

# A trade-off between the amount and distance of pollen dispersal triggered by the mixed foraging behaviour of *Sephanoides sephaniodes* (Trochilidae) on *Lapageria rosea* (Philesiaceae)

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## A B S T R A C T

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Nectar thieves may increase or decrease pollinator-mediated pollen flow and thus may have positive or negative effects on plant reproductive success. In temperate rainforests of South America, the hummingbird *Sephanoides sephaniodes* acts as both a pollinator and non-destructive nectar thief on *Lapageria rosea*. Although pollinators that also act as nectar thieves have the potential to significantly modify plant reproductive success, no previous study has addressed this. To determine how the mixed behaviour of *S. sephaniodes* affects pollen flow, we experimentally exposed some flowers to nectar theft and excluded nectar thieves from other flowers. We then assessed pollen dispersal into the floral neighbourhood. Thieved flowers exported less pollen, but the pollen exported was transferred farther into the neighbourhood. Our findings indicate a trade-off between distance and amount of pollen flow.

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### Keywords:

Pollination

Nectar theft

Foraging behaviour

Pollen flow

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## 1. Introduction

Plants that offer rewards (e.g. nectar, oils) to entice pollinators can also attract non-pollinating floral visitors, among them nectar robbers and nectar thieves (Zimmerman and Cook, 1985; Higashi et al., 1988; Arizmendi et al., 1996; Traveset et al., 1998; Irwin and Brody, 1999; Maloof and Inouye, 2000; Navarro, 2000). While nectar robbers obtain nectar destructively, nectar thieves acquire nectar by foraging between petals in a non-destructive manner (sensu Inouye, 1980). Nectar thieves (mostly antagonists) and pollinators (mostly mutualists) usually belong to two distinct assemblages of animals. Nevertheless, pollinators may also behave as nectar thieves. For instance, numerous hummingbirds, usually acting as legitimate pollinators, may also behave as nectar

thieves, even on the same plant (McDade and Kinsman, 1980).

Nectar thieves may modify the flower structure (i.e. direct effect) as well as the quantity and quality of nectar. Any modification could trigger changes in the foraging behaviour of pollinators, which may alter the reproductive success of plants (i.e. pollinator-mediated indirect effect) (Maloof, 2001; González-Gómez and Valdivia, 2005). Additionally, the decrease in nectar volumes triggered by nectar thieves may increase the distance pollinators must fly (Kadmon and Shmida, 1992). In turn, this would decrease the number of flowers visited per plant as well as the time a pollinator spends foraging on an individual flower (Pyke, 1982; Maloof and Inouye, 2000). Although these modifications may be advantageous because they increase the pollen flow and consequently the probability of outcrossing (Inouye, 1983), it may also translate into lower foraging times per visit and consequently a lower quantity of ovules fertilised (Thomson and Plowright, 1980). Additionally, pollinators may not visit such plants if nectar

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volumes drop below a certain threshold, which would negatively affect plant fitness (McDade and Kinsman, 1980; Maloof and Inouye, 2000).

Differences in pollinator behaviour triggered by nectar thieves may also affect patterns of pollen. Consequently, this would impact gene dispersal (Linhart, 1973) and, therefore, neighbourhood size. The genetically effective population size in plants (i.e. the local neighbourhood) is determined by the combination of pollen and seed movement (cf. Wright, 1943). Neighbourhood size influences the extent of genetic drift and natural selection in populations by affecting the connections between individuals and/or populations (Austerlitz et al., 2004).

Although pollinators that also act as nectar thieves have the potential to significantly modify the reproductive success of plants, no study has addressed this (Maloof and Inouye, 2000). In this article, we evaluate how the mixed foraging behaviour, both pollination and non-destructive nectar theft, of the green-backed firecrown hummingbird *Sephanoides sephanioides* (Trochilidae) affects pollen dispersal of the hummingbird-pollinated vine *Lapageria rosea* (Philesiaceae).

## 2. Materials and methods

### 2.1. Species and study site

We conducted fieldwork during May 2003 at Los Queules National Reserve (35°59'S–72°41'W) in the southern temperate rainforest of Chile. In this forest, *L. rosea* (Philesiaceae) is a self-compatible hummingbird-pollinated vine bearing red-coloured bell-shaped flowers (Humaña and Riveros, 1994). Each flower is composed of six tepals (three outer and three inner), which bear a single brown-coloured nectary in the base exposed towards the inner part of the flower (Humaña and Riveros, 1994). It blooms in the austral autumn from May to June (Humaña and Riveros, 1994; Henríquez, 2002). The flower longevity is 9–15 days with no significant protogyny (Humaña and Riveros, 1994). *L. rosea* is pollinated by the hummingbird *S. sephanioides* and the bumblebee *Bombus dahlbomii* (Humaña and Riveros, 1994). In the southern part of its distribution, *L. rosea* is not limited by pollinators for seed set (Humaña and Riveros, 1994). However, in the northern part of its distribution, where our study site is located, seed set is pollinator-limited (Valdivia et al., 2005).

### 2.2. Nectar quantity and sugar concentration, pollen load, and foraging behaviour of *S. sephanioides*

To test whether nectar quantity and sugar concentration differ between the inner and outer nectaries, we inserted a microcapillary tube into each nectary until no further nectar could be extracted. Then, for each nectar sample, we estimated sugar concentration (mass percent) with a hand-held temperature-compensated refractometer. This assessment was performed in 21 bagged flowers, each from a different plant, for 24 h. We performed our nectar assessments in sexually mature flowers during the peak of the flowering season (Humaña and Riveros, 1994; Henríquez, 2002).

To assess the frequency of hummingbird visits to flowers of *L. rosea*, the type of foraging behaviour exhibited during

each visit (illegitimate visits, i.e. theft behaviour; and legitimate visits, i.e. pollinating behaviour), and the time spent foraging an individual flower, we randomly selected 81 flowers from 21 plants (i.e. four flowers per plant approximately). We observed these flowers in 10-min periods from 08:00 to 14:00 h for 5 days during the peak flowering season (Henríquez, 2002).

### 2.3. Effect of nectar theft on pollen dispersal

To estimate the effect of nectar theft on pollen dispersal from flowers of *L. rosea*, 10 circular sampling areas were randomly selected. The area of each was 2826 m<sup>2</sup> (radius = 30 m). The centre of each sampling area was ≥ 80 m from the centre of all other sampling areas. Because hummingbirds do not carry pollen farther than 30 m from the emitting flowers (Linhart, 1973), we considered each sampling area to be a separate floral neighbourhood.

To determine the origin and trajectory of pollen, we chose two flowers from the same plant that were at identical phenological stages (i.e. pollen emission). These flowers were near the centre of the sampling area. In these flowers, we removed pollen borne in the anthers and replaced it with inert fluorescent powder (Kearns and Inouye, 1993). Of these two emitting flowers, we altered one to prevent nectar theft between tepals by applying transparent adhesive tape from the bottom to the mid-length of tepals. Here we replaced pollen borne on the anthers with green fluorescent powder. We tagged the second flower of each plant by replacing the natural pollen with pink fluorescent powder. We did not manipulate the tepals in these flowers, therefore permitting nectar theft by hummingbirds. We chose 10 additional flowers, located 0–30 m from the emitting flowers, in each sampling area to be tagged as receiver flowers. We determined the presence of fluorescent powder from thieved and non-thieved emitting flowers on the stigmatic surfaces of receiver flowers using an UV lamp. This determination was made at night, following 24–36 h of foraging by hummingbirds.

To estimate the pollen load on the stigmatic surfaces of receiver flowers, five categories were defined according to the percentage of the stigmatic area (9 mm<sup>2</sup> of stigmatic area approximately) covered with fluorescent powder. We assigned values of 0–4 to receiver flowers with 0%, 1–10%, 11–25%, 26–50%, and 51–100% of the stigmatic surfaces were covered with fluorescent powder, respectively. The stigmatic pollen load was then estimated in each floral neighbourhood with the following stigmatic pollen load index (SPLI), which we modified from the herbivory index of Dirzo and Domínguez (1995):

$$\text{SPLI} = \sum_{i=0}^4 X_i n / N$$

where  $n$  is the number of observations of the  $i$  powder load category,  $X_i$  is the powder load category, and  $N$  is the total number of observations.

We compared the frequency of pollinating and thieving visits by hummingbirds using non-parametric Mann–Whitney tests. Because comparison of nectar theft in altered flowers and in controls was assessed in the same neighbourhood, and thieved and non-thieved flowers in each sampling area

were from the same plant, we tested pollen load estimates with non-parametric Wilcoxon tests for dependent samples. Distances reached by fluorescent powder were assessed using a slope test after identifying significant correlations with regression analyses. We used Statistica 6.0 to perform all analyses. We report data as mean  $\pm$  S.E.

### 3. Results

#### 3.1. Nectar quantity, sugar concentration and foraging behaviour of *S. sephaniodes*

The amount of nectar from outer nectaries ( $4.86 \pm 0.53 \mu\text{l}$ ,  $N = 63$ ) was significantly greater than that from inner nectaries ( $1.99 \pm 0.36 \mu\text{l}$ ,  $N = 63$ ; Mann-Whitney test:  $U = 1071.0$ ,  $P < 0.001$ ). Sugar concentrations did not differ significantly between the outer and inner nectaries ( $20.18 \pm 0.67\%$ ,  $N = 40$  and  $19.96 \pm 0.67\%$ ,  $N = 27$ , respectively; Mann-Whitney test:  $U = 0.06$ ;  $P = 0.95$ ).

The frequency of legitimate visits ( $2.7 \pm 0.2$  visits/10 min/flower,  $N = 81$ ) was significantly higher than that of illegitimate visits ( $1.5 \pm 0.1/10$  min/flower,  $N = 18$ ; Mann-Whitney test,  $U = 852.56$ ;  $P < 0.01$ ). The duration of a legitimate foraging bout ( $1.87 \pm 0.26$  s) was significantly greater than the duration of an illegitimate bout ( $1.23 \pm 0.26$  s; Mann-Whitney test:  $U = 522.5$ ;  $P < 0.02$ ).

#### 3.2. Effect of nectar theft on pollen dispersal

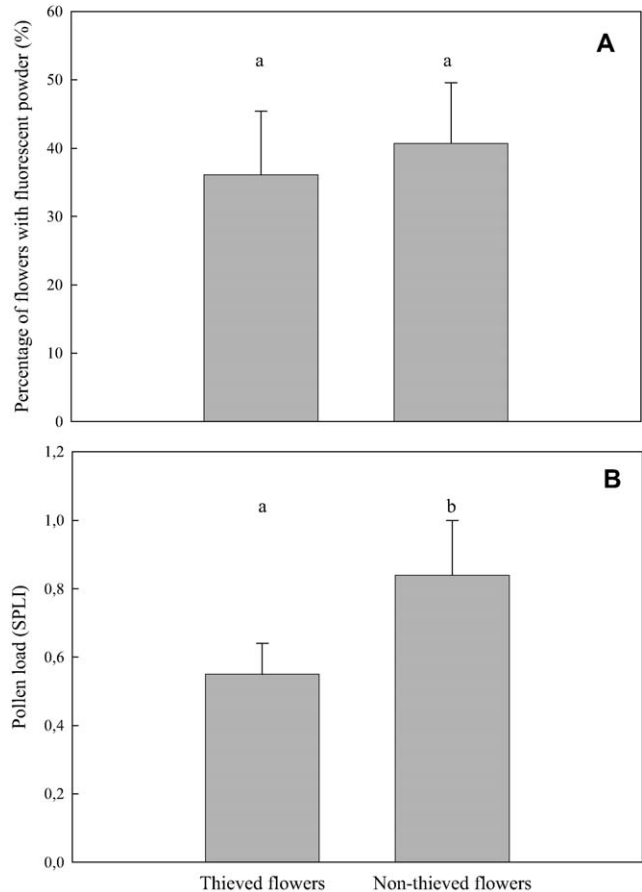
The proportion of receiver flowers bearing fluorescent powder was not different between thieved and non-thieved flowers (Fig. 1A. Wilcoxon test for dependent samples:  $Z = 1.19$ ,  $P = 0.234$ ). However, pollen load from non-thieved flowers was significantly higher on receiver flowers relative to that observed from thieved flowers (Fig. 1B. Wilcoxon test for dependent samples:  $Z = 2.07$ ,  $P = 0.038$ ). The distance to attain mean pollen load was 5.10 and 5.29 m from non-thieved and thieved flowers, respectively. Therefore, the distance of pollen dispersal from thieved flowers was significantly farther than from non-thieved flowers (slope test:  $t = -68.22$ ,  $P < 0.001$ ; Fig. 2).

### 4. Discussion

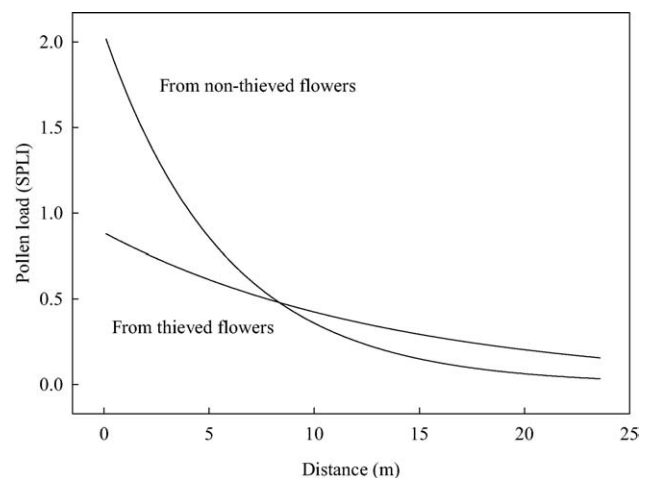
Nectar theft by *S. sephaniodes* on *L. rosea* influenced pollen flow in the floral neighbourhood: thieved flowers exported less pollen, yet it was exported over greater distances.

We observed that hummingbirds obtain nectar more frequently from the outer nectaries during thieving bouts compared to the inner nectaries. Therefore, it appears that the mixed foraging behaviour of *S. sephaniodes* results from the greater volume of nectar available in outer nectaries. However, hummingbirds spend less time foraging here. Our data suggests that hummingbirds obtain 70.9% of all nectar produced by flowers, but invest 34.2% less time when they forage nectar from the outer nectaries compared to that invested when they forage the whole flower.

We found no difference in the proportion of flowers receiving pollen from thieved and non-thieved flowers. However, in order to assess this finding in terms of plant perfor-



**Fig. 1 – Percentage of receiver flowers of *L. rosea* with fluorescent powder from thieved and non-thieved flowers (A), and fluorescent powder load (B) assessed through the SPLI (see text for methodological details).**



**Fig. 2 – Pollen dispersal of *L. rosea* from flowers thieved by *S. sephaniodes* and non-thieved flowers (Logarithmic equations for thieved flowers:  $y = -0.12\ln(x) + 0.75$ , and non-thieved flowers:  $y = -0.46\ln(x) + 1.59$ ).**

mance, two factors must be considered. First, the quantity of pollen exported from thieved flowers was significantly lower in comparison to non-thieved flowers. In terms of plant male function, this is negative: nectar theft reduces the number of pollen grains exported into the plant neighbourhood. The second factor concerns the distance of pollen dispersal. Nectar theft increased this distance, thereby increasing the outcrossing probability. This may confer an important advantage given the negative consequences of inbreeding, even in self-compatible plants such as *L. rosae* (Charlesworth and Charlesworth, 1987).

Our findings suggest that nectar theft results in a trade-off: a lower quantity of pollen is dispersed (negative), yet outcrossing may be increased (positive). Additionally, in terms of female function, the lower amount of pollen received by flowers as a result of nectar theft may be a positive consequence. That is, it should increase the likelihood of multipaternity. If a flower visitor carries away a small pollen load after each visit, other flowers are more likely to receive pollen from other visits and/or plants, resulting in a higher genetic diversity of the seeds within single fruits (Snow, 1996). Although we did not assess the female function of *L. rosae* in this work, another trade-off, as a result of nectar theft by *S. sephanooides*, is possible. The lower quantity of pollen flow that results from thieved flowers may be offset by 1) the greater dispersal distance, and 2) the potential increase in multipaternity of seeds.

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