natural selection, and thus to different trajectories of coevolution (Thompson 1994). An example is the system constituted by *Fuchsia magellanica* Lam. (Onagraceae) and

its main pollinator, the Hummingbird *Sephanoides galeritus* Lessou & Garnot (Trochilidae). At the southern extreme of its distribution, Tierra del Fuego, southern Chile, this Hummingbird, the only one present in the area, is very rare and localized and the plant is commonly visited by another bird, *Phrygilus patagonicus* Lowe (Fringillidae), which pierces the corollas and extracts nectar without pollinating the flowers.

In the present study, this plant–pollinator interaction in Tierra del Fuego was examined. Our main goal was to determine how detrimental was the impact of the fringillid on plant reproductive success. We experimentally evaluated the effect of nectar robbery on fruit set and compared the levels of such robbery among three habitats where the plant is found: (1) in the open, (2) inside the forest and (3) outside the forest edge. Flower-visiting birds in all three habitats were recorded. Insects behaving as secondary nectar thieves in both open and forested habitats were also censused. *Fuchsia magellanica* is polymorphic for flower colour and the levels of robbery between the normal and the rare morph were compared.

STUDY PLANT

Fuchsia magellanica usually grows in forest clearings and margins, especially in mixed evergreen deciduous *Nothofagus* sp. forests and coastal *Drimys–Nothophagus* spp. forest (Moore 1983). The flowering period lasts from November to March or April, at least in more northern parts of its range (Riveros 1991; Smith-Ramírez 1993); in Tierra del Fuego it may begin flowering later (Moore 1983). Flower size varies both within plants and, especially, among plants. *Fuchsia magellanica* is self-compatible but its potential for autogamy has been reported to be low (14%) in southern continental Chile (Riveros 1991). The flowers are open an average of 6 days (*n* = 14 flowers) and they are protogynous; the stigma is receptive (sticky) as soon as the flower opens and remains so even after the anthers have dehisced. The eight stamens are of two lengths; four extend slightly beyond the corolla and four are much longer, sometimes as long as the style. Anthers and stigma occasionally contact each other and are usually only several mm apart; delayed selfing may actually be a mechanism to ensure fertilization in case flowers are not visited by pollinators. Occasional flowers are solely male, lacking ovary, style and stigma altogether. This species has a classically ornithophilous, nectar-rich flower, with flared red sepals and straight purple petals skirting a long corolla tube. In Chile, the flowers are pollinated mainly by the Hummingbird *S. galeritus* (Smith-Ramírez 1993), although a small Flycatcher, *Elaenia albiceps* Hellmayr, is also commonly seen visiting the flowers 'legitimately' (effectively) in the island of Chiloé, Chile, at 42 ° S (M. F. Willson & C. Sabag, personal observations). Some *F. magellanica* individuals produce either white/pale

pink flowers or lavender/dark pink flowers. In Tierra del Fuego, these pale-flowered morphs were rare: of thousands of *F. magellanica* shrubs in our study sites, only 10 had pale flowers (four shrubs with white/pale flowers and six with lavender/dark pink flowers). Most pale-flowered individuals were found relatively close together (within 50 m) of each other but others grew in widely scattered portions of the main study population. The petals of all morphs became lighter in hue as the flower aged. The fruits of *F. magellanica* are elliptical or ovoid, 20–25 mm long and 6–8 mm wide (*n* = 10), usually dark red (not black, as given in Moore 1983) when mature and filled with hundreds (306 ± 73, *n* = 25) of tiny seeds. The fruits of the pale-flowered morphs are green when mature and contain similar numbers of seeds (268 ± 88, *n* = 25). Various frugivorous, seed-dispersing birds and mammals consume the fruits (Sabag 1993; A. Traveset, M. F. Willson & C. Sabag, personal observations), as well as some vertebrate seed predators.

Materials and methods

The *F. magellanica* populations under study were located near Puerto Arturo, at a latitude of about 55 ° S, in south-western Tierra del Fuego. The principal study site (where the effect of nectar robbery was examined) was a large grassy clearing with scattered *Nothofagus betuloides* (Mirb.) Verst and abundant *F. magellanica* shrubs. Additional observations in open habitats were made in nearby patches of disturbed forest, composed chiefly of *N. betuloides*, *Drimys winteri* Forst. and *Maytenus magellanica* (Lam.) Hook f. All fieldwork was carried out between 7 and 22 February 1995.

Direct observations of avian visitors to *F. magellanica* flowers were made, using binoculars and from a minimum distance of 10 m, in three habitats: (1) open, early successional habitat, with a high density of *F. magellanica* shrubs surrounded by grass and scattered *N. betuloides,* (2) inside disturbed forest, with a relatively low density of *F. magellanica* shrubs growing under a broken canopy of *N. betuloides*, *M. magellanica*, and *D. winteri* and (3) outside forest edge, with a relatively high density of *F. magellanica* shrubs mixed with *Berberis buxifolia* Lam., *Berberis ilicifolia* L.f., *Ribes magellanicus* Poir. and scattered young *N. betuloides*. All observations (> 43 h) were made between 5 and 19 February.

The effect of robbery on fruit set was evaluated by marking flowers on 10 plants of the normal morph. This was carried out in the open habitat, where the plant and the nectar robber are most abundant. On each plant, we labelled 20 flowers that had been robbed and 20 flowers of about the same developmental stage on which the ovary was surrounded with tape to prevent nectar robbery. The tape, which we are quite confident did not alter floral display, did not interfere with 'legitimate' visits to extract nectar from

the flowers and it was removed soon after the flowers were no longer receptive and the stamens had dehisced to avoid any possible effect on fruit development. Twelve days later, the proportion of flowers that set fruit was recorded for each plant. On three pale-flowered individuals 10 intact flowers were similarly marked to determine fruit set; the final sample size was 25 flowers as some labels were lost.

Because some flower buds bore a hole made by birds, 50 buds from each of 15 individuals in an open site were examined to determine what proportion of buds is attacked. Five buds from five individuals were also marked and monitored to learn if attacked buds develop into normal flowers.

The frequency of flower robbery in the three habitats was determined by assessing the proportion of mature flowers (with dehisced anthers) that had a hole at the base of the corolla in 176 individuals of the normal morph: 65 from four open sites, 81 from four forested sites and 30 from two sites outside forest edges. A total of 50 haphazardly chosen flowers were examined from each individual, except in those cases where the number of flowers was low (in those cases, the minimum number observed was nine). The level of flower robbery between normal ($n = 15$ plants) and pale-flowered morphs ($n = 6$ plants; this category pooled both pale morphs, because they were so rare) was also compared in an open site.

The probability that a flower had abundant available nectar, filling the tubular base of the corolla, was determined by observing 15 flowers randomly chosen from each of 10 shrubs inside the forest and 13 in open and edge sites (seven red, six pale); we recorded whether the flower had been robbed or not in order to compare nectar availability in robbed *vs* non-robbed flowers and between habitats.

The number of insects behaving as secondary nectar thieves (stealing nectar from the holes made by birds) was recorded, from 20 to 22 February, by examining a total of 50 flowers from each of 10–30 individuals in open and forested areas and counting the total number of insects observed sucking nectar. Most censuses were carried out between 09.00 h and 14.00 h. Two of the censuses were carried out simultaneously in an open site and inside the forest between 18.00 h and 20.00 h.

For data analyses, non-parametric tests were employed when data could not be normalized even after using the adequate transformation. Throughout the paper, means are accompanied with their standard deviations unless otherwise indicated.

Results

FLOWER VISITORS

The most common flower visitor was the fringillid *P. patagonicus*; it represented 80% of all visits to *F. magellanica* shrubs and 75% of all flowers visited (Table 1). Overall, the Hummingbird (*S. galeritus*) was the next most common visitor (11% of visits, 21% of flowers) but this species was observed only in the forest. The Flycatcher, *E. albiceps*, made 9% of the visits (4% of flowers). However, almost none of the visits by *P. pagatonicus* was likely to accomplish pollination (no part of their body contacted either the stamens or the stigma), whereas all of the visits by the Hummingbird and 16% of visits by the Flycatcher were potentially effective (Table 1).

Phrygilus patagonicus hopped from branch to branch, piercing flowers or probing previously made holes. Only occasionally did their backs or tails touch the anthers and stigmas, possibly depositing or picking up pollen. This species usually pierced a hole at the base of the corolla and could puncture eight to 10 flowers min^{-1}. Sometimes, they plucked whole flowers and squeezed them between their mandibles to extract the nectar or held them against a branch with a foot, while pecking at the corolla. Occasionally *P. patagonicus* flew away with a flower in the bill. Birds moved around the area in flocks of mixed adults and juveniles. Flock size sometimes numbered in the hundreds and therefore large numbers of flowers were robbed in a short time. Although *E. albiceps* commonly visited holes made by *P. patagonicus* they were never observed making holes in the corolla.

Large Bumble-bees (*Bombus* sp.) occasionally visited *F. magellanica* flowers, collecting pollen

Table 1. Frequency of flower visitation and nectar robbery by *Phrygilus patagonicus*, *Elaenia albiceps* and *Sephanoides galeritus* in three habitats in western Tierra del Fuego. 'Effective' visits refers to flower entries in which the flower was potentially pollinated. In parentheses are the proportion of individuals and of flowers visited, by habitat, and the proportion of all floral visits that were effective, by species

Habitat	No. hours observation	Species	No. individuals	No. flowers visited	No. effective visits
Open	13 h 5 min	*P. patagonicus*	109 (92%)	332 (97%)	0 (0%)
		E. albiceps	9 (8%)	12 (3%)	3 (25%)
Forest	23 h 10 min	*P. patagonicus*	45 (59%)	60 (32%)	1 (2%)
		E. albiceps	9 (12%)	12 (7%)	1 (8%)
		S. galeritus	22 (29%)	115 (61%)	115 (100%)
Forest edge	6 h 53 min	*P. patagonicus*	5 (100%)	19 (100%)	1 (5%)

and/or nectar. They probably are effective pollinators, as their abdomen touches the anthers and stigma when the bee enters the flower. Another likely pollinator observed on the flowers, but even more rarely, was a large (unidentified) bee. Other insects, mainly flies and small bees, do not act as pollinators but as nectar thieves, and were observed extracting nectar from the hole made by birds in the corolla tube.

EFFECT OF NECTAR-ROBBERY

Robbed flowers set fewer fruits than unrobbed flowers (80% ± 4·4% (SE) *vs* 100% ± 0%; *t*-test $F_{1,18} = 41·6, P = 0·0001$ on angular-transformed data). In most cases, this was because the ovary was damaged when the corolla was pierced; excised styles and stamens were also sometimes observed in robbed flowers. Fruit set on marked unrobbed flowers of the pale morph appeared to be also high (92%).

The frequency of flower robbery increased from forest to open habitat (Kruskal–Wallis test: $\chi_2^2 = 29·4$; $P = 0·0001$; Fig. 1). This result was not surprising, as *P. patagonicus* was more common in open sites and forest edges than in disturbed-forest sites (M. F.
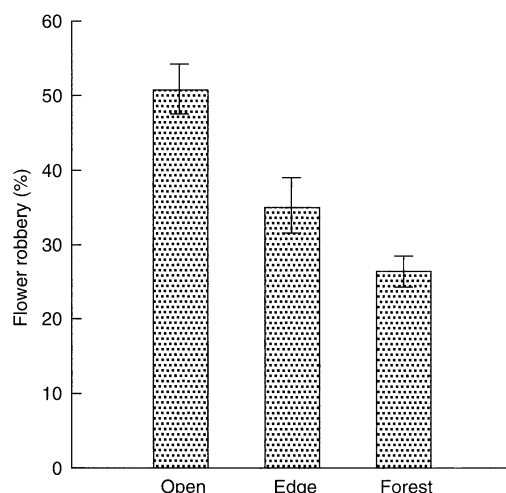

Fig. 1. Proportion of flowers of *Fuchsia magellanica* robbed by *Phrygilus patagonicus* in three different habitats. A total of 50 flowers were observed from 65 shrubs in four open sites, 81 shrubs from four forested sites and 30 shrubs from two sites outside forest edges. Standard error bars are shown.

Table 2. Relative abundance (based on point counts) of the avian flower visitors of *Fuchsia magellanica* in Chiloé and in Tierra del Fuego. *Second value pertains to season when *F. magellanica* fruits ripen. Data from Chiloé are from M. F. Willson & C. Sabag (unpublished data)

Species	Chiloé Island (spring) (birds point^{-1} day^{-1})	Tierra del Fuego (summer) (birds point^{-1} day^{-1})
Sephanoides galeritus	1·4	0
Elaenia albiceps	2·6	1·4 (0·4)*
Phrygilus patagonicus	0·3	2·1

Willson, A. Traveset & C. Sabag, unpublished data). Flocks of this species, which can visit hundreds of flowers in a short time, were also observed only in open sites. There was, however, variation within each study area in frequency of robbery and, when testing the effect of habitat in a mixed-model nested ANOVA (using plant within each habitat as the error term), the difference between forest and open sites was only marginally significant ($F_{1,6} = 4·62$; $P = 0·07$).

Advanced flower buds contain some nectar and were also attacked, although at a lower frequency (6% ± 5% of 750 buds observed in the open habitat) than open flowers. All damaged buds monitored were capable of developing into mature flowers.

The probability of finding abundant nectar was consistently lower in robbed flowers than in non-robbed flowers of the normal morph, and lower in forest (0% *vs* 27%; $\chi_2^2 = 26·4$; $P = 0·001$) than in open habitat (15% *vs* 77%; $\chi_2^2 = 24·9$; $P = 0·001$). Similarly, abundant nectar was rare in robbed flowers of the pale morph compared with non-robbed ones (8% *vs* 65%; $\chi_2^2 = 27·4$; $P = 0·001$).

The proportion of flowers robbed was much lower on the pale-flowered morph [14% ± 6% (SE), range = 0–38%] than on the normal morph [74% ± 4% (SE), range = 42–98%] (Wilcoxon's test, $\chi^2 = 12·3$; $P = 0·0004$).

Insects found foraging on nectar from the corolla holes made by birds were significantly more abundant in forest [21·1 ± 2·1 (SE) insects/1000 flowers, $n = 9$ censuses] than in open habitats [9·4 ± 1·7 (SE) insects/1000 flowers, $n = 14$] (Wilcoxon's test, $\chi^2 = 10·01$; $P = 0·002$).

Discussion

Sephanoides galeritus pollinated only a small fraction of the flower crop in a very limited subset of habitats (disturbed forest) occupied by *F. magellanica* in Tierra del Fuego. These results contrast with observations made in more northern parts of Chile, where this Hummingbird is abundant and commonly visits *F. magellanica* flowers (Smith-Ramírez 1993). *Elaenia albiceps* is another effective pollinator of *F. magellanica* in Tierra del Fuego and is known to pollinate other species, such as *Embothrium coccineum* Forst. in the island of Chiloé (C. Smith-Ramírez, unpublished data; M. F. Willson & C. Sabag, personal observations) but it visited a very small proportion of flowers as well. In contrast, *P. patagonicus*, the 'parasite' of the mutualism, was the most common flower visitor in the Tierra del Fuego study sites, being much more abundant there than in Chiloé, the contrary of what happens with the other two species (Table 2; Willson *et al.* 1994).

Phrygilus patagonicus negatively affected the reproductive success of the plant, mainly by reducing fruit set substantially (20%) as they damage ovaries when piercing flowers. Secondary robbers or thieves such as *E. albiceps*, flies and bees, took advantage of

the holes made by the fringillid, but apparently they were of little detriment to the plant. Nectar robbery by birds in other species of *Fuchsia* has also been documented from New Zealand (Delph & Lively 1985), although there is no report on their effect on plant success, and from Mexico, where a species of *Diglossa* robs nectar from *Fuchsia microphylla* HBK flowers but has a negligible effect on fruit set, mainly because of the rarity of the bird and because it does not damage the flowers (Arizmendi, Domínguez & Dirzo 1996). In the present system, the nectar robber might also depress plant reproductive success by interfering with Hummingbird pollination and promoting more autogamy than cross-pollination. One reason why *S. galeritus* forages chiefly in the forest might be that it has a higher probability of finding intact (non-robbed) flowers here. Robbed flowers with very low levels of nectar were much more frequent in open habitats than inside the forest. The stronger Hummingbird foraging activity in the forest, and thus the higher probability of cross-pollination in this habitat, is indicated by the greater frequency of intact flowers depleted of nectar compared with open areas; in these areas most seeds are probably produced by autogamy. Furthermore, if Hummingbirds 'prefer' and select intact flowers (we do not have evidence for this), the chances that robbed flowers are cross-pollinated are slight.

Preliminary data obtained from forest edges in north-east Chiloé show that the frequency of flower robbery in *F. magellanica* is quite low compared with Tierra del Fuego, not exceeding 15% of the flowers in sites where avian pollinators are abundant but up to about 45% at a site where Hummingbirds were scarce (M. F. Willson, unpublished data). *Fuchsia magellanica* begins to flower in November in Chiloé, when adult *P. patagonicus* are still in their breeding territories, but flowering in Tierra del Fuego occurs later in the breeding season of this species. Therefore, both the larger population of these birds in Tierra del Fuego and the fact that many adults have left their breeding territories and have joined the flocks by the time most *F. magellanica* flowers are available might cause a higher frequency of flower robbery there than in areas further north.

Elsewhere in Chile, *P. patagonicus* is known to visit flowers of some species (e.g. *E. coccineum*) legitimately and to be capable of pollen transfer among flowers (C. Smith-Ramírez, unpublished data). Thus, this fringillid can be a mutualist for some plant species but a nectar robber for others, as appears to be the case for the well-known professional nectar robbers of the genus *Diglossa* (e.g. Graves 1982).

The low frequency of animal pollinators observed in the populations of *F. magellanica* in Tierra del Fuego, together with the high fruit set found in the intact flowers, suggest that a large fraction of the seeds, presumably much larger than the 14% found by Riveros (1991) further north, are the result of selfing. Pollination systems of flowering plants commonly change with the

available array of pollinators or revert to autogamy where pollen vectors are scarce or unreliable (e.g. Amadon 1947; Grant & Grant 1965; Galen 1989). The consequences of selfing for levels of inbreeding depression in the genus *Fuchsia* are undetermined.

The pale-flowered morphs were very rare and localized in western Tierra del Fuego, as in other parts of Chile (Hoffman 1982; E. Pisano, personal communication). Although Hummingbirds were rare in open areas, they would be expected to favour the normal, red-flowered morphs. In contrast, flower robbery by *P. patagonicus* did not exert any selection against pale flowers, as these birds robbed a much greater proportion of flowers of the red morph. Selection against pale morphs has been found in *Delphinium nelsonii* Greene, in which the pollinators (Hummingbirds and Bumble-bees) appear to discriminate against the pale flowers because of difficulty of extracting nectar from them (Waser & Price 1981). Selection against the pale morph might occur during the seed-dispersal phase of the reproductive cycle, if the green-coloured fruits tend to be rejected by vertebrate foragers, but we lack data to examine this possibility.

Phrygilus patagonicus not only affects negatively the reproductive success of *F. magellanica* but, apparently, also reduces seed dispersal. This bird was commonly observed pecking out pieces of the fruit, thus rendering them less attractive to more effective seed dispersers. In contrast, *E. albiceps* acts as a mutualist of the plant, not only by pollinating flowers effectively but also by swallowing entire fruits and defecating intact seeds (A. Traveset, M. F. Willson & C. Sabag, personal observations) and thus being a legitimate seed disperser.

The interactions of *F. magellanica* with its avian floral visitors varies both at a geographic and at a local (habitat) scale. Variation in interactions has the potential to translate into variation in patterns and intensities of natural selection. In areas where pollinators are scarce the plant is 'forced' to reproduce mostly by autogamy, besides having to cope with an intense nectar robbing, so the selective pressures on floral traits probably differ significantly from those in areas where pollinators are not limiting. Furthermore, variation in interactions can have important consequences for the conservation of biodiversity and the development of long-term land-management plans for sustainable resource use. For instance, *F. magellanica* can colonize clear-cuts as the forests of Tierra del Fuego are being logged but, as this study suggests, their pollinators, the population of which is decreasing with extensive clear-cutting, will be unlikely to 'follow' their food plant into the open areas.

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