# FUCHSIA'S FIERY-THROATED DEFENDERS: THE EFFECT OF HUMMINGBIRD TERRITORIALITY ON THE REPRODUCTIVE SUCCESS OF *FUCHSIA ARBORESCENS*

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*Abstract.* *Fuchsia arborescens* flowers are pollinated by several species of hummingbirds, including fiery-throated hummingbirds, volcanoes, and gray-tailed mountain-gems. Patches of fuchsia are sometimes defended by hummingbirds who restrict visitations to these patches by other hummingbirds and should cause plants in defended patches to produce a lower seed set than plants in undefended patches. The average visit time by hummingbirds was 5-fold greater in undefended patches but there was no difference in number of fruits per inflorescence (representing seed set), number of visits by hummingbirds, or total foraging time in defended and undefended patches of fuchsia. Apparently fuchsia reproduction is not limited by inter-patch visitation of hummingbirds. This could be due to: 1) lack of strong self-incompatibility, 2) frequent pollination by insects, or 3) presence of enough genetically-distinct individuals within patches to maintain a viable population through intra-patch pollination.

*Key Words: genetic diversity*, Lampornis castaneoventris, *nectar production*, Panterpe insignis, *pollination*, Selasphorus flammula

## INTRODUCTION

Hummingbirds feed on the nectar of tubular, red or orange flowers and frequently serve as pollinators for these flowers. Male birds often defend territories that include patches of flowers and tend to prevent other hummingbirds from visiting flowers in their territories by calling and chasing them away. Because territory defense may reduce visitation to flowers, we hypothesized that undefended patches of flowers should have a higher reproductive success than defended patches because there is a higher probability of cross-pollination when more birds are able to visit a patch and when birds move among patches. Thus, by defending a patch of flowers, hummingbirds may be helping themselves but hurting the plants.

One example of a hummingbird pollinated flower is *Fuchsia arborescens.* (Onegraceae), and it is abundant in the Cerro de la Muerte mountain range of Costa Rica. Once pollinated, females produce cylindrical, dark purple berries containing numerous tiny seeds (Gentry, 1993). We observed three common generalist hummingbirds visiting flowers of fuchsia: volcano hummingbirds (*Selasphorus flammula*), gray-tailed mountain-gems (*Lampornis castaneoventris cinereicauda*), and fiery-throated hummingbirds (*Panterpe insignis*), two of which were defending flower patches. Fiery-throats continuously defend rich patches of flowers, and also allow females to share their patches during the breeding season (Stiles and Skutch, 1995). We tested for affects of fiery-throated hummingbird territoriality on the reproductive success of *Fuchsia arborescens.*

## METHODS

We located 5 fuchsia patches near the Estación Biológica Cuerici at Cerro de la Muerte, Costa Rica. Patches were classified as defended if there was continued presence of one bird throughout the day, feeding, perching, and chasing away intruders. Two defended patches and three undefended patches were observed for three 30-minute periods on 28 and 29 January 1998: once between 05:50 and 09:15, and twice between 15:30 and 17:50. We recorded the species and length of visit for each hummingbird feeding in the fuchsia patch. We assumed that hummingbirds visiting fuchsia flowers were also capable of pollinating them, because fuchsia has a very short corolla length. To control for observer bias, both observers circulated between all five patches.

We measured reproductive success of fuchsia patches by counting fruits on 20 inflorescences in each patch, with the assumption that numbers of fruits were a good index of seed





set. Only those inflorescences with at least one open flower were considered. We chose inflorescences haphazardly and were limited to inflorescences that were easily viewed - those that were close to the ground or could be viewed fully with binoculars. We counted only large, mature purple fruits. To control for observer bias, each observer counted fruits on 10 inflorescences in each patch.

We used nested ANOVAs to compare fruits per inflorescence, total bird visits, total foraging time for all birds, and average visit length excluding the defending male, in defended and undefended patches of fuchsia, and across patches within both categories.

## RESULTS

There was no effect of patch defense on number of visits by hummingbirds (overall mean ± SE = 3.73 ± 0.69) or total foraging time in a fuchsia patch (overall mean ± SE = 23.90 ± 5.30), nor did these variables differ among patches (Table 1). The average length of time spent in a patch by a visiting bird was 5-fold greater in undefended patches ($F_{1,10}$ = 5.98, p = 0.037; Fig 1), but did not differ among patches within defense treatments ($F_{3,10}$ = 0.84, p= 0.51). The resident fiery-throated hummingbird accounted for most of the total time spent by all birds in defended patches. There was no effect of patch defense on mean number of fruits per inflorescence nor did they vary among patches within defense treatments (Table 2). However, there was considerable variation among inflorescences within a patch (mean ± SD = 22.68 ± 25.55).

Frugivorous birds such as collared redstarts (*Myioborus torquatus*) and sooty-capped bush-tanagers (*Chlorospingus pileatus* ) foraged on the fuchsia fruits in all patches. Bees were also seen regularly visiting flowers in all patches. Defending hummingbirds did not react to either of these types of visitors.

TABLE 1. ANOVA model for hummingbird activity that includes defense and patch nested within defense, with defense and patch both treated as significant effects. Total visits per patch were measured over 3 half hour observation periods, and total foraging time was bird*minutes spent in a patch for each half hour period. All p values > 0.20.

| | | Total Visits | | Total Foraging Time | |
|---|---|---|---|---|---|
| Source | df | MS | F | MS | F |
| Defended | 1 | 0.5 | 0.09 | 0 | 0.00 |
| Patch(Defended) | 3 | 11.67 | 1.85 | 564 | 1.34 |
| Error | 10 | 6.33 | | 420 | |

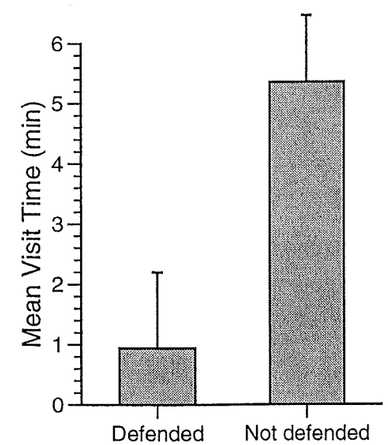


FIG. 1. Mean time spent foraging in *Fuschia* patch by visiting hummingbirds.

TABLE 2. ANOVA model for fuchsia reproductive success that includes defense and patch nested within defense, with defense and patch both treated as significant effects.

| | | Fruits/Inflorescence | |
|---|---|---|---|
| Source | df | MS | F |
| Defended | 1 | 8 | 0.01 |
| Patch(Defended) | 3 | 350 | 0.52 |
| Error | 95 | 669 | |

## DISCUSSION

There was no apparent effect of hummingbird territoriality on the reproductive success of fuchsia. It may be that fuchsia plants lack strong self-incompatibility (i.e., can reproduce with their own pollen equally well as with the pollen of another plant). Another explanation is that because there were several individual fuchsia plants within each of our patches, cross pollination among patches was not critical to the plants' reproductive success. In undefended patches, visiting birds may facilitate a similar level of cross-pollination within the patch as territorial birds in defended patches.

We cannot judge how much pollen was carried into defended patches. In defended patches, the mate of the territorial male may move among patches and facilitate some outcrossing among patches. Furthermore, volcano hummingbirds, unlike other visiting species, often poached nectar along the edges of defended patches and thus may have contributed pollen from other fuchsia patches. Perhaps their small size made them less noticeable or more tolerable to fiery-throated defenders. Visiting birds could be less important for pollination than we had hypothesized if they were frequently carrying pollen from another plant species when they arrived at a fuchsia patch.

Our hypothesis rested on the assumption that fuchsia reproduction was limited by pollinators in general and hummingbird pollinators in particular. The considerable variation in fruit production among inflorescences is consistent with pollinator limitations, but pollen addition experiments are needed to separate the effects on plant reproduction of pollen limitations vs. carbohydrate and nutrient limitations. Butterflies, bees, and frugivores regularly visited all patches, so their effect on pollination and fruit numbers were presumably the same in defended and undefended patches. However, if insects pollinate a large number of fuchsia flowers, the potential effects of hummingbird territoriality on the reproductive success of fuchsia would be less important and more difficult to detect.

Both of our defended patches were occupied by fiery-throated hummingbirds. At other times of year, volcanoes, gray-tailed mountain-gems, and magnificents may defend patches of fuchsia. To our knowledge, nothing is known about the effects of territorial behavior in these species on the reproductive success of fuchsia. Although no hummingbird species specializes on *Fuchsia arborescens* , it would be interesting to examine the effects of a specialist hummingbird's territoriality on its host species, such as the green violet-ear hummingbird (*Collibri thalassinus*) and *Centropogon*.

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