PATTERNS IN NECTAR PRODUCTION AMONG PATCHES OF HUMMINGBIRD-POLLINATED FLOWERS

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Abstract: Hummingbird pollinators tend to visit large patches of flowers more frequently than small patches. This would be an optimal foraging strategy that reduces travel time between flowers, assuming nectar production per flower is the same in small and large patches. However, variation in nectar per flower, as a function of patch size, may offer an additional explanation for high hummingbird visitation at larger patches. Here, we test the hypothesis that nectar production per flower is greater in patches with many flowers than in those with few. Contrary to our hypothesis, we found that flowers in small patches had greater nectar production, both in terms of proportion of nectar-producing flowers and amount of nectar produced per flower, than flowers in large patches. We propose that patches with few flowers may produce more nectar per flower to maximize hummingbird visits, and consequently, cross-pollination.

Key words: cross-pollination, Gesneriaceae, *hummingbird pollinators, optimal foraging*

INTRODUCTION

Optimal foraging theory predicts that foragers should spend more time in larger and denser resource patches to maximize net energy gain by minimizing travel distance (Begon et al. 1990). At Cuerici Biological Station at Cerro de la Muerte, Costa Rica, patches containing more flowers receive more hummingbird visits per patch than patches with fewer flowers (Biedron et al. 2003). The authors attributed these patterns to a hummingbird foraging strategy that both reduces travel time between flowers and allows access to the greatest number of resource-providing flowers. However, the pattern could also be caused by greater resource availability per flower in large patches.

Several mechanisms could potentially cause higher per-flower nectar production by plants with more flowers. We define patches as individual plants separated from conspecifics by at least 0.5 m. In a patch, the number of flowers may be positively correlated with the status of the plant (i.e., water and nutrient access, photosynthetic potential). These patches with greater access to water and nutrients or greater photosynthetic potential may also produce more nectar per flower. The hummingbird visitation rate may increase with increasing amounts of flower nectar. Therefore, the relationship between number of flowers in a patch and hummingbird visitation rate may be correlated, but not causally related.

In this study, we hypothesized that flowers in large patches (i.e., on plants with many flowers), which seem to be preferred by hummingbird pollinators, would have greater nectar resources than flowers in small patches (i.e., plants with few flow-

ers). We predicted that proportionally more flowers would produce nectar in large patches than in small patches, and that flowers in large patches would produce more nectar per flower than flowers in small patches.

METHODS

We selected patches of a shrub containing varying numbers of red, tubular flowers (family Gesneriaceae), along the trail east of the small farm near the Cuerici Biological Station, Cerro de la Muerte, Costa Rica. At Cuerici, this shrub is typically 1-2 m in height, and is found in second-growth habitat. Each patch we sampled consisted of a single plant, and was separated by at least 0.5 m from the nearest conspecific. Nectar volume was measured by probing the base of the corolla with a 5 μl glass capillary tube.

From 1530 to 1800 on 28 January 2005 we removed nectar from 10 individual flowers in each of 10 patches. We then covered these flowers with mesh tied at the base of the stem, to prevent feeding by hummingbirds. We assessed nectar volume in five of the covered flowers between 0530 and 0630 on the next morning and in the remaining five between 1030 and 1200 later that morning.

Linear regressions of nectar volume on the number of flowers in each patch were performed using JMP 4.0.0. Data met or were transformed to meet the assumptions of parametric tests. For regressions of average nectar production on the number of flowers in a patch, we log-transformed the x-axis to linearize the relationship.

RESULTS

We found that average nectar production per flower declined as the total number of flowers in a patch increased, for both the overnight period ($r^2 = 0.11$, df = 48, P = 0.02; Fig. 1a) and the overnight + morning period ($r^2 = 0.09$, df = 47, P = 0.03; Fig. 1b). The mean volume of nectar per nectar-producing flower (i.e. excluding flowers that produced no nectar) was greater for flowers in small patches than in large patches, although this result was not statistically significant ($r^2 = 0.39$, df = 6, P = 0.10; Fig. 2). Finally, small patches had a greater proportion of nectar-producing flowers than large patches ($r^2 = 0.77$, df = 6, P = 0.004; Fig. 3).

DISCUSSION

Contrary to our hypothesis, we found that flowers in small patches had greater nectar production, both in terms of proportion of nectar-producing flowers and amount of nectar produced per flower, than flowers in large patches. Biedron et al. (2003) observed more hummingbird visits to large patches than small patches, but the patterns we observed would tend to increase hummingbird visitation to flowers in small patches. We infer that the pattern in hummingbird visitation reported by Biedron et al. probably results primarily from the numbers of flowers per patch.

Because they receive fewer hummingbird visits, flowers in small patches may have a lower rate of cross-pollination than flowers of large patches. Pollination is one of the most important components

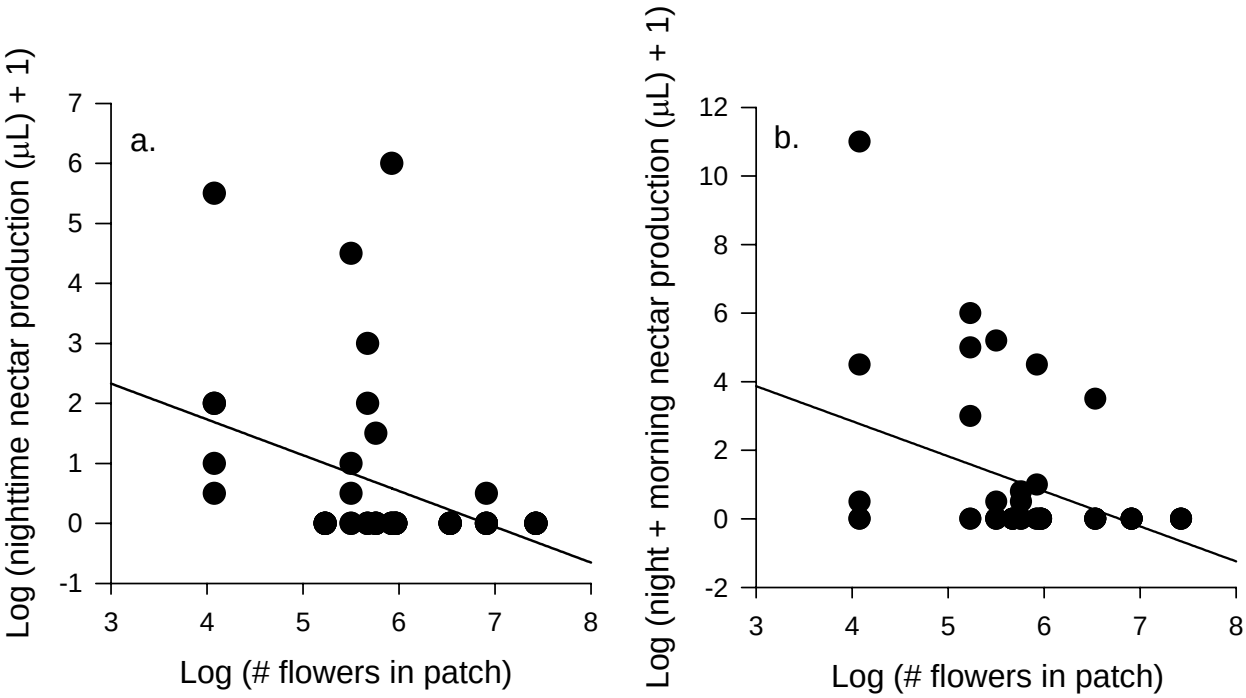

Figure 1. (a) Average night-time nectar production per flower and (b) average night and morning nectar production per flower decreased with increasing number of flowers in a patch (a: y = -0.0004x + 0.47, b: y = -0.0005x + 0.56). The x-axis was log-transformed to linearize the relationships. Lines were fit by least squares linear regression.

of fitness in flowering plants, and nectar rewards are provided to hummingbirds to manipulate the dispersal of pollen. We suggest that flowers of small patches may compensate for a lower hummingbird visitation rate by providing higher nectar rewards to encourage pollinator visits. Offering higher nectar rewards can increase the time spent or the return rate of hummingbird pollinators, but cannot initially attract hummingbirds because they cannot detect nectar prior to probing (Shannon et al. 2000). However, the hummingbird species which feed on gesneriad flowers at Cerro de la Muerte, such as the Volcano Hummingbird, *Selasphorus flammula*, are known to be territorial, and thus may learn patterns in nectar availability among plants in their territory (Stiles and Skutch 1989). Our informal observations of high hummingbird re-visitation of flowers also suggest that the birds can learn to feed at flowers that produce large quantities of nectar. Therefore, high nectar production may be an effective strategy to increase cross-pollination rates for plants with few flowers.

The exponential relationship between nectar production and number of flowers in a patch suggests that, as patch size increases, nectar production per flower decreases at a diminishing rate. Experimentally establishing the relationship between per-flower nectar availability or proportion of nectar-producing flowers in a patch and hummingbird visitation rate would strengthen the conclusions of this research. Furthermore, a future experiment could examine patches of flowers separated by a greater distance than 0.5 m,

since the presence of neighboring patches of varying size may have a greater influence on the energy consumption and consequent foraging behavior of wide-ranging hummingbird foragers. An assessment of leaf area to flower ratio in large and small patches would shed light on differential carbon investment strategies by demonstrating whether small patches fix more carbon to devote to nectar production, or simply devote a greater proportion of fixed carbon to nectar than larger patches.

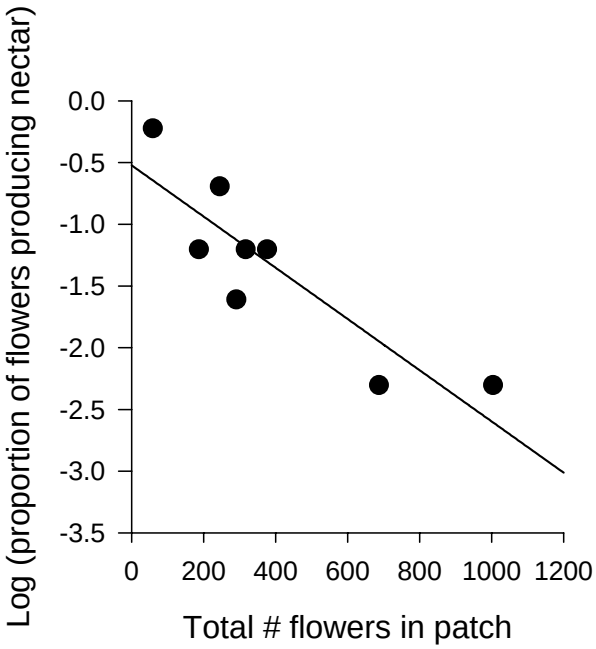

Figure 3. Proportion of nectar-producing flowers decreased with increasing number of flowers in a patch (y = -0.002x – 0.52). Line was fit by least squares regression.

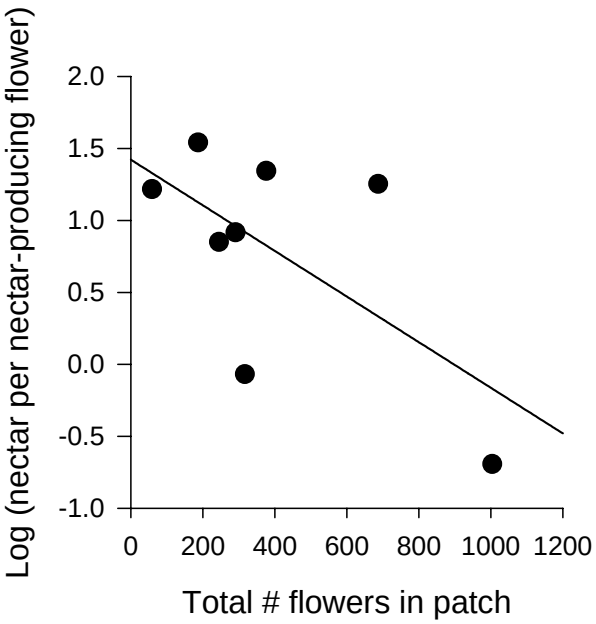

Figure 2. Average amount of nectar produced per nectar-producing flower decreased with increasing number of flowers in a patch (y = -0.002x + 1.42). Line was fit by least squares regression.

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