

Foraging behaviour of bird pollinators on *Embothrium coccineum* (Proteaceae) trees in forest fragments and pastures in southern Chile

CECILIA SMITH-RAMIREZ^{1,2*} AND JUAN J. ARMESTO^{1,2}

¹Laboratorio de Sistemática & Ecología Vegetal, Facultad de Ciencias, Universidad de Chile, Santiago, Chile and ²Center for Advanced Studies in Ecology and Biodiversity, P. Universidad Católica, Santiago, Chile (Email: csmith@netline.cl)

Abstract We investigated the effects of forest patch size on the behaviour of birds feeding on the flower nectar of the proteaceous tree *Embothrium coccineum* J. R. et G. Forster, which is typically restricted to forest edges in agricultural landscapes in southern Chile. We quantified reproductive parameters of trees (no. inflorescences per branch, total and open flowers per inflorescence) in forest fragments varying from 1 ha (small), to 20 ha (medium) and to >150 ha (large), and in remnant trees in pastures. Visits to flowers by nectar-feeding birds were recorded during 30-min observation periods, spread throughout the day during two flowering seasons, November 1992 and 1993 ($n = 242$ periods overall). Aggressive encounters among flower visitors were recorded in 1992. We expected less visits to trees in pastures and small forest patches because abundances of *Embothrium*'s main pollinators, the flycatcher *Elaenia albiceps* and the hummingbird *Sephanoides sephaniodes*, decreased in smaller patches. We found, however, that pollinator visiting rates were negatively correlated with forest patch area and were highest for pasture trees. This trend was largely due a decline in the number of visits by *E. albiceps*, the main flower visitor, in larger patches. Hummingbird visits did not change with forest patch size. Lower visitation rates to flowering trees in larger forest fragments seemed to be a consequence of territorial defence by *E. albiceps* and were unrelated to differences in floral display.

Key words: *Elaenia albiceps*, *Embothrium coccineum*, forest edges, hummingbirds, passerine pollination, *Sephanoides sephaniodes*, territorial defence, tree reproductive ecology.

INTRODUCTION

Plant–pollinator interactions are greatly affected by the subdivision of natural habitats resulting from human activities, such as the conversion of forest land to pastures, timber plantations or crop fields (Linhart & Feinsinger 1980; Sowig 1989; Aizen & Feinsinger 1994a,b). Species richness of animal pollinators is often reduced in habitat fragments relative to undisturbed continuous habitat (Linhart & Feinsinger 1980; Spears 1987; Jennersten 1988; Aizen & Feinsinger 1994a). Species composition and abundances of pollinators are also affected by the area of habitat fragments, as well as by the degree of modification of the environmental matrix surrounding the fragments (Gilbert 1980). Handel (1983) showed that the behaviour of animal pollinators, and hence the number of pollen grains they transfer between conspecific plants is likely to be a function of the geometry of habitat fragments (size, density and shape) and the quality of the surrounding matrix. Changes in pollinator assem-

blage and pollinator behaviour can greatly influence gene flow and plant evolution in fragmented habitats (Aizen & Feinsinger 1994a,b; Aldrich & Hamrick 1998).

In the present study we characterized the behaviour of birds feeding on flower nectar of *Embothrium coccineum* (Proteaceae), a tree species belonging to a monotypic genus, endemic to southern South American forests. *Embothrium* trees are frequently found in edges of forest fragments as well as in open, agricultural landscapes in southern Chile. Two bird species, the hummingbird *Sephanoides sephaniodes* and the passerine flycatcher *Elaenia albiceps* are the main pollinators of *Embothrium* in agricultural landscapes of Chiloé Island (Smith-Ramírez & Armesto 1998). Although *E. albiceps* and *S. sephaniodes* are not the only birds that feed on *Embothrium* nectar, these two species accounted for almost 90% of the visits to the flowers during two consecutive flowering seasons (Smith-Ramírez & Armesto 1998).

The dissection of formerly continuous forest habitat in southern Chile has altered the abundances and diversity of avian species feeding on specialized plant resources, such as fleshy fruits or nectar (Willson *et al.* 1994; Armesto *et al.* 1996). In remnant patches of

*Corresponding author.

†Address for correspondence.

Accepted for publication August 2002.

Table 1. Characteristics of study sites (two sites for each of four groups: isolated pasture trees, small, medium and large forest fragments), estimated fragment area, total no. trees observed per site, and average and standard error of reproductive parameters of trees related to floral display and fruit production in each site

	Fragment area (ha)	Total no. trees observed per site	Inflorescences per branch	Flowers per inflorescence	Open flowers per inflorescence	Fruit per inflorescence
Pasture trees	†	4	5.4 ± 1.5	8.1 ± 1.0	5.6 ± 0.8	2.1 ± 0.2
	†	5	10.0 ± < 0.01	8.2 ± 1.1	5.7 ± 0.7	1.2 ± 0.1
Small	1	30	3.4 ± 1.0	6.3 ± 0.5	3.7 ± 0.9	1.9 ± 0.1
	1	20	8.3 ± 1.3	6.4 ± 0.9	4.4 ± 0.5	2.2 ± 0.2
Medium	23	12	8.2 ± 1.3	6.9 ± 1.4	5.4 ± 1.2	1.2 ± 0.1
	18	15	5.0 ± 1.3	4.4 ± 0.6	2.6 ± 1.8	–
Large	>150	7	5.8 ± 1.3	4.7 ± 0.7	8.1 ± 0.6	4.2 ± 0.8
	>150	6	–	–	–	–

†Average ground cover of 0.004 ha was used in regression analyses. No data on flower production were available in one large fragment and fruit production was unavailable for one medium and one large fragment. Significant effects of fragment size were found only for fruits per inflorescence (one-way ANOVA, $F = 17.7$, d.f. = 3,256; $P < 0.0001$). There were no significant trends for other reproductive parameters.

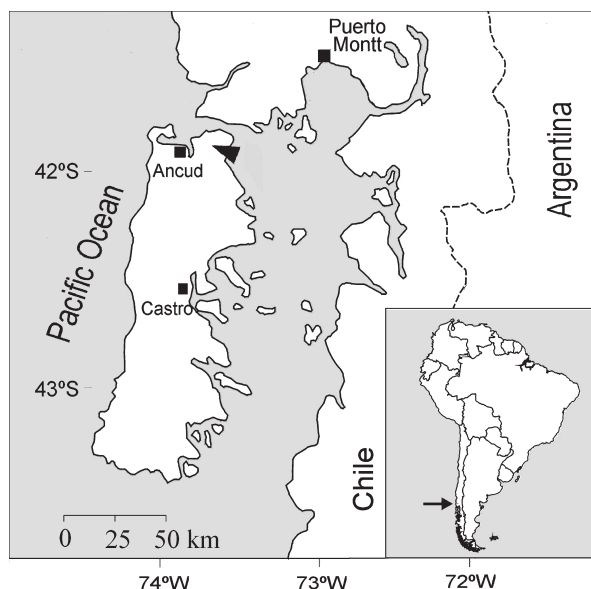


Fig. 1. Location of study area in northern Chiloé Island (arrow).

primary forest in Chiloé Island, both *E. albiceps* and *S. sephaniodes* decline in population density with decreasing forest patch area (Willson *et al.* 1994). This leads to the prediction that trees in small forest fragments are likely to receive fewer pollinator visits and hence decreased pollen flow compared to trees in larger fragments. Accordingly, we investigated how the area of forest fragments affected the foraging behaviour of the main bird pollinators of *E. coccineum* trees occurring in forest edges and pastures, and examined the potential consequences of behavioural patterns of pollinators for tree reproduction in the landscape mosaic. There are few other studies of pollinator–plant interactions in fragmented forests, and these have generally focused on plants and animal pollinators that are restricted to

the interior of forest patches (Spears 1987; Jennersten 1988; Aizen & Feinsinger 1994a), rather than on interactions among edge species, which are the subject of the present work.

METHODS

Study area

Observations of trees were conducted in six remnant forest fragments and two pastures (Table 1, Fig. 1) located in northern Chiloé Island (41°50'S, 73°35'W), between the rural localities of Manao and Caipulli. Sites were separated from one another by 15 km or less and were approximately 20 km east of Ancud (Fig. 1). Many forest fragments in the local landscape mosaic are approximately 1 ha in size, but there are a small number of larger (>150-ha) forest patches (Willson *et al.* 1994). Most forest patches are either rounded in shape or have dendritic shapes following streams. Forest fragments are remnants of extensive temperate rainforests that covered Chiloé island in the mid 1800s (Willson & Armesto 1996). Forests clearing in the past 100 years has generated a landscape mosaic dominated by open pastures and fields, with scattered remnant forest patches. Forest edges with pastures often bear narrow belts of second-growth vegetation, including a mixture of shrubs, which are absent from the forest interior, and a high density of juvenile trees (<10 m tall). Vegetation along forest edges is subjected to occasional grazing and trampling by cattle, especially in patches surrounded by pasture. Even small forest patches retain an emergent tree layer, characterized by tall (30–35-m) *Nothofagus nitida* (Nothofagaceae) and *Eucryphia cordifolia* (Eucryphiaceae). Most patches had limited selective logging but none had been completely clearcut prior to the study. *Eucryphia*

cordifolia, *N. dombeyi* (emergents in primary forests), *Amomyrtus meli*, *Amomyrtus luma* (Myrtaceae), *Drimys winteri* (Winteraceae) and *Caldcluvia paniculata* (Cunoniaceae) dominate the canopy of the forest remnants. Shrub species, *Baccharis* sp. (Asteraceae), *Berberis darwinii* and *B. microphylla* (Berberidaceae), grew only along forest edges (Willson *et al.* 1994; Diaz *et al.* 1999).

Tree species studied

Embothrium coccineum (Proteaceae), a firebush, is distributed from central Chile to southern Patagonia and Tierra del Fuego (35–55°S). It is generally associated with open meadows, forest edges and second-growth areas. On Chiloé Island (approx. 42°S), this species blooms in spring (September–November). Trees produce large numbers of conspicuous red flowers in groups of 20–50 per inflorescence. The tubular flowers (2 cm long) are protandrous, with four yellow stamens totally fused to the four curved red tepals, which are free almost the entire length of the corolla. Flowers are open for 3–5 days, secreting 7–15 µL of nectar daily (Smith-Ramírez 1993; Smith-Ramírez & Armesto 1998). Nectar can sometimes be seen dripping from open flowers. When in bloom the entire tree acquires a bright red colour. Fruits are 5–10-cm-long dry pods that ripen 3 months after flowering. Pods open longitudinally, releasing around five winged seeds, approximately 2.4 cm long. Trees from the mainland have been reported as partly self-incompatible and strongly dependent on pollinators for seed-set (Riveros 1991). Field assays on Chiloé have shown that seed production requires the manipulation of the flower by nectar-feeding birds (C. Smith-Ramírez, unpubl. data, 1994).

Avian flower visitors

Embothrium coccineum's red blossoms attract nine species of birds, mostly passerines, that feed on flower nectar (Smith-Ramírez & Armesto 1998; Table 2).

Four species are likely to be significant pollen vectors because of their visitation rates. Two of them, *S. sephanioides* and *E. albiceps*, have been shown to carry pollen of *E. coccineum* on their bodies (Smith-Ramírez & Armesto 1998). Occasional visitors included the parrot *Enicognathus leptorhynchus* (Psittacidae) that visited trees in one small fragment, destroying many flowers, and the Icterinae *Molothrus bonariensis* that visited only flowers of isolated pasture trees.

Field methods

Observations of birds visiting flowers of *E. coccineum* trees were conducted during days in the second and third week of November 1992, and in the third week of November 1993, during the peak of the flowering season. For each observation period we selected groups of 2–4 individual trees of *E. coccineum* growing contiguously along edges of small, medium and large forest patches (Table 1). No flowering trees were located in the interior of forest fragments. Bird visits to each group of trees were recorded during 30-min periods. We also conducted observations on a number of trees that remained as isolated or shade trees in the middle of two different open pastures (Table 1). In the latter case one individual tree was observed at a time because the distance to nearest neighbours (>50 m) prevented simultaneous observation. Overall, we made observations on four isolated trees in each of two open pastures. For statistical analyses we averaged the reproductive features and observations on these four trees at each pasture site. Each year we observed only trees that were >8 m tall and exhibited similar massive flower production. A noticeable, but uniform decrease in flowering was observed for all trees during the second year.

Forest fragments selected for the present study were classified in three groups according to their area: (i) small patches of approximately 1 ha each; (ii) medium size fragments approx. 30 ha; and (iii) large fragments approximately 150 ha. Two patches in each size category were chosen (Table 1). Isolated trees were

Table 2. Birds observed feeding on flower nectar of *Embothrium coccineum* in northern Chiloé Island[†]

Family	Species	Body mass [‡] (g)	Feeding habits	Frequency of visits (%)
Tyrannidae	<i>Elaenia albiceps</i>	17.0	F, I, N	76.6
Trochilidae	<i>Sephanoides sephanioides</i>	6.5	N, I	11.8
Fringillidae	<i>Carduelis barbatus</i>	14.6	G	5.6
Fringillidae	<i>Phrygilus patagonicus</i>	22.0	F, G	5.0
Emberizidae	<i>Curaeus curaeus</i>	73.0	I, F	0.5
Emberizidae	<i>Molothrus bonariensis</i>	— [§]	I	0.2
Psittacidae	<i>Enicognathus leptorhynchus</i>	— [§]	G	0.1
Emberizidae	<i>Zonotrichia capensis</i>	21.5	F, I, G	0.1
Tyrannidae	<i>Anairetes parulus</i>	6.2	I	0.1

[‡]From Sabag (1993). F, frugivore; I, insectivore; G, granivore; N, nectarivore (Rozzi *et al.* 1996). [§]Data unavailable. [†]Relative frequency of visits based on $n = 1647$ records (Smith-Ramírez & Armesto 1998).

separated from one another by at least 50 m and were located >400 m away from the nearest forest edge. In small patches, trees that occurred along the entire perimeter of the patch were observed. In medium and large patches we observed several groups of trees present in a randomly selected area equivalent to the perimeter of small fragments. Trees in these sampling areas represented only a fraction of all trees found in the entire perimeter of medium and large patches. The absolute density of *E. coccineum* trees along forest edges decreased with increasing patch size and increasing extension of edge habitat (Table 1).

In November 1992, sites (patches and pastures) were monitored in a random order by one observer over the course of 3 weeks. In the second year (1993), three randomly selected sites were monitored simultaneously each day by different observers over a 2-week period. Simultaneous observations were useful to control for changes in bird activity due to day-to-day variation in weather. Records of birds visiting *E. coccineum* flowers were kept during an average of eight observation periods of 30 min each day, distributed evenly from 07.00 to 21.00 hours, except for interruptions due to inclement weather. When a bird was observed feeding on an *E. coccineum* flower it was recorded as one 'visit'. For each 30-min period, we recorded the number of individuals of each bird species visiting the flowers, the number of flowers visited by each bird, and the number of aggressive interactions (physical contact and/or chasing behaviour) among individuals of the same or different species. We also recorded the simultaneous occupation of one tree by different bird species as a measure of interspecific territorial defence. Based on records from the first year, we established the time of day with the greatest frequency of bird visitation. In 1993 30-min observation periods were limited to times of maximum activity (07.00–10.30 hours,

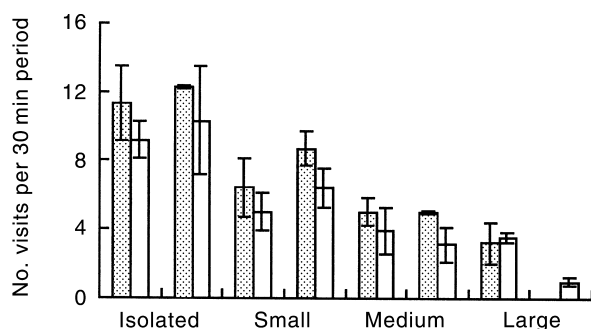


Fig. 2. Number of visits by all nectar-feeding birds to flowering *Embotrium coccineum* trees in small, medium and large forest patches, and remnant trees in pastures. Values are the average number of visits per 30-min observation period. Standard error bars are also shown. Visiting rates differed between years and decreased from pasture trees to large patch sizes (two-way ANOVA; significant effects of both year and patch size, $F_{1,7} = 17.4$, $P < 0.005$ and $F_{3,3} = 64.0$, $P = 0.0032$, respectively). (■), 1992; (□), 1993.

17.30–22.30 hours). A total of 242 30-min observation periods were accumulated in the 2 years of study and 1647 bird visits were recorded. To compare results between fragments and between years, we used the average number of bird visits to flowers per 30-min observation period at each site.

Availability of nectar resources in each pasture tree and forest patch was estimated by the abundance of nectar-secreting flowers. To examine the effect of variation in resources on the visiting rates of nectar-feeding birds, during November 1992, we quantified daily the following variables of the target *E. coccineum* trees: (i) the number of open flowers per inflorescence ($n = 12–18$ inflorescences per tree); (ii) the number of inflorescences per branch <50 cm long ($n = 1–7$ branches) for four to six trees per study site; and (iii) the average number of unopened and open (nectar-secreting) flowers during the entire flowering period. The latter was an indicator of the overall floral 'display' of the trees. We also estimated the number of fruits produced at the end of the ripening period (January) by counting pods per inflorescence in 2–4 branches per target tree in the different forest fragments.

We used Pearson's correlation to assess the relationship between bird visitation rates to flowers (pooling data for both years) and number of aggressive interactions among birds, and Spearman's rank correlations to assess the relationship between fragment size (a categorical variable) and bird visitation rates (overall and by species) and resource supply. In the analyses, remnant trees in pastures were ranked as the smallest patch size with an average ground cover of 0.004 ha. This area was calculated by multiplying the average cover of 0.0007 ha per tree (1.5 m mean crown diameter), times the number of target trees in one pasture. We pooled data on bird visiting rates for both years of study, despite the decrease in flowering in the second year, because trends of visitation across sites remained unchanged (Fig. 2). One-way ANOVA was used to assess the effect of forest fragment area on reproductive parameters of trees (Table 1). A two-way ANOVA was used to assess the effects of year of study (as a random factor) and area of forest fragments (four groups: isolated trees, small, medium, and large fragments; Table 1), on the number of bird visits to flowering *E. coccineum* trees.

RESULTS

Visitation rates

The passerine *E. albiceps* and the hummingbird *S. sephaniodes* were the two most numerous visitors to *E. coccineum* flowers, accounting, respectively, for 77% and 12% of all the birds observed during 1992 and

1993 (Table 2). The average number of visits per observation period to *E. coccineum* flowers by all bird species was greater for isolated pasture trees and for trees on edges of small forest patches than for trees in medium and large patches (Fig. 2). Results of two-way ANOVA indicated that the number of visits to flowers by all bird species listed in Table 1 differed between years ($F = 17.4$, d.f. = 1,7; $P < 0.005$) and decreased from pasture trees and small fragments to large fragments ($F = 64.0$, d.f. = 3,7; $P < 0.0001$). There was no significant interaction between year and fragment area ($F = 0.13$, d.f. = 3, 7; $P = 0.94$). Fragment size was also negatively correlated with visiting rates to flowering trees by all bird species (both years pooled, Spearman's rank correlation, $r_s = -0.72$; $P < 0.05$; $n = 8$). When each bird species was analysed separately, hummingbird visits to flowering trees were unrelated to fragment size ($r_s = 0.24$; $P > 0.05$; $n = 8$). Consequently, the greater number of visits to individual trees in pastures and groups of trees growing along edges of small fragments reflected primarily a greater number of visits to these trees by the most frequent flower visitor, *E. albiceps* (Spearman's rank correlation, $r_s = -0.80$; $P < 0.01$; $n = 8$). Visits by the passerine *Carduelis barbatus*, the third most important visitor to *E. coccineum* flowers (6% of all visits; Table 2), were not related to tree location ($r_s = -0.31$; $P > 0.05$; $n = 8$). In contrast, *Phrygilus patagonicus*, which accounted for only 5% of all visits to flowers (Table 2), had a significantly higher number of visits to trees in medium and large patches ($r_s = 0.70$; $P < 0.05$; $n = 8$).

Bird visits and resource supply

Excluding pasture trees, more *E. coccineum* trees were observed along edges of small fragments than in

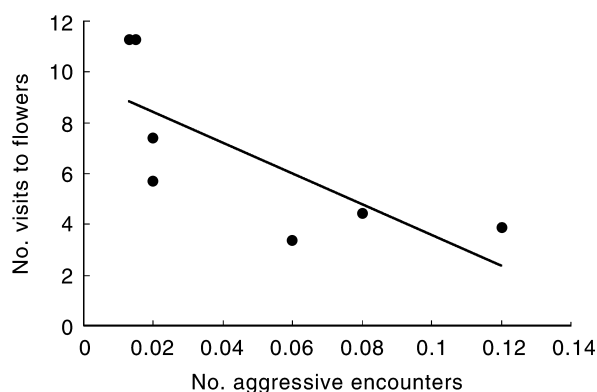


Fig. 3. Relationship between the average number of visits by nectar-feeding birds (per 30-min observation period) and the average number of intraspecific or interspecific aggressions in flowering *Embothrium coccineum* trees in pastures and forest patches. Regression model, $Y = 9.61 - 60.3X$ ($F_{1,5} = 6.13$; $P = 0.056$). $R^2 = 0.551$.

medium and large fragments (Table 1). Consequently, there was a significant correlation between the total number of *E. coccineum* trees present in a given site and the number of visits to target trees by *E. albiceps* ($r_s = 0.92$; $P < 0.01$; $n = 8$). This correlation did not hold, however, when all bird species and trees in pastures and forest fragments were considered together ($r_s = -0.06$; $P > 0.05$; $n = 8$). Only for *S. sephaniodes* was there a positive correlation between the number of visits and the number of open flowers per inflorescence ($r_s = 0.70$; $P < 0.05$; $n = 7$). For other bird species (*E. albiceps*, *C. barbatus* and *P. patagonicus*) the number of visits to target trees was unrelated to either the number of flowers per inflorescence and per branch or the abundance of flowers per tree.

Aggression and territoriality

We frequently observed aggression among nectar-feeding birds visiting trees of *E. coccineum*. Generally, aggression occurred between conspecific individuals but occasionally it was observed among individuals of different species. Most commonly a bird already perched in a tree expelled an arriving visitor. We observed individuals of *E. albiceps*, *S. sephaniodes*, *C. barbatus* and *P. patagonicus* actively expel other birds, both conspecific and non-conespecific, from flowering *E. coccineum* trees. We interpret aggressive behaviour to be territorial resource defence, particularly in the case of the arriving migrant *E. albiceps*. This species established breeding territories that included a number of flowering *E. coccineum* trees contiguous to one another along a forest edge. We did not observe aggression among the infrequent visitors to *E. coccineum* flowers. Most observed incidents of aggression (86%) occurred between two individuals of *Elaenia albiceps*, and 76% of these took place in medium and large patches. Aggression rates among visiting birds was correlated positively with the area of the forest fragment (Spearman's rank correlation, $r_s = 0.65$; $P < 0.05$; $n = 8$). Consequently, agonistic behaviour was negatively related to total bird visitation rates because more birds visited undefended pasture trees (Fig. 3). In these isolated trees we also recorded the maximum number of individuals (11) and species (6) perching and feeding simultaneously on a single tree (Table 3). Consequently, pollinating birds stayed longer and were able to visit a larger number of flowers in trees that were not defended (Fig. 3).

Overall, neither the number of aggressive interactions nor the number of birds simultaneously visiting flowers in one tree were correlated with availability of resources, measured as the number of open flowers per site (pasture trees and patches). Thus bird pollinators defended trees with similar yields to those that were not defended.

Table 3. Average and standard error of visiting rates (1992 and 1993) to *Embothrium coccineum* flowers (no. bird visits/no. observation periods) for all nectar-feeding bird species and for the two major bird pollinators *Elaenia albiceps* and *Sephanoides sephaniodes*

Fragment Size category	Visiting rates all birds	Visiting rates <i>E. albiceps</i>	Visiting rates <i>S. sephaniodes</i>	Simultaneous occupation average Species	Simultaneous occupation average Individual	Rate of aggression
Pasture tree	11.3 ± 1.8	8.9 ± 1.5	1.9 ± 0.4	4.8 ± 0.02	6.5 ± 0.02	0.015 ± 0.04
Small	11.3 ± 1.7	7.7 ± 0.9	0.2 ± 0.09	2.0 ± 0.08	2.1 ± 0.1	0.013 ± 0.05
	7.4 ± 0.6	5.9 ± 0.6	0.7 ± 0.04	2.2 ± 0.06	2.4 ± 0.1	0.02 ± 0.01
Medium	5.7 ± 1.2	4.7 ± 1.2	0.5 ± 0.1	2.2 ± 0.04	1.9 ± 0.08	0.02 ± 0.01
	4.5 ± 0.7	2.6 ± 0.6	0.9 ± 0.2	1.2 ± 0.04	1.4 ± 0.08	0.08 ± 0.05
Large	3.9 ± 0.2	3.1 ± 0.2	0.5 ± 0.2	1.4 ± 0.09	1.4 ± 0.1	0.12 ± 0.06
	3.4 ± 0.8	1.7 ± 0.6	1.6 ± 0.2	1.1 ± 0.09	1.1 ± 0.2	0.06 ± 0.01
	1.3 ± 0.2	0.4 ± 0.2	0.6 ± 0.2	1.1 ± 0.08	1.1 ± 0.2	No data

The simultaneous occupation average is the mean no. species and individuals simultaneously feeding on a single tree. Rate of aggression is the no. aggressions observed per tree divided by the numbers of bird visits in 1992.

DISCUSSION

Most studies of pollination in fragmented forest landscapes have documented that the number of pollinator (insects or hummingbirds) visits to flowers decreased progressively with a reduction in the area of habitat fragments (Linhart & Feinsinger 1980; Powell & Powell 1987; Jennersten 1988). In forest fragments in the Argentinean Chaco, Aizen and Feinsinger (1994a) reported that the total number of pollinator visits to flowers of several native plant species remained constant across a broad range of sizes of habitat fragments because of a compensatory increase in the density of an introduced pollinator, the European bee *Apis mellifera*, in smaller forest fragments. Otherwise, the number of visits by native pollinators decreased in smaller patches.

In contrast to previous studies, in a human-dominated landscape mosaic in northern Chiloé Island the main pollinator of the proteaceous tree *E. coccineum*, the Tyranid *E. albiceps*, visited flowering pasture trees and trees in edges of small (1-ha) rainforest fragments more frequently than trees in larger (>20-ha) patches. We did not observe compensatory increases in the number of visits by other nectar-feeding species in larger forest fragments, although the second most important pollinator, the hummingbird *S. sephaniodes*, had similar visiting rates regardless of patch size and site (Table 3). Thus, flowering trees in edges of medium and large forest patches received fewer visits by a less diverse pollinator assemblage than pasture trees.

This result was inconsistent with our prediction based on the reported decline in abundance of both *E. albiceps* and *S. sephaniodes* in small compared to large forest fragments in the same area (Willson *et al.* 1994). This discrepancy is due in part to the fact that Willson *et al.* (1994) studied birds along transects in the interior of forest fragments. Rozzi *et al.* (1996) reported that in Chiloé island both *E. albiceps* and

S. sephaniodes tend to be more common in forest edges than in forest interiors. Consequently, a better understanding of pollinating-bird responses to habitat fragmentation may require a systematic comparison of bird abundances in a diversity of habitats characteristic of the human-dominated landscape (Aldrich & Hamrick 1998; Daily *et al.* 2001).

Lower rates of pollinator visitation to trees in larger patches were not compensated for by changes in pollinator density. Therefore, we attributed these differences in visitation rates to the fact that pasture *E. coccineum* trees and trees in small fragments are less likely to be defended by the main pollinator, *E. albiceps*. This is consistent with the observation that territorial defence by *E. albiceps* was largely restricted to clumps of trees in edges of medium and large forest fragments. Flowering *E. coccineum* trees are an important food source for *E. albiceps* early in the breeding season (Smith-Ramírez & Armesto 1998), probably influencing the location of nests and territories. Generally, a defended territory included three to 3–5 adjacent flowering trees, in addition to an undetermined number of fleshy-fruited trees or shrubs present nearby in the forest edge, such as *A. luma*, *Drimys winteri*, *Luma apiculata* and *Berberis* spp. Fruiting trees and shrubs are an important food source for the opportunistic *E. albiceps* from December to January, after *E. coccineum* ceases flowering (Sabag 1993; Rozzi *et al.* 1996). The ability of this bird species to switch from feeding on nectar to feeding on fleshy fruits and on insects is remarkable (Sabag 1993). From our observations of territorial defence, we infer that *E. albiceps* nested mainly in forest fragments >20 ha, where a variety of food resources (nectar, fleshy fruits and insects) required during the entire breeding and rearing periods was available. Defence of scattered pasture trees by the birds is probably impractical because of the long distances between neighbouring trees and lack of understory.

Behavioural patterns of nectar-feeding birds may have important consequences for the reproductive

success of trees growing in forest fragments and in other habitats in human-dominated landscape mosaics. A population genetic analysis by Aldrich and Hamrick (1998) demonstrated that pasture trees were the main source of seedlings and saplings found in forest patches in a fragmented landscape in Central America. In our study the number of fruits matured per inflorescence was greater for trees in large forest fragments than for trees in small fragments or pastures (ANOVA, $F = 17.7$; d.f. = 3,256; $P < 0.0001$; Table 1). Accordingly, the larger number of bird visits to flowering trees in small fragments and in pastures seems to be in excess with respect to the number of visits required for successful pollination and did not contribute to increased fruit yields. Because of the lack of effect of pollinator visitation rates on fecundity, it is likely that other reproductive variables not examined in the present study, such as seed-set and the amount of pollen grains transferred to receptive stigmas, may vary with fragmentation (Aizen & Feinsinger 1994b). In particular, the quality of pollen transferred between stigmas in patches of different size may differ.

The small proportion of fruits matured per inflorescence (7–20% of all flowers, data not shown) suggests that in *E. coccineum* the fruit production may be subject to other selective forces. For instance, fruit set in Australian Proteaceae may be affected by pollen or nutrient limitation, and by insect predation on flowers and seeds (Ayre & Whelan 1989). In the case of *E. coccineum*, pollinators may have an effect on the probability of exogamy (i.e. the quality of pollen transferred between stigmas) and hence on the genetic makeup of the progeny. *Embothrium coccineum* trees in large forest patches are more likely to be defended by *E. albiceps*. In the absence of territorial defence, trees in small fragments and isolated trees in pastures have a lower probability of exogamy (pollen transfer between trees) because birds stay longer and visit more flowers within individual trees. Trees that were actively defended in larger patches received less visitation, compared to smaller patches, and birds moved sooner to another tree, thus promoting greater pollen flow among conspecifics. Other studies have documented that pollen flow is highly dependent on the relationship between pollinator behaviour and patch size in fragmented habitats (Aizen & Feinsinger 1994b; Aldrich & Hamrick 1998).

ACKNOWLEDGEMENTS

We are grateful to M. F. Willson, T. de Santo, E. Elgueta, E. Couve and E. Salazar for advice, company, and assistance in the field. R. Vasquez, E. Rivera and two anonymous reviewers provided valuable comments on earlier versions of the manuscript. We acknowledge the support of a J. S. Guggen-

heim Fellowship (JJA), Biocores Project (INCO-DC Program, EU), an Endowed Presidential Chair in Science (JJA), Millennium Nucleus Project No. P99–103FICM and grant FONDAP-FONDECYT 1501–0001 to the Center for Advanced Studies in Ecology and Biodiversity. The hospitality of the Institute of Ecosystem Studies, New York, USA, while preparing the final version, is also appreciated.

REFERENCES

- Aizen M. & Feinsinger P. (1994a) Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine 'Chaco Serrano'. *Ecol. Appl.* **4**, 378–92.
- Aizen M. & Feinsinger P. (1994b) Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest. *Argentina Ecol.* **75**, 330–51.
- Aldrich R. P. & Hamrick J. L. (1998) Reproductive dominance of pasture trees in a fragmented tropical forest mosaic. *Science* **281**, 103–5.
- Armesto J. J., Smith-Ramírez C. & Sabag C. (1996) The importance of bird–plant mutualisms in Chilean temperate rain forests. In: *Riparian Temperate Rain-Forest* (eds R. Lawford, P. B. Alaback & E. Fuentes) pp. 248–65. Springer, Berlin.
- Ayre D. J. & Whelan R. J. (1989) Factors controlling fruit set in hermaphroditic plants: Studies with the Australian Proteaceae. *Trends Ecol. Evol.* **4**, 267–72.
- Daily G. C., Ehrlich P. R. & Sanchez-Azofeifa G. A. (2001) Countryside biogeography: Use of human-dominated landscape matrices by the avifauna of southern Costa Rica. *Ecol. Appl.* **11**, 1–13.
- Díaz I., Pápic C. & Armesto J. J. (1999) An assessment of post-dispersal seed predation in temperate rain forest fragments in Chiló Island, Chile. *Oikos* **87**, 228–38.
- Gilbert L. E. (1980) Food web organization and conservation of neotropical diversity. In: *Conservation Biology: An Evolutionary-Ecological Perspective* (eds M. E. Soulé & B. A. Wilcox) pp. 19–34. Sinauer, Sunderland, Massachusetts, USA.
- Handel S. N. (1983) Pollination ecology, plant population structure, and gene flow. In: *Pollination Biology* (ed. L. Real) pp. 63–211. Academic Press, London, England.
- Jennersten O. (1988) Pollination in *Dianthus deltoides* (Caryophyllaceae): Effects of habitat fragmentation on visitation and seed set. *Conserv. Biol.* **2**, 359–66.
- Linhart Y. & Feinsinger P. (1980) Ecological and behavioral determinants of pollen dispersal in hummingbird-pollinated *Heliconia*. *Am. Nat.* **107**, 511–23.
- Powell A. H. & Powell G. V. N. (1987) Population dynamics of male Euglossine bees in Amazonian forest fragment. *Biotropica* **19**, 176–9.
- Riveros M. (1991) Aspectos sobre la biología reproductiva en dos comunidades del sur de Chile, 40°S. Doctoral Thesis, Facultad de Ciencias, Universidad de Chile, Chile.
- Rozzi R., Martínez D., Willson M. F. & Sabag C. (1996) Avifauna de los bosques templados de Sudamérica. In: *Ecología de Los Bosques Nativos de Chile* (eds J. J. Armesto, C. Villagrán & M. T. K. Arroyo) pp. 135–52. Editorial Universitaria, Santiago, Chile.
- Sabag C. (1993) El rol de las aves en la dispersión de semillas en un bosque secundario de Chiló. Tesis de Magister, Universidad de Chile, Facultad de Ciencias.

- Smith-Ramírez C. (1993) Los picaflores y su recurso floral en el bosque templado de la isla de Chiloé, Chile. *Rev. Chil. Hist. Nat.* **66**, 65–73.
- Smith-Ramírez C. & Armesto J. J. (1998) Nectarivoría y polinización por aves en *Embothrium coccineum* (Proteaceae) en la isla de Chiloé, Chile. *Rev. Chil. Hist. Nat.* **71**, 51–63.
- Sowig P. (1989) Effects of flowering plant's patch size on species composition of pollinator communities, foraging strategies, and resource partitioning in bumblebees (Hymenoptera: Apidae). *Oecologia* **78**, 550–8.
- Spears E. E. (1987) Island and mainland pollination ecology of *Centrosema virginianum* and *Opuntia stricta*. *J. Ecol.* **75**, 351–62.
- Willson M. F. & Armesto J. J. (1996) The natural history of Chiloé: On Darwin's trail. *Rev. Chil. Hist. Nat.* **69**, 149–161.
- Willson M., DeSanto T., Sabag C. & Armesto J. J. (1994) Avian communities of fragmented south-temperate rainforest in Chile. *Conserv. Biol.* **8**, 508–20.