

SHORT COMMUNICATION

Reproductive biology of *Macleania rupestris* (Ericaceae), a pollen-limited Neotropical cloud-forest species in Costa Rica

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The reproductive success of hummingbird-pollinated plants often depends on complex interactions between environmental conditions and pollinator biology (Navarro 1999, Stiles 1985, Wolf *et al.* 1976). The effect of environment on reproductive success of hummingbird-pollinated plants is particularly pronounced at high altitudes, where large daily fluctuations in temperature, relative humidity and solar radiation limit the effective time for photosynthesis (Cavieres *et al.* 2000) and affect foraging activity (Navarro 1999) and abundance of pollinators (Rahbek 1997). At high altitudes in the tropical cloud forests of Costa Rica these factors may have serious impacts on fruit production.

Three main hypotheses have been proposed to explain the factors limiting fruit production in ornithophilous plants. The resource-limitation hypothesis claims that variation in fruit production is regulated by variation in available resources over time or space (Lloyd 1980). The pollinator-limitation hypothesis states that insufficient pollen deposition, mainly due to inadequate pollinator services, prevents many flowers from developing into fruits (Schemske 1980). Finally, low fruit set may be explained by trade-offs between male and female fitness; an increase in flower number may augment male fitness via pollen production, thus compensating for the reduction in female fitness due to low fruit-set (Bateman 1948, Janzen 1977, Stephenson 1983, Willson 1979).

Here, we explicitly test predictions of the pollinator-limitation and fitness-trade-off hypotheses by investigating the phenology and pollination biology of *Macleania*

rupestris H.B.K. (Ericaceae), an epiphytic or terrestrial shrub common in the understorey of Neotropical cloud forests. These data, collected over 12 mo of field observation in a Costa Rican cloud forest, suggest that pollinator limitation is the primary cause of low fruit set in high-altitude populations of *M. rupestris*.

Flowers of *M. rupestris* are hermaphroditic with tubular red corollas (*c.* 3 cm long) tipped by white lobes (Wilbur & Luteyn 1978). The main pollinators of this plant are the fiery-throated hummingbird *Panterpe insignis* Cabanis & Heine and the green violet-ear *Colibri thalassinus* Swainson (Trochilidae). Fruits bend upward and turn purple-black when ripe, allowing for easier removal by frugivorous birds such as the sooty thrush (*Turdus nigrescens* Cabanis) and the sooty-capped bush-tanager (*Chlorospingus pileatus* Salvin). The study was conducted at the Cerro de La Muerte Biological Station (09°33'N, 83°44'W; 3100–3350 m asl) in the Costa Rican Talamanca mountain range. The Cerro de la Muerte region receives an average annual precipitation of 2500 mm, mostly between April and December. The mean temperature is *c.* 12 °C, with large daily fluctuations (from –5 °C to 35 °C), particularly during the dry season. The study site includes mainly high-altitude oak forest and páramo vegetation. The landscape is a mixture of trees and shrubs such as *Quercus*, *Viburnum* and *Gaiadendron*, with patches of páramo vegetation dominated by herbs of the Asteraceae and Poaceae as well as dwarf shrubs from the Rosaceae, Hypericaceae and Ericaceae and the bamboo *Chusquea* (Cleef & Chaverri-Polini 1992).

We marked and counted the number of inflorescences, number of newly opened flowers and number of fruits per inflorescence every week between January 2004 and January 2005 on 33 plants of *M. rupestris* along a

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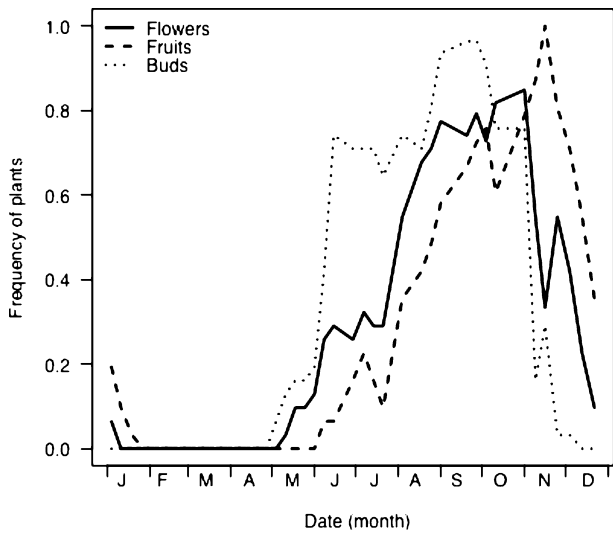


Figure 1. Relative frequency of *Macleania rupestris* plants ($N = 33$) with flower buds (dotted line), flowers (solid line) and fruits (dashed line) over a period of 12 mo.

1.5-km transect ranging in altitude from 3100 to 3350 m asl. Total flower production was estimated following Fuchs *et al.* (2003). Four species of hummingbird were observed at the study site: *P. insignis*, *C. thalassinus*, the magnificent hummingbird (*Eugenes fulgens*), and the volcano hummingbird (*Selasphorus flammula*). Of these, only *P. insignis* and *C. thalassinus* were regular visitors of *M. rupestris*; we recorded the number of visits and number of flowers visited per plant by both species. Observations were performed between 6h00 and 11h00, 3 d wk⁻¹ during the study period, on two randomly selected plants each day.

Additionally, we conducted three censuses of hummingbirds at five different altitudes in the highlands of Costa Rica: Cerro de la Muerte (Talamanca mountain range), Irazú, Barva and Poás volcanoes (Central mountain range) to evaluate changes in abundance of *P. insignis* along an altitudinal cline (2650–3300 m asl). To make these censuses comparable we conducted them during the hummingbird breeding season (i.e. November–January) and in habitats with vegetation characteristics similar to the study area (Barrantes & Loiselle 2002). In each location, we counted the number of hummingbirds along a 1.5-km transect, walking at a steady pace from 6h00 to 7h30. All data were Box–Cox-transformed for regression analyses.

In our high-altitude population of *M. rupestris*, flowering extended from May to January, with a maximum during the months of highest precipitation (July–November, Figure 1). Each branch bore a mean (\pm SE) of 4 ± 1.05 inflorescences and each plant on average produced 2 ± 1.05 open flowers per day and a total of 571 ± 88.6 flowers over a 9-mo period. Fruit production

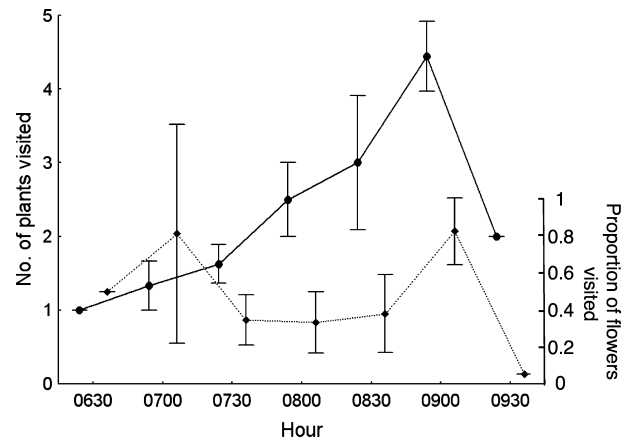


Figure 2. Mean (\pm SD) number of plants visited (solid line) and proportion of flowers (dotted line) visited by hummingbirds (number of flowers visited in a single feeding event/total flowers on a plant) in the Cerro de la Muerte population.

lasted from June to January. Fruit-set was low, averaging 0.10 ± 0.02 , and inflorescences produced between 0 and 23 fruits, with an average of 3.75 ± 0.07 fruits. Peak fruit production occurred in December at the onset of the dry season (Figure 1), when all plants in our population bore fruits. Plants produced an average of 31 ± 3.71 fruits.

Panterpe insignis was the predominant pollinator in our population, visiting the majority of flowers ($n = 362$) and plants ($n = 18$) in the study area. *Panterpe insignis* also visited individual plants more often (6.22 ± 1.07 visits) than did *C. thalassinus* (4.02 ± 1.09 visits), though both species visited similar numbers of flowers during a given foraging bout (*P. insignis* 5.06 ± 1.68 ; *C. thalassinus* 5 ± 3.05). In contrast to its behaviour at lower altitudes, *P. insignis* did not establish territories in our population, behaving instead as a trap-liner, visiting several plants in sequence in a short period of time. This behavioural difference is likely due to the relatively low abundance of flowers in our study site. During the entire study period, *C. thalassinus* was recorded visiting only five of the censused plants, perhaps reflecting the more aggressive behaviour of *P. insignis*, which limits access of other hummingbirds to flowering plants (Wolf *et al.* 1976). Furthermore, *P. insignis* is present year round in the study site, although part of the population may migrate to lower altitudes after the breeding season (Stiles & Skutch 1989), whereas *C. thalassinus* occurs in the area at very low density and for only few months a year (Wolf 1976).

Feeding activity of hummingbirds, measured as the number of flowers visited in a single feeding event divided by the number of available flowers on a plant, showed two peaks during the morning, the first one at 7h00 and the second at approximately 9h00, whereas visits to plants increased steadily during the morning, from dawn to 9h00 (Figure 2). Hummingbird activity decreased

Table 1. Average abundance (no. individuals per census) of *Panterpe insignis* censused along a 1.5-km transect at five localities of Costa Rica highlands.

Locality	Altitude (m asl)	Mean abundance (SD)	Visits
Volcán Poás	2650	20.7 ± 8.4	3
Volcán Barva	2850	13.0 ± 5.7	2
Volcán Irazú	3000	6.3 ± 2.9	3
Talamanca	3200	7.7 ± 3.5	3
Talamanca	3300	2.0 ± 2.0	3

drastically after 9h00, with a moderate increase at dusk (G.B. pers. obs.). The first peak of flower visitation is possibly determined by the energetic requirement of hummingbirds, which generally coincides with the peak of nectar production in hummingbird-pollinated flowers (Stiles & Wolf 1979). After satiation, flower visitation decreases only to rise again after a short period to fulfil the energy needs imposed by the low temperatures prevalent during the morning hours (Calder & King 1974). The increase in plant visitation observed during the morning likely reflects the depletion of nectar that occurred after the first period of visitation: hummingbirds have to visit more plants to satisfy their energy demands.

The fitness-trade-off hypothesis predicts that plants with larger floral displays should receive more pollinator visits. We observed no such relationship (linear regression, $P = 0.26$). We did, however, observe the positive relationship between pollinator visitation and fruit set ($\beta = 1.27$, $R^2 = 0.58$, $P < 0.001$) predicted by the pollinator-limitation hypothesis. Results from our hummingbird census (Table 1) point to an overall negative correlation between altitude and pollinator abundance ($\beta = -0.026$; $R^2 = 0.88$; $P = 0.019$), consistent with the idea that pollinator habitat may deteriorate with altitude (Rahbeck 1997). In our transect at Cerro de la Muerte, however, we see no such relation ($\beta = 0.002$, $R^2 = 0.005$, $P = 0.664$), likely due to the much smaller range of altitudinal variation within the site as well as its place at the upper end of the altitudinal range. Additionally, we cannot rule out the potentially important role of locally varying habitat and climatic conditions in patterning the spatial and temporal abundance of pollinators. For example, extreme early morning temperatures along our transect at Cerro de la Muerte likely affect the foraging activity of hummingbirds and the number of effective foraging hours (Gómez 1986).

Our data thus strongly suggest that low fruit set in our population is not explained by fitness trade-offs via an increase in male fitness as flower production increases, and instead support the idea that fruit production is limited by pollinator availability. While we cannot explicitly test the resource-scarcity hypothesis with our data, they nonetheless suggest that resource limitation

is of less significance than pollinator limitation in our population. For example, resource scarcity may place an upper limit on the number of fruit produced in the harsh environments of high-altitude cloud-forest populations, and might explain the lower (cf. Wolf *et al.* 1976) flowering intensity and extended flowering period of *M. rupestris* in our population. But resource scarcity alone cannot explain the relationship between hummingbird visitation and fruit set, and the observed pattern may be better explained by variation in pollinator abundance. The prolonged flowering period observed is likely to be a consequence of pollinator limitation, since the rate of visitation by hummingbirds to individual plants is largely dependent on the phenology of an individual or population (Feinsinger *et al.* 1986, Rathcke 1992). When faced with pollinator scarcity, plants may adopt a bet-hedging strategy (Udovic & Aker 1981) in which the flowering period is prolonged in order to take full advantage of rare periods of pollinator availability and ensure reproductive success. Selfing may also become more prevalent at high altitudes due to pollinator scarcity (Berry & Calvo 1989, Kalisz & Vogler 2003) which may contribute to the observed lack of correlation between fruit-set and altitude in the transect at Cerro de la Muerte. Recent evidence suggests that our observation of pollinator limitation is common in biodiversity hotspots like the Neotropical cloud forest (Vamosi *et al.* 2006), and may act synergistically with habitat loss or climate change (Rull & Vegas-Vilarrúbia 2006) to increase extinction risk. Finally, this study additionally serves to highlight the importance of considering both biotic and abiotic factors in further investigations of plant reproductive success.

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