TEMPORAL PATTERNS IN ABUNDANCE OF GENERALIST BUTTERFLY SPECIES

BRENDA M. WHITED AND JILL L. HARRIS

Abstract: Costa Rica has high butterfly biodiversity with over 500 species. Many of these butterflies are generalists that coexist on the same nectar resources. Temporal niche partitioning may explain this high biodiversity. We investigated diel patterns of abundance of several generalist butterfly species feeding on a localized nectar source. Butterfly peak abundance did not occur at different times of day for different species, suggesting that temporal niche partitioning is not a factor maintaining biodiversity. Rather, butterfly biodiversity may be explained by other mechanisms, e.g. spatial partitioning. Our data suggest that other factors, including time of day and temperature appear to drive general patterns in total butterfly abundance.

Key words: Anartia fatima, *biodiversity,* Heliconius erato petiverana, *Hesperiidae,* Phoebis argante, *temporal niche partitioning*

INTRODUCTION

One of the great puzzles of the tropics is the high biodiversity, and ecologists have proposed many theories to explain this diversity. One leading theory is that tropical organisms divide resources into many narrow niches, allowing many species to coexist.

In Costa Rica alone, there are over 500 species of butterflies (DeVries, 1987). Most of these butterflies occupy the same nectar-feeding niche as either specialist feeders on specific nectar-producing plants or as generalists. The distributions of many species overlap, such as the several hundred species that can be found at La Selva (Janzen 1983). How can so many species coexist as generalists on the same resource?

Janzen (1983) notes that in many areas, different butterfly species have peak abundances on popular plants at different times of the day. This variance in time of peak abundance may be an example of temporal niche partitioning in a common nectar resource, which allows for high biodiversity of butterflies.

To determine if generalist butterflies temporally partition a nectar resource, we studied the temporal patterns of butterfly abundances on a localized nectar resource (Verbenaceae: *Stachytarpheta frantzii*). *S. frantzii* supports a number of taxa, including hummingbirds, bananaquits, Hymenopterans, Dipterans, and butterflies (pers. obs.). If butterflies partition resources temporally on *S. frantzii*, then we expect to observe peaks in species abundances at different times of day. Conversely, if we find no peaks in abundance or if all species peak at the same time, factors other than niche partitioning may drive butterfly abundance, and other mechanisms not tested here may maintain butterfly diversity.

METHODS

We observed a patch of 26 *S. frantzii* stems on 14 - 16 February 2004, at Estación Biológica La Selva, Costa Rica. Stems had approximately 85 inflorescences, with three to twelve flowers per inflorescence. From 0800 - 1600, we conducted hourly censuses of butterfly abundances, noting counts of individuals of each species present and ambient and black body temperature as a measurement of sun intensity. Black body measurements were taken with a BAT-12 thermocouple inside a piece of dark foam attached to a *S. frantzii* branch.

We measured nectar production over the course of one day. We bagged eight inflorescences at 0800 on 14 February. Every three hours

until 1700, we used 20 μL micropipets to measure nectar volume of each flower within each inflorescence.

We determined best fit models with lack of fit analyses. Linear fit models were rejected when the lack of fit P < 0.05 and second order polynomial models were accepted.

RESULTS

We observed ten different species of butterflies on the *S. frantzii* plants. However, six of these species were observed less than twice daily and were excluded from analysis. The most common species were *Anartia fatima*, *Phoebis argante, Heliconius erato petiverana*, and long-tailed skippers (Hesperiidae). Abundances ranged from zero individuals of a species to as many as eight (long-tailed skippers observed at 0900, Fig. 1B) during any ten minute census. All species were generalist feeders that utilize many different plant species as a source of nectar

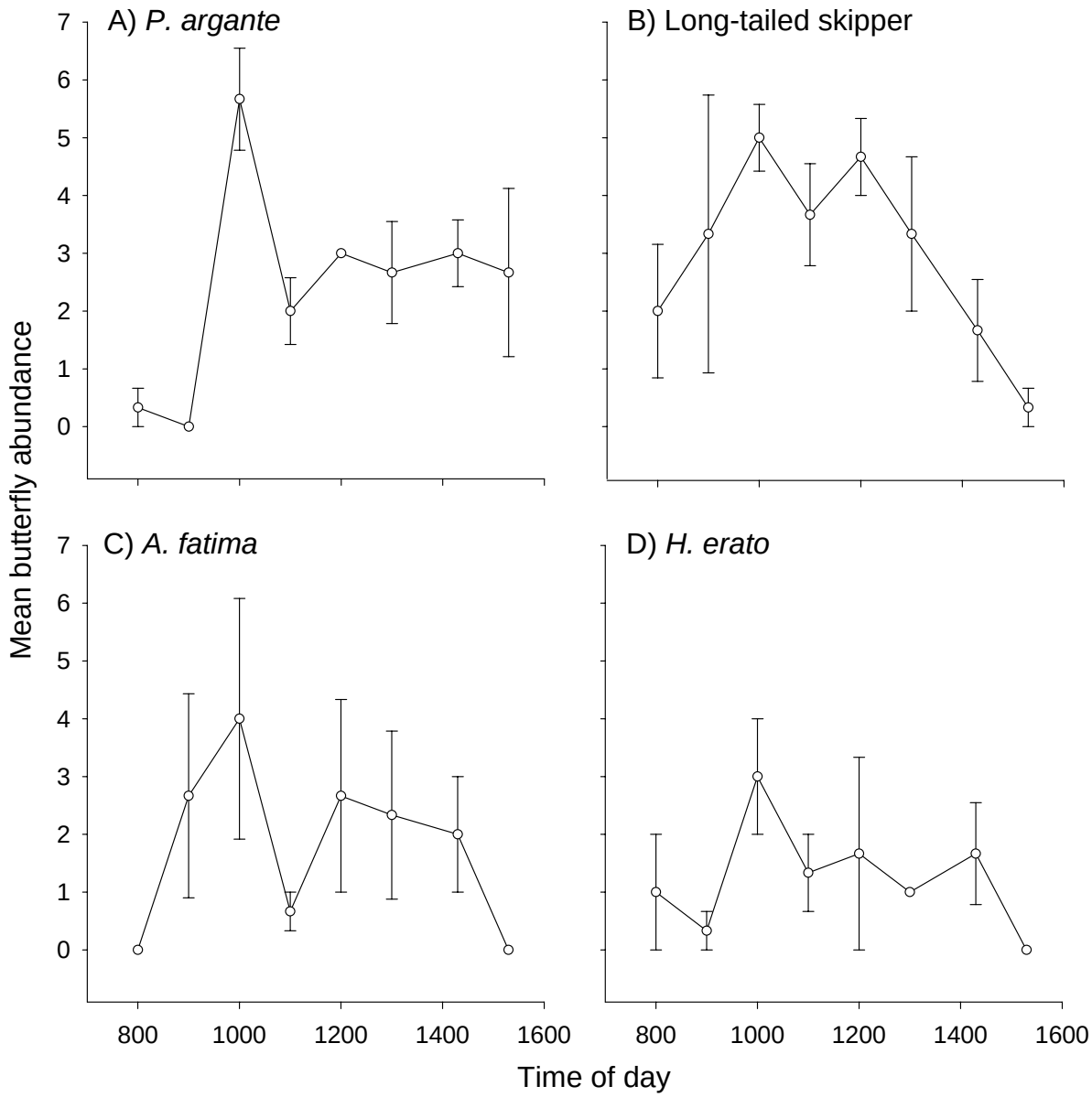

Figure 1. Mean abundance ± SE of each of four common butterfly species over the course of the day. Regression analyses showed no significant fit for *P. argante* (A), *A. fatima* (C), or *H. erato* (D). For long-tailed skipper abundance (B), we cannot reject a linear model based on lack of fit analysis (P = 0.21), though the fit was not significant (r^2 = 0.095, P = 0.14). We accept the second-order polynomial because the model is a significant fit (r^2 = 0.39, P = 0.005).

(DeVries 1987). *H. erato* may also consume pollen from flowers in addition to nectar (DeVries 1987).

Peak abundances of each species tended to occur at the same time of day (Fig. 1). *P. argante* abundance was highest at 1000 (ANOVA, $F_{7,23} = 5.59$, $P = 0.002$; Fig. 1A). Long-tailed skipper abundance tended to be highest at 1000 ($F_{7,23} = 1.75$, $P = 0.17$; Fig. 1B) but the mean abundance was not significantly different than abundances at other times. However, regression analysis of long-tailed skipper abundance showed a significant relationship between time of day and abundance, with peak abundances between 1000 - 1200 ($r^2 = 0.39$, $P = 0.005$; Fig. 1B). Highest abundances of *A. fatima* and *H. erato* occurred at 1000 but were not significantly different than abundances at other times (ANOVA, *A. fatima*: $F_{7,23} = 1.23$, $P = 0.34$; Fig. 1C and *H. erato*: $F_{7,23} = 1.11$, $P = 0.40$; Fig. 1D). There was a single peak in total abundance between 1000 - 1200 ($r^2 = 0.35$, $P = 0.01$; Fig. 2).

Rainfall rendered the black body measurements inaccurate; the foam was soaked, and evaporation cooled the black body to temperatures equal to or below ambient temperatures. However, there was a significant relationship between ambient temperature and time of day, with highest temperatures peaking at approximately 1300 ($r^2 = 0.70$, $P < 0.0001$; Fig. 3). Butterfly abundance varied with temperature, with peak abundance occurring at 28 - 30°C ($r^2 = 0.27$, $P = 0.04$; Fig. 4). However, temperature does not completely explain butterfly abundance since this optimum temperature occurs twice daily (from 1000 - 1200 and again from 1500 - 1600) and butterfly peak abundance occurs only once, between 1000 - 1200.

We were unable to extract any nectar with our methods thus we cannot report any data on diel patterns of nectar production.

Discussion

Peak abundances of species did not occur at different times of day. Thus, butterfly species that utilize *S. frantzii* do not exhibit temporal niche partitioning and may partition this resource in other ways in order to maintain high biodiversity. For example, there may be some spatial partitioning such that different butterfly species feed on *S. frantzii* flowers at different

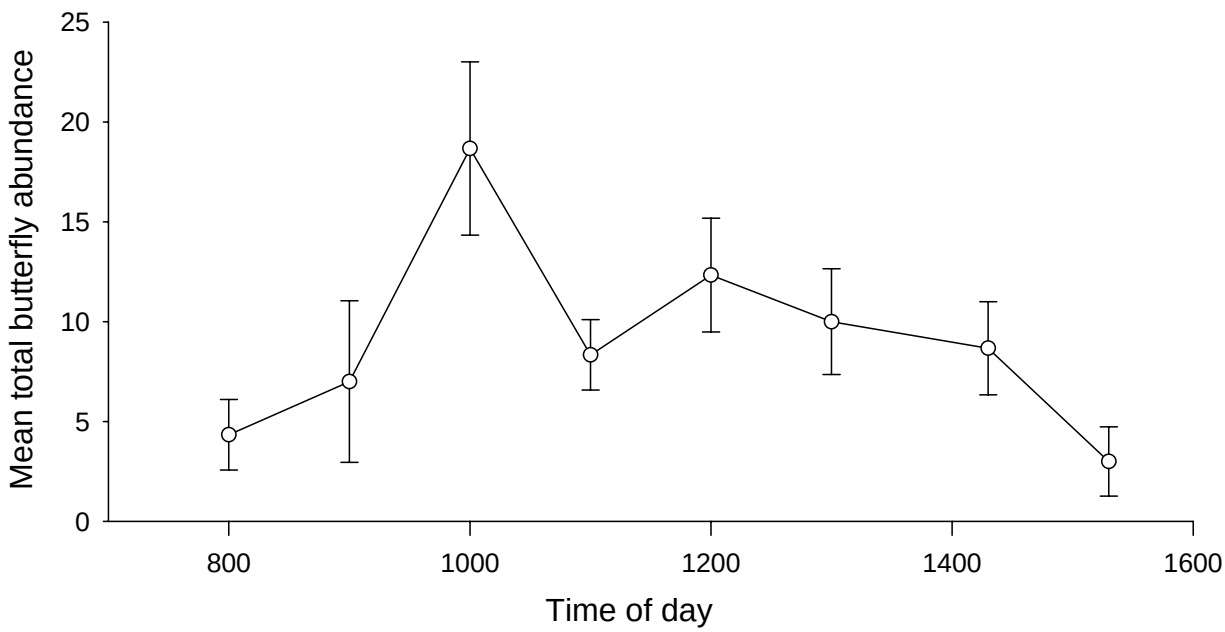

Figure 2. Total mean abundance ± SE over the course of the day. Means were obtained from abundance sampling over three consecutive days. Linear model was rejected (lack of fit: P = 0.03) and second order polynomial accepted (P = 0.20).

heights from the ground. Butterflies may also feed on different parts of the flower, since it is suggested that *H. erato* feeds on pollen. It is also possible that while many butterfly species are generalist feeders, they can maintain high diversity by specializing on specific host plants for larvae.

Although patterns in abundance did not occur as we predicted, there was a general pattern, with abundance of each common species and total abundance peaking at 1000. Time of day and temperature both appear to be significant factors in patterns of abundance. However, since optimal temperature occurs twice daily, and butterfly abundance only peaked once, time of day appears to have a more significant effect on abundance than temperature. It is also possible that high abundance of potential predators (e.g. insectivorous birds) occurs at the second daily optimal temperature, limiting butterfly activity. A diel pattern in nectar production may also determine butterfly abundance, with times of highest nectar production corresponding to peak abundances. Unfortunately, our methods of bagging flowers and extracting nectar with micropipets were unsuccessful, so we could not study this effect.

Temporal niche partitioning does not appear to explain the high butterfly biodiversity in the system that we studied. Yet the puzzle remains that over 500 species of butterflies coexist on the same nectar resource. Butterflies may partition niches in other ways not tested here, and future studies should investigate partitioning of multiple resources at different levels.

Literature Cited

DeVries, P. J. 1987. The Butterflies of Costa Rica. Princeton University Press: Princeton, NJ.

Janzen, D. H. 1983. Costa Rican Natural History. University of Chicago Press: Chicago, IL.