frequently. When all other inflorescences were eliminated, the pollinators visited the higher inflorescences more. Thus, size (in this case the majority of the inflorescences on the plant) and height are interrelated, and perhaps both contribute to reproductive strategy for *Senecio*.

Results suggest that contemporary selection is not favoring further increases in inflorescence size because larger inflorescences did not receive enough additional insect visitors to balance the larger number of florets that require pollination. Instead, inflorescence size appears to currently be under stabilizing selection. This conclusion assumes that each insect visitor pollinated an equal number of florets per visit, irrespective of inflorescence size. If instead, average visitors stay longer and pollinate more florets in larger inflorescences, then selection might be favoring further increases in inflorescence size. Future studies are required to discriminate among these alternative interpretations.

Our sexual selection hypothesis was supported, but alternative hypotheses remain. The sexual selection hypothesis as we have developed it would be weakened by finding cases of gigantism in plants that are wind pollinated. *Alnus*, a wind-pollinated giant also found at Cuerici Biological Reserve, might be an example of gigantism selected for through a mechanism other than sexual selection. In addition, *Senecio* sp. is wind dispersed and a higher inflorescence might have higher dispersal success. It is possible that wind dispersal and pollinator preference are working in conjunction to select for larger plants. This hypothesis would be weakened by examples of gigantism in species that employ biotic seed dispersal agents. Gigantism may also be a result of abiotic conditions unique to Cerro de la Muerte such as increased soil nutrients or light availability. Finally, it is possible that gigantism is not the result of selection, but rather a neutral trait that has persisted through time.

Although sexual selection mediated by pollinators may be a mechanism by which *Senecio* sp. has evolved, it would be interesting to examine the distribution of other giants with respect to potential pollinator limitations. Clearly, pollinator limitation by itself does not necessarily lead to gigantism, as in the Arctic tundra where pollinator limitations are frequent but plant stature is greatly reduced. Our study suggests that sexual selection via insect visitation choices may lead to gigantism in the Costa Rican cerro, but gigantism can still evolve in suitable abiotic environments.

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EFFECTS OF FOOD ABUNDANCE ON TERRITORIAL DEFENSE IN THE FIERY-THROATED HUMMINGBIRD

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Abstract. Male fiery-throated hummingbirds (*Panterpe insignis*) defend their territories using a loud, high-pitched, double chip. Birds occupying territories with high densities of flowers spend more time chipping, defend smaller territories, and receive more visits by females. They also spend relatively more time chipping in the morning, when nectar production is the greatest and interspecific competitors are most abundant. Inflorescence density apparently affects hummingbird territoriality and is positively correlated with breeding success.

Key Words: Fiery-throated hummingbird, Panterpe insignis, *territory quality, territorial defense, intraspecific competition*

Introduction

Territorial defense is very common among bird species, presumably because of benefits in ensuring food resources and breeding opportunities. For the fiery-throated hummingbird (*Panterpe insignis*), territory quality is determined mainly by the abundance of three flowers that it visits for nectar rewards: *Fuchsia* sp., *Bomarea* sp., and *Tropaeolum* sp. (Stiles 1983). We hypothesized that flower density is a limiting factor that determines the amount of male chipping, territory size, and number of visits by females. Specifically, we predicted that: (1) a higher quality habitat will require more territorial chipping than a lower quality habitat because it will attract more competitors; (2) birds will chip more frequently in the morning, when nectar production is greatest, than in the afternoon (Holmes, pers. comm.); (3) birds in habitats with high flower densities will hold smaller territories than those in habitats with low flower densities; and (4) females, which harvest nectar from male territories (Stiles 1983), will be more frequent in territories with high flower densities.

Methods

To test these hypotheses, we chose five fiery-throated hummingbird males to observe in Cuerici Biological Preserve, Costa Rica. On 25 January 1996, we followed all birds by sight and sound to map their territories and ranked the territories from one to five according to size, with one being the smallest. The resource quality of each territory was assessed by estimating the relative densities of three flowers that they were visiting for nectar: *Fuchsia* sp., *Bomarea* sp., and *Tropaeolum* sp., and ranking them from one to five (with one being the highest flower density).

On 26 January 1996, we measured total chipping time for each bird in the morning and afternoon. From 0700 - 1000 and again from 1400 - 1700, we timed each bird's total chipping for 30 minutes. Chipping was considered continuous when breaks between chips lasted less than one second in duration. While chipping time was being assessed, one of us recorded other activities in the territory such as countercalling, interspecific and intraspecific interactions, the presence of females, and general movement and activity of the male hummingbird.

We analyzed total chipping time between territories as well as those observed at different times of day using an analysis of covariance and a paired t-test, respectively. We tested for correlations between territory size and flower density and between number of female visits and flower density with Spearman's rank tests.

Results

Territories of male fiery-throated hummingbirds varied in size and flower density. Territory size was inversely correlated with flower density; i.e., the smallest territories were characterized by the highest densities of preferred food sources ($r = -1.00$, $P < 0.0001$; Fig. 1). The number of female visits was greatest in territories with high flower density ($r = -0.9747$, $P < 0.005$; Fig. 1). Resident males chipped for a greater percentage of time in the small, flower-rich territories than in the larger, flower-poor territories ($F = 7.82$, $df = 4$, $P < 0.001$). Across the full

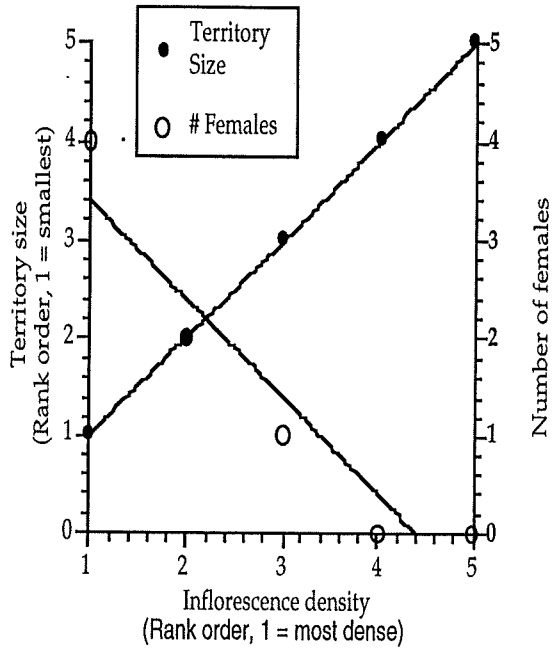

Figure 1. Territory size and number of females as a function of inflorescence density at Cuerici Biological Preserve, Costa Rica.

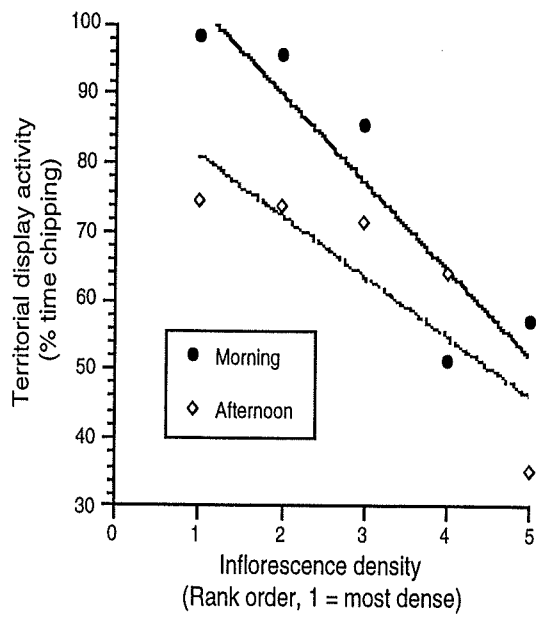

Fig. 2. Territorial display activity by fiery-throated hummingbirds as a function of inflorescence density at Cuerici Biological Preserve, Costa Rica.

range of flower densities, males spent approxi mately 20% less time chipping in the afternoon than in the morning ($t = -7.09$, $df = 4$, $P = 0.002$; Fig. 2). In addition, interspecific interactions appeared to be more frequent on high-quality than on low-quality territories, although we were unable to quantify this.

Discussion

Fiery-throated hummingbirds are a highly territorial species whose breeding success depends on the quality of their territories, as measured by flower density (Stiles 1983). At Cuerici Biological Preserve, males with flower-rich territories spend more time chipping than males with flower-poor territories, perhaps because the high flower density allows the males to ingest adequate nectar in less time and to call for more time than males on low quality territories. Additionally, males with flower-rich territories might spend more time chipping due to increased interspecific and intraspecific competition.

Temporal variation in chipping (Fig. 2) might be due to diurnal variation in territory quality. Because daytime nectar production is highest in the morning, males may spend more time defending nectar-rich flowers during the morning than after nectar resources are depleted. Greater defenses could also be a reflection of typical weather conditions in which clear morning skies often give way to heavy clouds and afternoon mists. Perhaps, both territory holders and potential competitors are more active in the morning than in the afternoon when energy expenditures might be greater due to wet, cool conditions.

Flower density apparently also affects the presence of females, intraspecific competitors, and interspecific competitors. Females were only observed in the three highest quality territories. Similarly, interspecific competitors such as the slaty flower piercer (Diglossa plumbea) and the volcano hummingbird (Selasphorus flammula) were more abundant in the two most flower-rich territories. Nevertheless, the male hummingbird's defenses indicate that despite additional interspecific competition, it may be beneficial for males to defend the best territories due to increased mate attraction.

Our results support the hypothesis that territory quality affects chipping rates, territory size, and number of visits by females. The population dynamics of fiery-throated hummingbirds appear to be heavily resource driven, and future studies might center on the hummingbird's susceptibility to decreased resource abundance. This might aid the preservation of this species by highlighting the extent to which flower resources dictate fiery-throated hummingbird populations.

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