persistence of the less common white morph in the population. This inference is based on the assumption that higher visitation rate by pollinators is correlated with reproductive success. We conclude that frequency-dependent selection is probably operating in this system, through pollinator choice.

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Influence of *Fuchsia arborescens* patch size on hummingbird visitation and territorial defense

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Abstract: According to optimal foraging theory, organisms forage in dense areas of high quality food to minimize travel distance and maximize the rate of net energy intake. Some hummingbird species at the Cuerici Preserve, Costa Rica may invest energy in defending patches with high quality and quantity of resources. We observed hummingbird visits to *Fuchsia arborescens* patches. We tested the hypothesis that as the number of inflorescences in a patch increases, the number of pollinator visits per unit time, as well as territorial defense, would increase. Our results supported the first prediction, but not the second. Over the course of a day, the number of hummingbird visits to patches of low and high densities should become more similar as resources in the most preferred patches are depleted. This hypothesis remains to be tested.

Key Words: optimal foraging theory, resource density, territoriality

Introduction

Optimal foraging theory predicts which feeding strategies an organism will use under various conditions, based on the assumption that natural selection favors foraging strategies that maximize an organism's rate of energy intake (Begon et al. 1990). An optimal forager will choose to feed in patches providing a high quantity and quality of resources. Time spent traveling between feeding sites should be minimized and net energy gain maximized. Larger patches, defined as local areas with more inflorescences, should therefore attract more hummingbird visits. A previous study has shown that resource patch size is positively correlated with the mean number of visits by non-resident territorial hummingbirds (Preuss 1993). In addition, it could be advantageous for hummingbirds to defend large patches because they provide a substantial resource.

Fuchsia arborescens is a flowering shrub pollinated by Fiery-throated Hummingbirds, Volcano Hummingbirds, and Gray-tailed Mountain Gems, all of which are territorial species (Dickenson 1998, Stiles and Skutch 1989). These hummingbirds maintain territories containing *F. arborescens* to secure food resources and attract mates. Territories in the tropics are relatively stable over time, so securing a food resource may be vital for reproductive success. Individuals should invest more energy in defending large patches because they are higher quality food sources than small patches.

We predicted that both the number of hummingbird visits per hour and the number of territorial chases per hour would increase with the number and density of inflorescences per patch.

Methods

Between the hours of 07:30 and 10:30 on 28 - 29 January 2003, we observed hummingbird visits to patches of *Fuchsia arborescens* near the Cuerici Biological Station in Cerro de la Muerte, Costa Rica. We chose a range of patch sizes based on the number of inflorescences present. We defined a patch as a cluster of *F. arborescens* inflorescences that was distinctly separated from neighboring clusters. For each patch, we counted inflorescences, estimated the surface area of the shrub facing the observer, and calculated density of inflorescences.

We observed each patch for 30 minutes and recorded the number of hummingbird visits and the number of chases. A visit was defined as at least one hummingbird probe to a flower before leaving the patch, and a chase was defined as one hummingbird aggressively evicting another from the patch. Because we could not distinguish

between resident and non-resident hummingbirds, visits by both were recorded.

Results

We observed 34 *F. arborescens* patches ranging in number of inflorescences from 10 to 400. The number of hummingbird visits per patch ranged from 0 to 10, and the number of chases per patch varied from 0 to 8. We found that the number of inflorescences per patch and the number of visits to the patch per hour were positively correlated (Fig. 1; Spearman's Rho = 0.57, P = 0.01). However, there was no correlation between the density of inflorescences and the number of visits per hour (Spearman's Rho = 0.25, P = 0.31), between number of inflorescences and number of chases per hour (Spearman's Rho = 0.11, P = 0.54) or between density of inflorescences and number of chases per hour (Spearman's Rho = -0.04, P = 0.84).

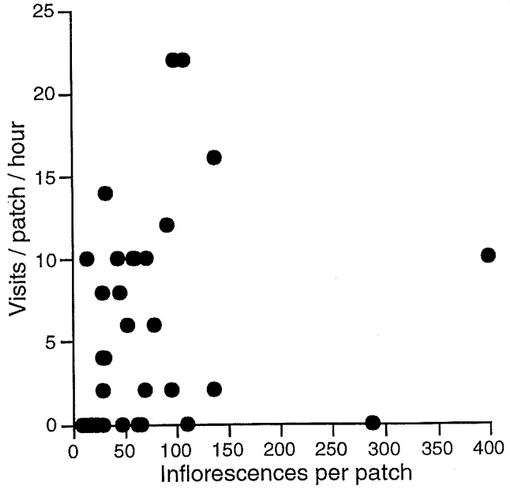

FIG. 1. Patch visitation rate by hummingbirds was positively correlated with number of inflorescences per patch of *Fuchsia arborescens* (Spearman's Rho = 0.57, P = 0.01). Patches (n = 34) were near the Cuerici Biological Station in Cerro de la Meurte, Cosa Rica.

Discussion

The frequency of hummingbird visits increased with the number of inflorescences per patch. This suggests that hummingbirds are attracted to larger patches with greater food resources, in accordance with our predictions. The number of hummingbird visits per patch may also be affected by resource quality, such as volume and sugar concentration of nectar (Trombulak 1990), which we did not account for in our study.

Patch size was not significantly correlated with chasing behavior. Because our patch selection was limited by our field of vision from one point on the ground, our patches probably did not represent entire hummingbird territories. Therefore, the chase rates we observed might reflect defense of a larger territory than the patch under observation. In that case, we would not expect the number of chases to differ significantly between patches.

Furthermore, number of chases may not be a reliable indicator of the vigor of territorial defense. Vocalizations, for example, may deter intruders prior to a physical intrusion. Also, few chases may result from few invaders rather than lack of territorial defense behavior. If we had been able to distinguish accurately between resident and non-resident birds, we could have more effectively assessed territorial defense. It is also possible that territorial aggression in hummingbirds varies throughout the year due to changes in food resources and breeding season (Begon 1990).

Our results indicate that foragers are attracted to dense resource patches. However, these are likely to become depleted over time. Foragers may then move to less dense patches that have not yet been depleted. Over the course of a day, the number of hummingbird visits to patches of low and high densities should become more similar, as resources in the most preferred patches are depleted. This hypothesis remains to be tested.

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