SYNCHRONOUS FRUITING IN *DIPTERYX PANAMENSIS* AND THE RELATIVE ROLES OF SEED PREDATORS AND DISPERSERS

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Abstract: Dipteryx panamensis, a large emergent tree at La Selva biological station, displays temporally synchronous fruiting among trees. The relative roles of seed predators and dispersers likely influence the spatial scale at which synchronous fruiting occurs. We evaluated the relative roles of fruit and seed consumers, as well as spatial patterns of fruiting and non-fruiting trees, with the hypothesis that the scale of synchronous fruiting would reflect the identity of the predominant seed predator or disperser. Almost all seed movement occurred on the ground, and synchronous fruiting occurred at the small scale of tree clusters, suggesting that ground seed consumers like rodents are the dominant drivers of patterns in the synchronous fruiting of *D. panamensis*.

Key words: agouti, emergent tree, great green macaw, masting

INTRODUCTION

Dipteryx panamensis (Fabaceae) produces very large seeds covered by a thick, hard shell and fleshy fruit, which attract a number of large vertebrate dispersers and seed predators. At La Selva Biological Station, many *Dipteryx* trees seem to fruit simultaneously, which could be an adaptive strategy in two ways: more seed dispersers could be attracted to a large patch of fruiting trees and/or mass fruit production could swamp seed predators.

The spatial scale of fruiting synchrony may be determined by the relative importance of different seed dispersers and predators (i.e., which animals have the greatest positive or negative impact on seed dispersal). If wide-ranging predators such as great green macaws (*Ara ambigua*) are the most important animal species in this system, then *Dipteryx* trees should display large-scale synchrony in order to swamp the macaws with an overabundance of seeds. Small-scale or no synchrony would be an ineffective strategy against macaws because the birds could easily locate small fruiting patches or lone individuals and would exploit those trees exclusively. However, if wide-ranging dispersers such as toucans or bats are the important species, then local *Dipteryx* trees should show little or no temporal synchrony in fruit production. Far-flying birds and bats would be able to locate lone trees (especially since most reproducing *Dipteryx* are very large emergents), so synchronous fruit production would not necessarily attract any more dispersers; in fact, providing too many seeds at once would reduce the number of dispersers per tree.

Terrestrial vertebrates, unlike animals consuming fruit and seeds in the canopy, can act as both dispersers and predators, mostly through the scatterhoarding behavior of such animals as agoutis (Guariguata et al. 2002). These and other rodents are capable of cracking the *Dipteryx* shell and eating the seed, but they also cache uneaten seeds (scatterhoarding), which can facilitate dispersal. If these terrestrial animals, which are not as far-ranging as birds and bats, are most important for *Dipteryx*, then the trees should display small-scale synchrony. This strategy will both attract larger numbers of potential terrestrial dispersers and induce more scatterhoarding behavior (Guariguata et al. 2002), because the animals would have *Dipteryx* seeds only during a limited time each year. Large-scale synchrony would be less effective in this case because dispersers would be swamped

and would not be attracted to particular trees; no synchrony would be ineffective at attracting dispersers and inducing scatterhoarding behavior.

To test alternative hypotheses regarding the seed dispersal strategies of *Dipteryx*, we examined the distribution of fruiting and non-fruiting *Dipteryx* in the La Selva forest and observed the prevalence and activities of different types of seed dispersers and predators. We hypothesized that the spatial scale of fruiting synchrony would be determined by the identity of the major disperser or predator, as predicted above.

METHODS

To determine spatial distribution and fruiting synchrony of *Dipteryx* trees at La Selva, we haphazardly walked trails (primarily CCC, CCL, SUR, SOR, STR, and LOC) and recorded the location and fruiting state of all large *Dipteryx* seen. We spent a total of 20 hours observing fruiting trees for the presence of frugivorous animals (both seed dispersers and predators). For all animals seen, we recorded time spent at the tree, and made notes on foraging behavior, including number of fruits or seeds consumed.

At two fruiting trees, we recorded the number of cracked nuts, whole nuts, chewed fruits, and intact fruits in 2 x 2 m plots located every 5 m along 30 m transects (four at one tree, three at the other) beginning at the base of each tree. On each transect, we also noted the distance of the canopy edge from the base of the trunk. At these same two trees, we marked all fallen fruits in four 3 x 3 m plots located haphazardly in areas of high fruit density underneath the canopy, and recorded the number of chewed fruits and intact fruits in each plot. After 72 hours for Tree 1 and 48 hours for Tree 2, we returned to the plots and counted all marked fruits and new fruits in each plot.

RESULTS

Spatial distribution patterns of fruiting trees

We located 16 fruiting *Dipteryx* trees and 11 non-fruiting trees. Near the trails we surveyed, there appeared to be three local clusters of fruiting trees (i.e., at least three fruiting trees within a 200 m radius). We found some non-fruiting trees near but not within the fruiting clusters (Fig. 1).

Number and distribution of fallen fruits/seeds

Ground fruits were most dense directly underneath the canopy for both trees. Tree 1 showed higher density of fallen fruits underneath the outer canopy, while fruit density was highest near the trunk of Tree 2 (Table 1).

Observations of canopy feeding animals

We recorded two bird and two mammal species feeding on the fruits of *Dipteryx*. We observed one group of six great green macaws in a fruiting *Dipteryx* for 20 minutes, but did not directly witness any feeding events. The birds were eventually displaced by a group of spider monkeys (see below). Another group of four macaws was seen perched in the crown of a fruiting *Dipteryx* for 5 minutes; this group was not feeding. All other macaw sightings were of two to six birds flying over the canopy.

A group of eight spider monkeys fed actively for 30 minutes on *Dipteryx* fruit. Usually, they tasted a fruit briefly before dropping it, but occasionally (every 10 - 20 fruits) they spent several minutes eating a single fruit before dropping the intact seed. A group of six white-faced capuchins fed for 20 minutes in the same tree the following afternoon, displaying the same foraging behavior as the spider monkeys.

We observed two groups of six chestnut-mandibled toucans (*Ramphastos swainsonii*) in fruiting *Dipteryx* trees for 20 - 30 minutes each. The birds appeared mostly to be interacting so-

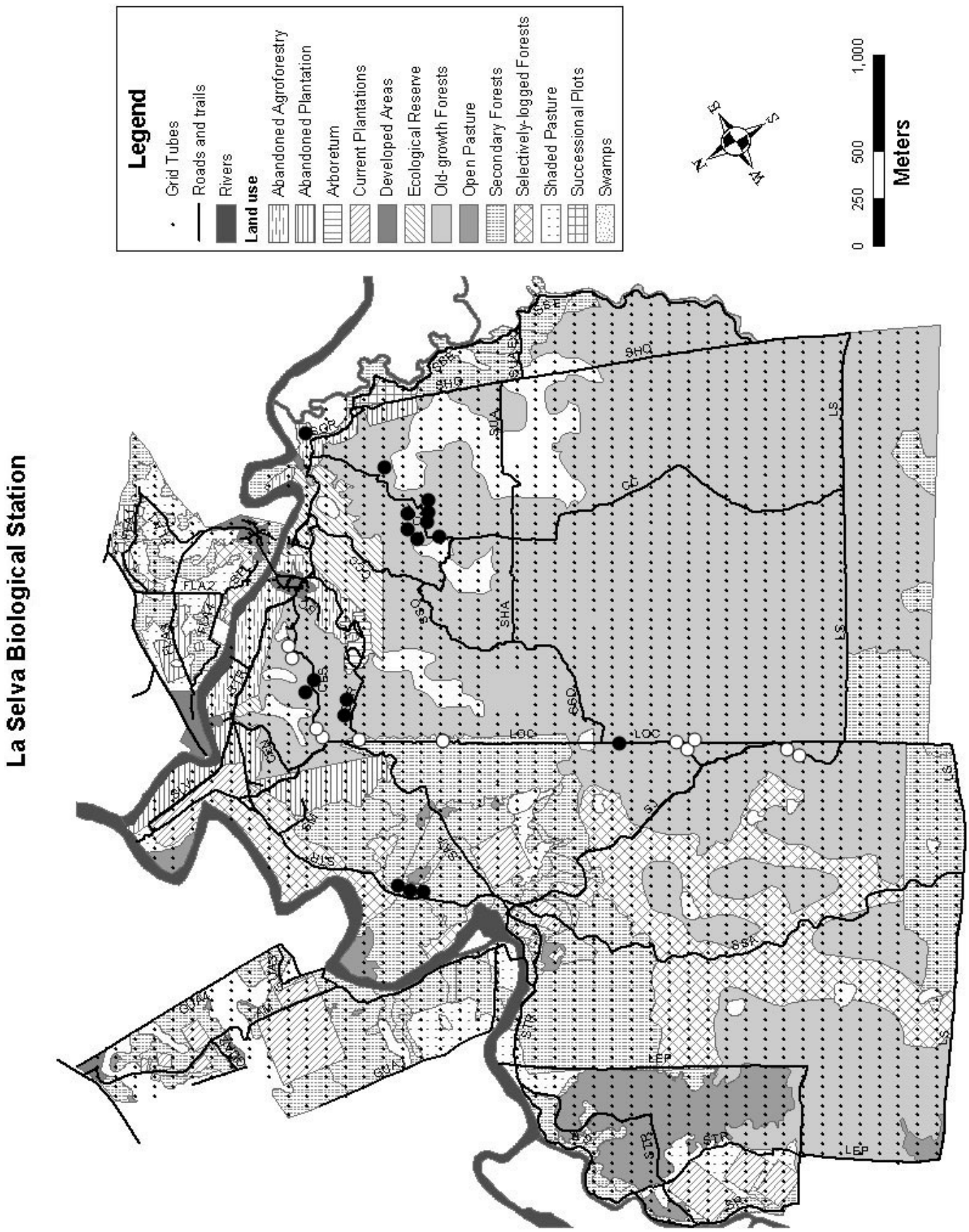

Figure 1. Distribution of fruiting (closed circles) and non-fruiting (open circles) trees of the species *Dipteryx panamensis* in La Selva Biological Station, Costa Rica.

cially and not feeding, though we did observe one toucan swallow a whole *Dipteryx* fruit. Other potential fruit-eating species observed in *Dipteryx* were two collared aracaris (*Pteroglossus torquatus*), three montezuma oropendolas (*Psarcolius montezuma*) and three parakeets (unidentified species), though none of these birds were feeding. Brief nocturnal observations (0140 - 0210) revealed a small, unidentified mammal species in the canopy and several bats flying overhead, none of which were seen to be feeding on fruits, though there was a high number of fruits dropping from the trees.

Table 1. Average number of fallen *Dipteryx* fruits/seeds found in 2 x 2 m plots at six distances from the trunk (n = 4 plots at each distance for Tree 1; n = 3 for Tree 2). Samples estimated fruit density within concentric rings of width 5 m. Average canopy radius for Tree 1 = 21.8 m, Tree 2 = 13.3 m.

Radial distance (m)	Average fruits/plot	Area of ring (m^2)	Calculated total fruits
Tree 1			
25 - 30	2	864	432
20 - 25	8	707	1413
15 - 20	29	550	4018
10 - 15	34	393	3287
5 - 10	16	236	942
0 - 5	14	79	274
		Total =	*10366*
Tree 2			
25 - 30	1	864	144
20 - 25	1	707	118
15 - 20	5	550	687
10 - 15	6	393	589
5 - 10	13	236	785
0 - 5	47	79	916
		Total =	*3239*

Marked seed plots

42 of 187 marked seeds (24%) had been removed from the plots after 72 hours at Tree 1; nine of 152 seeds (8%) had been removed after 48 hours at Tree 2. For both trees combined, 13% (39 of 302) of fruits that were initially chewed were removed, while 32% (12 of 37) of intact fruits were removed. Brief scans of the ground immediately surrounding the plots did not reveal any marked fruits.

DISCUSSION

Our results suggest small scale synchrony in the fruiting of *Dipteryx panamensis.* This is consistent with the hypothesis that ground dispersers like agoutis are driving the system. This was further supported by our high measure of ground seed removal (4 - 8% per day) relative to few observations of dispersal or predation by canopy feeders. However, this does not necessarily mean that other dispersers are unimportant. It is quite possible that dispersal by nocturnal canopy animals is common, but was overlooked due to limitations in our ability to observe them. Birds may be quite important even with few dispersal events, because the distances which they transport seeds is probably much larger than with ground dispersers and the likelihood of the seed being eaten after initial dispersal may be lower. The importance of dispersal by gravity should also not be ruled out completely. Low probability events such as ricocheting off high branches or rolling down hills may impact surprisingly many seeds given that there can be tens of thousands of fruits dropped by a tree (Table 1).

Since ground dispersers are focusing on the seed, it is curious that the seeds are surrounded by an edible flesh. Perhaps the fruit is there only to attract dispersers through the smell of the rotting fruit, or perhaps the fruit adds meaningfully to the rewards of animals

that eat the seed also. However, it is also possible that *Dipteryx* retains the fruit as an attractant to alternative dispersers. This would serve as a bet-hedging strategy, which may be especially important in such a long-lived species where abundances of specific dispersers or predators may vary drastically even within an individual tree's lifetime (> 1000 years). In fact, it is likely that the dispersal strategy of *Dipteryx* may have originally evolved in response to extinct megafauna (e.g., gomphotheres, Janzen 1982) and that some of the contemporary dispersers are attracted to the fruits only by accident.

Ideally, studies of seed dispersal should be carried out throughout the entire fruiting season and the fates of individual seeds determined. Also, all *Dipteryx* trees in a sector of forest should be mapped and monitored for multiple years to yield a detailed picture of spatial patterns in fruiting. Our short-term study suggests that, although multiple strategies may be important, the seed dispersal strategy of *Dipteryx* is presently best suited to ground dispersers.

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TEMPORAL PATTERNS IN ABUNDANCE OF GENERALIST BUTTERFLY SPECIES

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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

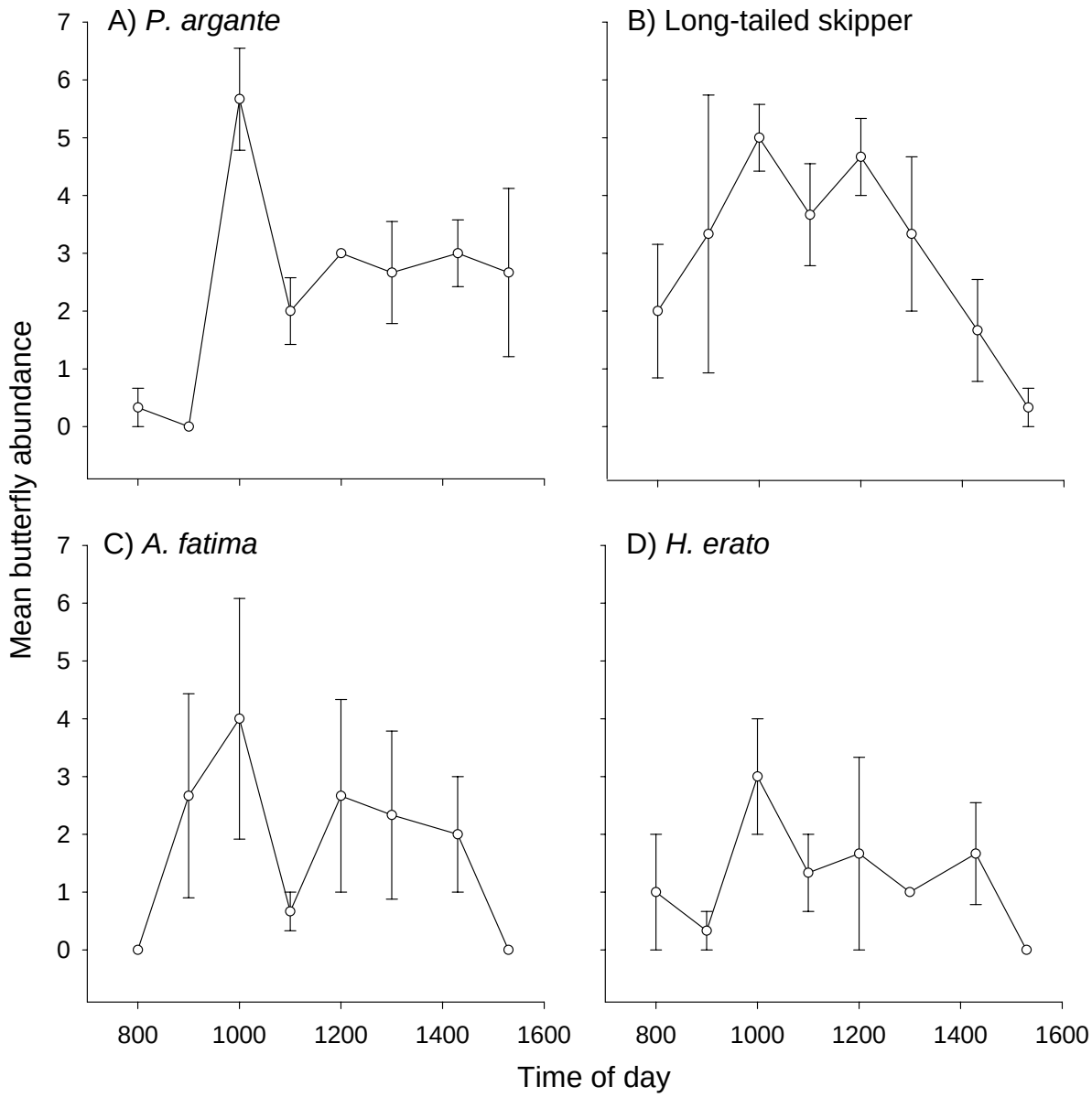

Figure 1. Mean abundance ± SE of each of four common butterfly species over the course of the day. Regression analyses showed no significant fit for *P. argante* (A), *A. fatima* (C), or *H. erato* (D). For long-tailed skipper abundance (B), we cannot reject a linear model based on lack of fit analysis (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

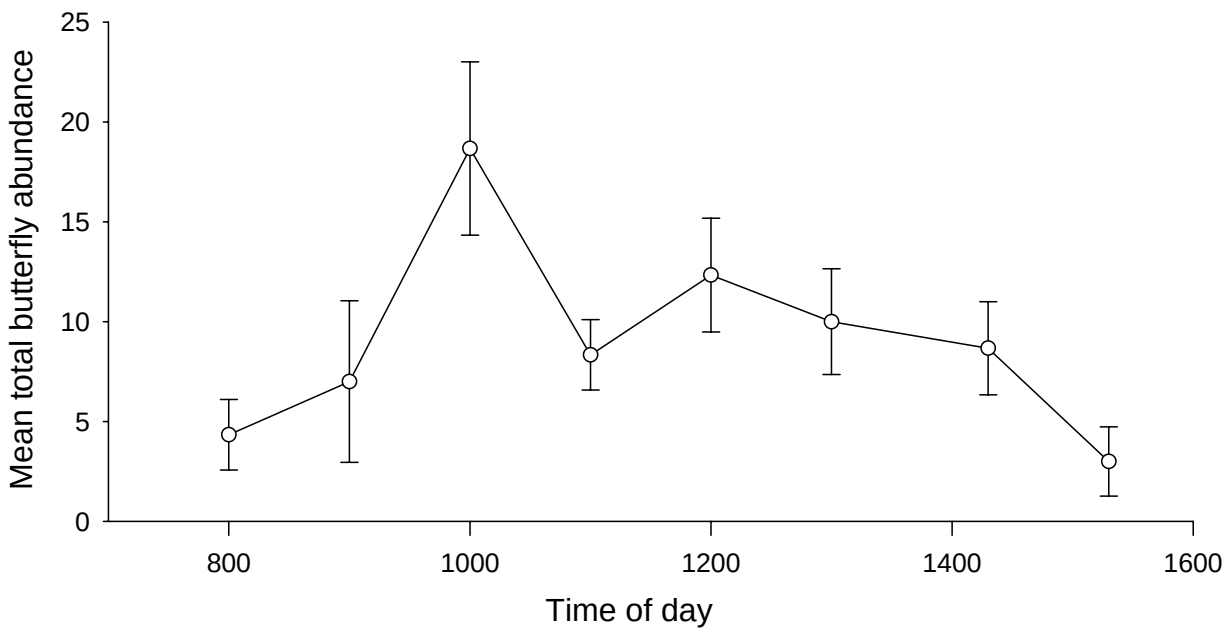

Figure 2. Total mean abundance ± SE over the course of the day. Means were obtained from abundance sampling over three consecutive days. Linear model was rejected (lack of fit: P = 0.03) and second order polynomial accepted (P = 0.20).

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.

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TO CHIRP OR NOT TO CHIRP: THE COSTS OF NON-BREEDING SEASON TERRITORIALITY IN *DENDROBATES PUMILIO*

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Abstract: The breeding season for strawberry poison dart frogs, (*Dendrobates pumilio*), peaks in the wet season in Costa Rica. However, males maintain breeding site territories throughout the year by vocalizing even though there are no immediate reproductive benefits. We investigated whether there are costs, such as reduced time spent foraging, associated with this behavior. We observed the behavior of *D. pumilio* males, and calculated time budgets for activities related to territoriality and foraging. In an experimental manipulation, we removed the nearest vocal neighbor from some frogs to determine whether their behavior would change when the pressure to maintain a territory was relieved. Males spent less time vocalizing in both control and when vocal neighbors were removed, with no variation between treatments. Their foraging behavior was also unaffected by frog removal. This suggests that there is a low cost to vocalizing in the non-breeding season, or that pressure from surrounding males is not a measure of that cost and predation may have a stronger effect.

Key words: strawberry poison dart frog, time budget, vocalization

INTRODUCTION

There are many benefits to being a territorial male, such as reduced competition for limited reproductive sites. There are also energetic costs and potential risks associated with acquiring and defending a territory. The poison dart frog, *Dendrobates pumilio*, maintains territories via vocalizations (bouts of quick, repetitive chirps) that result in males that are spaced evenly 2 - 3 m apart throughout their range in La Selva Biological Station (Robakiewicz 1989). *D. pumilio* maintain these territories from one month up to four years (Bunnel 1973; Robakiewicz 1989). These vocalizations also serve to attract females to ovipository sites. Territories allow for an elaborate courtship between male and female to take place undisturbed (Bunnel 1973). Donnelly (1989) reported seasonality in *D. pumilio* reproduction, with apparent peaks in female fertility at the onset of the rainy season. However, *D. pumilio* males maintain their territories with vocalizations throughout the non-breeding season.

We investigated the potential costs of maintaining territories in the non-breading season (e.g., time taken away from foraging). If vocalizing has a high cost, then individuals should reduce their time spent calling and increase their time spent foraging when pressure from nearby males is reduced. If vocalizing has a low cost, then we would expect to see calling behavior regardless of the presence of vocal neighbors.

Bunnell (1973) found that resident male vocalization peaked between 0600 and 1000 and Robakiewicz (1992) found that foraging behavior peaked later in the afternoon. If vocalization has a cost of reduced time foraging, then this pattern may be due to the limitations imposed by increased vocalization pressure in the morning.

METHODS

Between 0730 and 1630 on 15 - 17 February 2004, we located *D. pumilio* along the SUR, SOR, and STR trails and in the successional plots at La Selva Biological Station, Costa Rica. We identified 17 chirping frogs (with inflated throat pouches) as males and selected these for observation. We observed each focal frog from

~ 3 m away using binoculars, and noted the approximate distance to its nearest vocal neighbor and time of day. We recorded the length of time each frog spent vocalizing, walking, hopping, moving in place (foraging maneuvers), or sitting silently over a 10 min period or until the frog moved out of view. Foraging maneuvers and time spent walking were combined into one measure of foraging time (excluding instances when frogs were approaching other frogs). We calculated the percentage of time spent for each activity, and used correlation matrices to assess relationships between behaviors, distance to nearest neighbor.

For seven frogs that had not moved out of view after this first scan, we waited 20 minutes and repeated the 10 minute scan after an experimental manipulation. We removed the nearest vocal neighbor before repeating the scan for four frogs. To account for the effects of disturbance caused by the manipulation, we used three frogs as controls where we approached the neighboring frog but did not remove it. We assessed changes in behavior before and after the manipulation for both treatments and compared the amount of changes between treatments.

RESULTS

D. pumilio spent the majority of its time sitting silently or vocalizing (Table 1). The percent of time spent sitting was therefore strongly negatively correlated with percent of time spent vocalizing (Table 2). Other less common behaviors included hopping and foraging (Table 1). There was a significant correlation between foraging and time of day, with more foraging in the afternoon (Table 2). Vocalizing was more common in the morning, but this was not significant (Table 2). There was no correlation between the distance of a frog to its nearest vocal neighbor and any observed behavior, even in a model that also included time of day (t = 0.52, df = 15, P = 0.61; Table 2).

Table 1. Means ± SE of time budgets for 17 focal *D. pumilio*.

% time spent:	Mean ± SE
Sitting	73.73 ± 6.06
Vocalizing	22.10 ± 5.87
Hopping	0.44 ± 0.14
Foraging	3.58 ± 0.92
Total observation time (s)	540 ± 26
Distance to nearest vocal neighbor (m)	3.25 ± 0.33

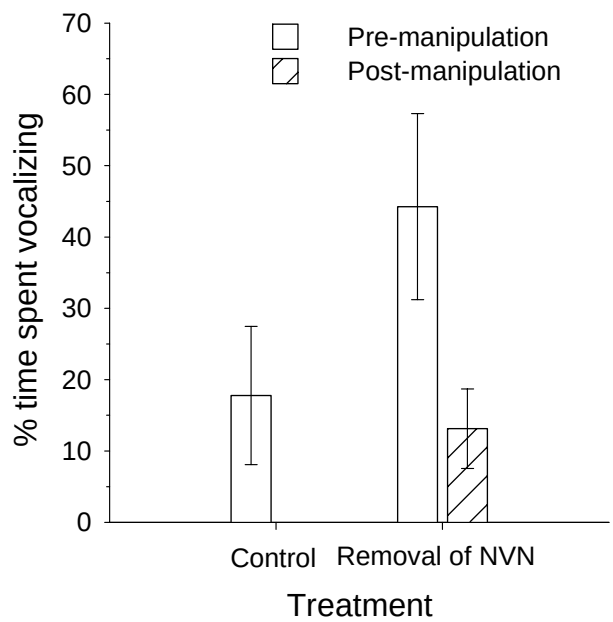

Figure 1. Percent of time spent vocalizing by *D. pumilio* before and after experimental manipulation. The nearest vocal neighbor (NVN) was removed from four experimental frogs, but not from three control frogs. Standard error bars are shown. The decrease in vocalizing time is significant for experimental frogs, but not control frogs, although post-manipulation yielded 0% time spent vocalizing. The magnitude of the decrease in vocalizing time did not differ significantly between treatments.

Frogs spent significantly less time vocalizing when their nearest vocal neighbor was removed (paired-t = 3.99, df = 2, P = 0.03; Fig. 1, 2). There was an insignificant decrease in vocaliza-

Table 2: Correlation matrix for *Dendrobates pumilio* behaviors, time of day, and distance to the nearest vocal neighbor (NVN) for 17 focal frogs observed for up to 10 minutes each. Only 16 focal frogs are included in analyses of distance to NVN. Foraging behaviors include walking and foraging maneuvers in place.

	Distance to NVN (m)	% time sitting	% time vocalizing	% time hopping	% time foraging
% time sitting	0.16				
% time vocalizing	-0.18	-0.99*			
% time hopping	0.33	-0.22	0.17		
% time foraging	0.04	-0.22	0.06	0.20	
Time of day	0.35	0.28	-0.39+	0.19	0.65*

* P < 0.05, + P = 0.12

tion in control frogs (paired-t = 1.83, df = 2, P = 0.21; Fig. 1). However, the change in vocalization behavior as a result of manipulation treatment did not differ between experimental and control frogs (t = 1.09, df = 5, P = 0.33; Fig. 1). In a model that encapsulated all these variables, there was a definite effect of disturbance caused by the experiment on vocalization ($F_{1,3}$ = 15.8, P = 0.01).

The amount of time a frog spent foraging was unaffected by the removal of its nearest vocal neighbor (paired-t = 0.17, df = 2, P = 0.88; Fig. 3). Control frogs also showed no change in foraging time before and after manipulation (paired-t = 0.46, df = 2, P = 0.69; Fig. 2). There were no differences in foraging time between control frogs and frogs with neighbors removed (t = 0.35, df = 5, P = 0.77; Fig. 2).

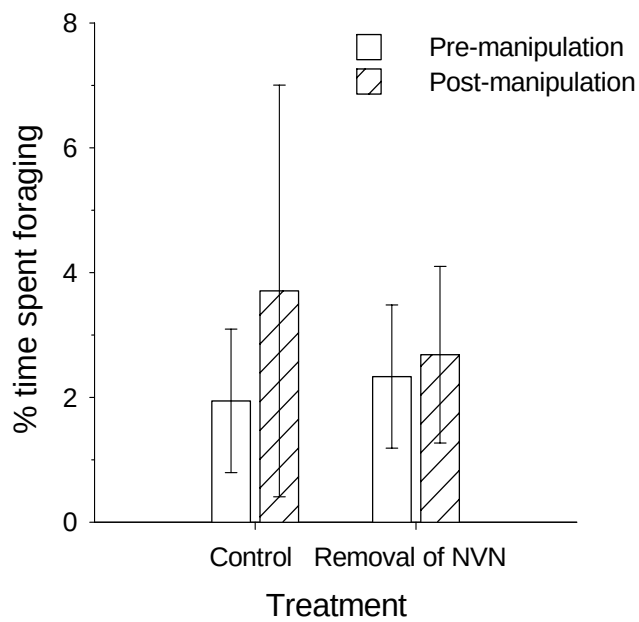

Figure 2. Percent of time spent foraging by *D. pumilio* before and after experimental manipulation. The nearest vocal neighbor (NVN) was removed from four experimental frogs, but not from three control frogs. Standard error bars are shown. There were no significant changes in time spent foraging before and after manipulation in either treatment, and no differences between treatments.

Discussion

The lack of a significant difference between treatments and the lack of correlations in behavior to nearest vocal neighbor distance suggests that there is a low cost to vocalizing, and that *D. pumilio* calls regardless of pressure to maintain territories. If we had found that vocalization was a costly behavior, this would imply that frogs already having claimed a territory when the breeding season begins would incur greater fitness through increased reproductive success early in the breeding season. However, since we found little cost to vocalization, the delayed benefits in the breeding season do not necessarily have to be large to offset these low costs. Even so, if there are large benefits, then to fail to maintain a territory by vocalizing may have

high fitness cost.

Regardless of the cost, *D. pumilio* does partition time between foraging and vocalizing. Foraging activity peaks in the afternoon, while vocalizing is more common in the morning. If the species is constrained to specific foraging hours, perhaps by food availability, then during the hours they do not forage their default behavior may be chirping, which is not costly.

Although our study suggests that there is no cost to vocalizing in the non-breeding season, frogs often stopped vocalizing in response to a slight disturbance. Also we lost sight of ten out of the 17 frogs we observed when they moved under the leaf litter. This suggests that *D. pumilio* exhibits predation avoidance behavior. Although *D. pumilio* is a Dendrobatid frog, its toxins are not as potent as other members of the poison dart frog family (Crump 1983). This suggests that it may still be vulnerable to predation, although little is known about its potential predators. Vocalizing calls attention to the frogs, leading to an increase in exposure. Therefore vocalizing may have a cost of increased predation risk. Future studies could investigate predation rates on these frogs and how they relate to male vocalization.

There were some limitations to our study. Our low sample size made it difficult to compare treatments in our manipulative study, and the effect of experimental disturbance confounded these results. Future studies should give more time after manipulation to allow frogs to habituate to experimental conditions. Furthermore, *D. pumilio* spent the majority of observation time sitting still, and we were unable to determine whether this behavior was related to foraging or territoriality. Robakiewicz (1992) defined sitting behavior as characteristic of an alert foraging stance, while Donnelly (1987) defined it as an alert territorial posture. Further investigation of the differences between these two stances is needed.

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THE ADAPTIVE NATURE OF FLORAL BRACTS IN FOUR *HELICONIA SPP.*

JULIA M. BUTZLER AND SARA M. HELLMUTH

Abstract: Inflorescences of *Heliconia spp.* include those that hang down from the stem (pendant), and those that have cup-like bracts filled with fluid (upright). These traits appear to be homoplastic, having evolved several times in different clades. We explored the potential benefits of upright bracts, hypothesizing that liquid in the bracts would reduce herbivory levels on the flowers, and/or prevent nectar-robbing mites from entering the flowers. In fact herbivory was lower in *Heliconia spp.* that had upright bracts. We also found a significant difference in herbivory levels between the two upright species, *H. imbricata* and *H. wagnerania*. Our tests for mite colonization of drained flowers were inconclusive because none of the manipulated flowers bloomed during our study. The multiple ecological processes probably contribute to the diversity of flowering plants.

Key words: Heliconia imbricata, Heliconia mariae, Heliconia pogonantha, Heliconia wagnerania, *herbivory, inflorescence, La Selva, orientation, phoretic mites*

INTRODUCTION

Flowering plants (Division: Anthophyta) are the largest and most successful plant group on earth today. The success of this group can be attributed in part to the diversity of structure and function in the reproductive organ, the flower itself. Clearly, the evolutionary diversification of flower structure has facilitated the diversification of flowering plants in habitats of all types (Heywood 1993).

Members of the genus *Heliconia* (Heliconiaceae: Zingibierales) are large-leaf herbs found throughout the neotropics. The floral parts of a plant are positioned within a bract, which are located in series on an inflorescence. Several species have inflorescences of pendant orientation with respect to point of attachment to the stem (e.g., *H. pogonantha*), while others (e.g., *H. wagneriana*) have upright inflorescences. The species exhibiting upright inflorescences often have unusual cup-like floral bracts that contain liquid, commonly thought to contain plant secretions. These bracts typically sustain surprisingly diverse communities of aquatic (or semi-aquatic) insects (Seifert 1980).

Phylogenetic analyses indicate that the upright inflorescence is the primitive state in *Heliconia*, and that the pendant state has independently evolved twice (Kress 1981). The same analysis, however, also indicated that upright bract orientation is a homoplastic trait as well, having evolved again from the pendant state. Such reversals make it reasonable to hypothesize that the current state of any species (upright vs. pendant) is a product of contemporary selection rather than an evolutionary anachronism.

Several hypotheses have been developed to explain the benefits of having an upright bract. Skutch (1933) was the first to suggest that the water-filled bracts served to prevent attacks from terrestrial insects and larvae that feed on flowers and flower parts. The flowers remain submerged until they are ready to be pollinated, and are therefore protected from herbivory by terrestrial insects. The bract liquid may also prevent hummingbird associated nectar-robbing mites from entering the flower. It seems that *H. wagneriana* at La Selva does not support a mite population below the top inflorescence (McDade, pers. comm., Hellmuth, pers. obs.). Two species of mite-carrying hummingbird visitors (*Phaithornis superciliosus* and *Glaucis aenea*) commonly visit *H. wagneriana* flowers. However, because the flowers remain sub-

merged until ready to pollinate, and then often senesce quickly to fall back into the liquid, mites may be selectively avoiding the upright *Heliconia* species. Top inflorescences may host mites because of the low volume of liquid.

To identify the benefit of having an upright orientation, we compared the occurrence of herbivory of two upright species (*H. wagneriana* and *H. imbricate*) and two pendant species (*H. mariae* and *H. pogonantha*). Both upright species hold water in their bracts that harbors a diverse invertebrate community, whereas the pendant species contained no water or aquatic invertebrates. Additionally, we tested whether the presence of bract water influenced the absence of mites in *H. wagneriana*.

METHODS

On 15 - 16 February 2004, we compared floral herbivory on two upright species (*H. wagneriana* and *H. imbricata*) and two pendant species (*H. pogonantha* and *H. mariae*). Inflorescences were collected from areas surrounding the OTS field station at La Selva National Park, Costa Rica. We located three distinct patches of each species along the SAZ trail, and sampled one inflorescence from each patch. On each inflorescence from each species, we quantified the herbivory levels on the top, middle and bottom flowers of each inflorescence (to partition variance due to flower age). We recorded the presence or absence of herbivory on the petals, seeds, and inside of the bracts of each flower. Herbivory on the inside of the bract was only recorded if it covered > 5% of the surface area. We used a chi-square test to compare the probability of herbivory on reproductive floral structures, on non-reproductive floral structures, and overall herbivory, between pendant and upright inflorescences, as well as between species within a bract type.

We also tested the effect of bract liquid on the colonization of mites on flower parts of *Heliconia wagneriana*. We did this by comparing mite abundance between drained bracts and intact bracts. On 14 February 2004, we used a dissection knife to slice 1 x 1 cm holes into the bases of the bracts of 140 flowers on 23 inflorescences in three different *H. wagnerania* patches located on the SAZ trail. We were careful to avoid damage to interior flower parts. For the next three days we checked each drained bract and neighboring intact bract for flowering, hummingbird visitation, and mites.

RESULTS

Bract orientation and species within bract orientation were related to herbivory intensity on both reproductive and non-reproductive tissue (Table 1). Bracts of the pendant inflorescences were more likely to have herbivory on the reproductive parts than bracts on upright inflo-

Table 1. The percent of *Heliconia* bracts with herbivory on the inside of the container bract, on the petals, or on the internal reproductive parts (stamen, pistil, ovary, or seeds).

Inflorescence type	Species	Bract herbivory (inside)	Petal herbivory	Reproductive herbivory
Upright	*H. imbricata*	88	77	44
	H. wagneriana	0	22	0
Pendant	*H. mariae*	11	33	44
	H. pogonantha	0	77	66

rescences (χ^2 = 4.21, df = 1, P = 0.04); however, herbivory on the non-reproductive parts, and overall herbivory was not different between bract orientations (χ^2 < 0.001, df = 1, P = 0.99 and χ^2 = 2.6, df = 1, P = 0.11, respectively). Within the upright floral structure type, *H. imbricate* had more herbivory on both reproductive (χ^2 = 5.14, df = 1, P = 0.02) and non-reproductive structures (χ^2 = 8.10, df = 1, P < 0.01) than *H. wagneriana*. There was no difference in the occurrence of herbivory between the two pendant species (reproductive, χ^2 = 0.90, df = 1, P = 0.34; non-reproductive, χ^2 = 1.60, df = 1, P = 0.21).

Unfortunately, none of the experimentally drained bracts or their undrained controls flowered during the experiment. Consequently, there was no hummingbird visitation, and no opportunity to evaluate whether mites associated with the hummingbirds were more likely to colonize drained flowers.

Discussion

Heliconia spp. with upright bracts sustained less flower herbivory than those with pendant bracts, which is consistent with the hypothesis that upright bracts have been selected for in *Heliconia* because the fluid retained within bracts protects reproductive parts. Pendant inflorescences, however, are not the ancestral condition of these plants, suggesting it too is an adaptation and implying that there must also be factors that can favor pendant bracts in *Heliconia* flowers. One possibility is that although upright bracts limit herbivory on the flowers by terrestrial insects, they expose the plant to potential aquatic herbivores (Seifert 1982). Additionally, it is possible that the pendant inflorescences evolved as an adaptation to increase pollination events (Seifert 1982).

We also found a significant difference in herbivory levels between the two upright species, *H. imbricata* and *H. wagnerania*. It has been suggested that the chemical composition of the fluid may mediate the structure of the aquatic (or semi-aquatic) community that is harbored in the bract (Bronstein 1986). The plant can regulate several aspects of the bract fluid, including the pH (Butcher 2002) and sugar concentration (Nutter 2000), which may then influence the composition and abundance of the community (e.g., eliminating aquatic herbivores). Further studies could compare the pH of the liquid and the aquatic communities found in the bracts of these two species to determine there is any relationship.

We were unable to evaluate the hypothesis that upright bracts protect flowers against nectar theft by mites associated with hummingbirds. Field observations revealed that mites are commonly found in top inflorescences, which hold a very small volume of water compared to the bracts that were lower down on the inflorescence. Furthermore, a pilot study on a single plant revealed that two bracts that were drained (and which subsequently bloomed) were both colonized by mites. Mites are selective in their choice of plants to colonize, sometimes avoiding entire families of plants such as the *Acanthaceae* (McDade, pers. comm.). It is possible that the mites have evolved a mechanism that prevents them from colonizing *H. wagnerania*; these flowers only bloom for a single day before falling back into the water, giving the mites little time to escape from the flower after feeding on nectar. Future studies could examine what cues the mites use in the decision of which flowers to colonize.

Our study indicates that herbivory is one selective pressure that influences the bract type of *Heliconia* flowers. It is likely that pendant inflorescences are associated with other advantages since they have evolved at least twice in this genus. Apparently, there are multiple ecological processes, involving numerous other organisms that influence the evolution of floral

morphology in *Heliconia*. This range of selective pressures influencing the evolution of flower structure in flowering plants is likely responsible for a large part of the diversity and success of the group as a whole.

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EFFECTS OF SUCCESSIONAL FOREST STAGE ON ARTHROPOD AND BAT COMMUNITIES

ELEANOR E. CAMPBELL AND LUKE M. EVANS

Abstract: Humans have had a large impact on forest structure in recent history. Practices in logging and conversion of forest to agricultural land have led to significant changes, especially in the age structure of forests, and it is consequently important to understand how these changes affect faunal communities. Because many arthropods feed on forest vegetation, and insectivorous bats feed on the arthropods, we hypothesized that the difference in vegetation between successional stages of the forest would affect these communities. We measured arthropod morphotype richness, abundance, and size, as well as bat richness and foraging time in early and late successional forest stages. There were arthropod morphotypes that overlapped between forest stages, but many were unique to one or the other. Bat morphotypes were completely unique to successional stage. However, we found that arthropod richness, abundance, and size did not differ between successional forest stages. Also, bat richness and foraging use was not significantly different between successional forest stages. It seems that the types of resources offered to the faunal communities vary across successional stages, and that species composition may depend of different varieties of resources.

Key words: bat foraging, forest structure, Petterson D240X

INTRODUCTION

In recent history humans have been changing tropical forest characteristics through such activities as logging and clearing land for agriculture. In particular, forest structure (e.g., successional stage) has been affected, and may be influencing the faunal communities within. We chose to study the tropical communities of arthropods and insectivorous bats. Many arthropods feed upon forest vegetation, therefore a change in vegetation may alter the arthropod community. As well, the insectivorous bat community might change in response to the arthropod community. We hypothesized that successional stage of a forest would affect the composition, abundance, and richness of the arthropod community, as well as the composition, foraging use, and richness of the insectivorous bat community.

There are many possibilities of how successional change in the forest could affect these communities. Vegetative types differ between successional forest stages, which may cause arthropod herbivory specialization and therefore community composition changes. Because early successional, pioneer plant species tend to be fast-growing and therefore poorly defended, it could be expected that the richness and/or abundance of arthropods in the early successional forest would be greater than in the early successional forest. Alternatively, it may be that successional stage has no affect on composition, richness, or abundance of the arthropod community.

Insectivorous bats may show a response to trends of composition, richness, and abundance in the arthropod community. If bats specialize on certain arthropod species, the bat community composition may change in response to the suite of arthropod species present in each forest stage. If arthropod abundance or richness is greater in early successional forests, it may follow that bat use or richness is also greater if there is more abundant prey. It is also possible that if there are other overriding factors than prey type and abundance, bat community composition, richness, and use between successional stages in forests may not differ or may not be congruent with patterns of arthropod

composition, richness, and abundance.

METHODS

We sampled the arthropod and bat communities in early and late successional growth 1 km north of the biological station in La Selva, Costa Rica on 16 - 17 February 2004. We sampled two older successional plots (at marker 850 on trail SOR and marker 350 on trail CCL) and two early successional plots (20 m from SOR on path between stages 0 - 1 year and 1 - 2 years, and 10 m from SOR on path between stages 3 - 4 years and 4 - 5 years). To sample the night arthropod community we hung three sticky traps (at 1 m, 2 m, and 3 m above ground) at each plot from ca. 1730 to 0630 each sampling day. Each arthropod was identified to morphotype and measured for length. Morphotype data were used to calculate arthropod richness and abundance.

To sample the bat community we used a Petterson D240X ultrasound detector, set at a listening frequency of 45 kHz, to record search-phase insectivorous bat calls. We sampled each plot once for 20 min during dusk (ca. 1730 to 1930) and during pre-dawn (ca. 0400 to 0600) when bat activity is likely to be highest. We recorded the total bat foraging time in our sampling area (10 m radius of ultrasonic detection) by noting the length of time we heard clicks through the detector in order to determine foraging minutes/sample. We also tried to record a sample of each call (Appendix 1). Call samples were analyzed using Sonobat 2.0, and sorted according to their duration, bandwidth, slope, and high and low frequencies. Species richness was determined by differentiating between distinct sonotypes.

All data were analyzed comparing early vs. late successional stages. Difference in insect richness was analyzed with an ANOVA model that included successional stage, day, plot nested within successional stage, and stage*night. Differences in insect abundance and insect length were analyzed with ANOVA models that included successional stage, day, height of the trap, plot nested within successional stage, stage*height, stage*night, and night*height. Differences in bat richness and foraging minutes/sample were analyzed with an ANOVA model that included day, time of day, successional stage, plot nested within successional stage, night*time of day, night*stage, and time*stage.

RESULTS

There were 27 arthropod morphotypes that occurred only early successional forest, ten that occurred only in late successional forest, and 14 that occurred in both (Fig. 1a). There were six bat morphotypes that occurred only in early successional forest, four that occurred only in late successional forest, and none that occ-

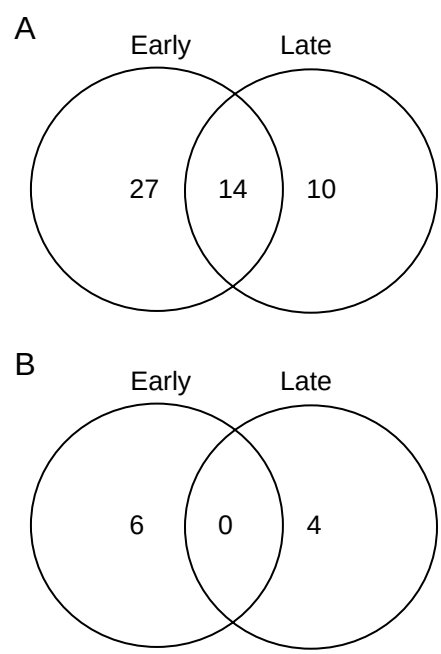


Figure 1. Number of morphotypes found in early and late successional forests; overlapping area indicates morphotypes found in both successional stages. A: Arthropod morphotypes. B: Bat morphotypes.

urred in both (Fig. 1b).

On average, arthropod richness and abundance per plot, and abundance per plot of arthropods ≥ 2 mm in length, were greater in early successional forest than in late successional forest (Fig. 2a, Fig. 2b, and Fig. 2c, respectively). However, none of the models were significant ($F_{5,7}$ = 2.23, P = 0.34; $F_{11,23}$ = 2.24, P = 0.09; and $F_{11,23}$ = 0.93, P = 0.55 for richness per plot, abundance per plot, and abundance per plot of arthropods ≥ 2 mm in length, respectively). Mean length of insects (mm) did not differ between successional stages of forest (mean ± SE = 3.05 ± 0.4 and 2.74 ± 0.40 for early and late successional forest respectively; $F_{11,23}$ = 0.40, P = 0.93). Average number of bat morphotypes per plot was not significantly different between early successional forest and late successional forest ($F_{8,14}$ = 0.64, P = 0.73 for the model; Fig 3a). Bat use, in foraging minutes/sample, did not differ between early and late successional forest ($F_{8,14}$ = 1.21, P = 0.42 for the model; Fig. 3b).

Discussion

We found that successional stage does affect arthropod and insectivorous bat communities. Bat composition was completely different between successional stages; there was overlap in insect species composition, but the majority of species were unique to their successional stage. Surprisingly arthropod abundance, richness, and length, as well as bat richness and foraging minutes/sample, did not change significantly with successional stage, although there were trends of increasing arthropod abundance and richness with early successional stages.

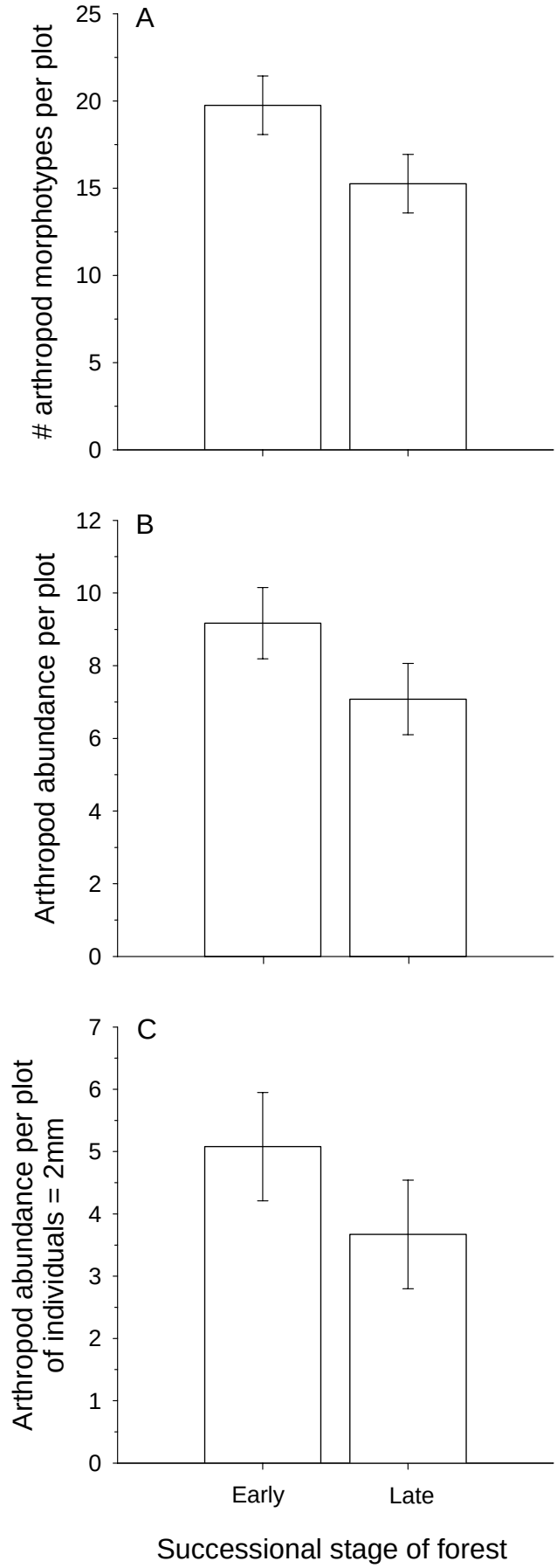


Figure 2. The effect of forest successional stage on the arthropod community. Means ± SE are reported for (A) arthropod richness per plot, (B) arthropod abundance per plot and (C) arthropod abundance per plot of individuals ≥ 2 mm in length.

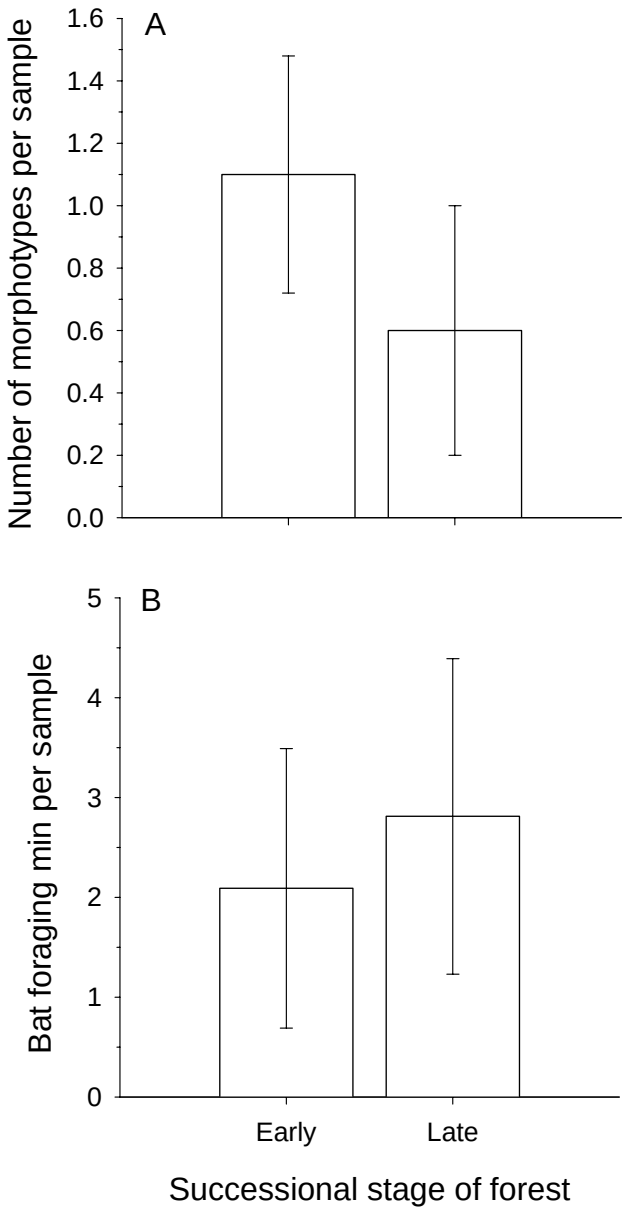


Figure 3. The effect of successional stage on the bat community: means ± SE are reported for (A) bat richness per sample and (B) bat use of plot in foraging minutes per sample.

The high instance of unique bat and arthropod morphotypes per successional stage may be explained by the differing range of available niches in forests of different ages. This shift of niches may be a result of forest structure changes through time. Arthropods, generally limited in mobility, depend on their immediate environment for resources to grow and reproduce. Arthropod species may show high preference for food type, and thus may be unique to specific areas where this food type is found. Insectivorous bats may prefer certain types of insects, and thus they may be unique to areas where those insects are supported. We speculated that different bats may prefer larger or smaller prey items, and that difference in arthropod size between the successional stages may help explain differences in bat community composition. There was no change in average arthropod size between stages, and so arthropod size difference likely is not a factor that affects bat community composition. However, our methods of collection may have only sampled a small sized subset of the arthropod community; such things as large moths, which may be an important food source for some bats, would not have been caught by a small sticky trap. Future studies should use a variety of collection methods to better sample the night aerial insect community.

It may also be that the forest structure affects bat foraging; dense and low early growth may be more difficult to fly through that higher and more open older growth. It would be interesting to determine how arthropod type and bat foraging success affect spatial preferences of feeding bats. Future studies could perhaps determine this by analyzing bat flight patterns, as well as stomach contents to determine prey preferences.

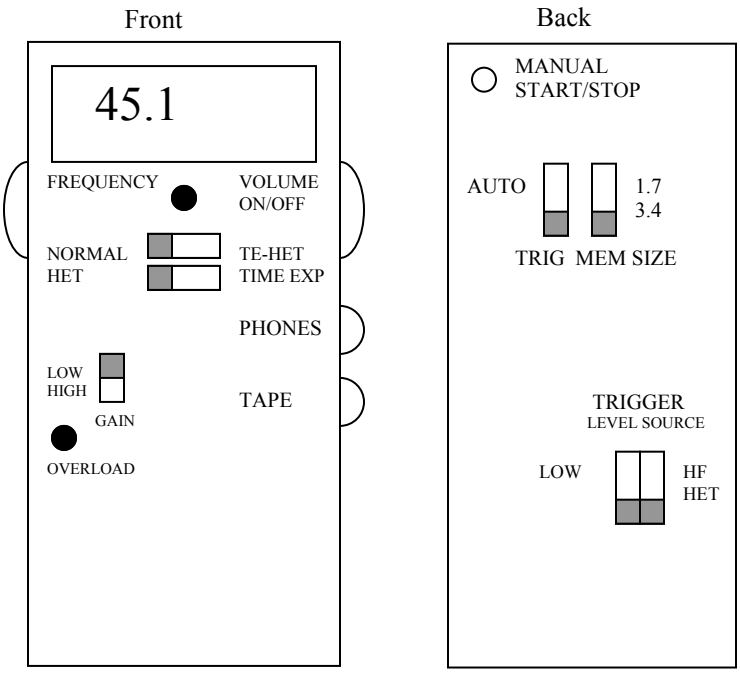
It has been thought that the fast-growing plants that characterize young successional plots are generally more edible, due to decreased secondary metabolites, which may explain the trends of increasing arthropod richness and abundance in early successional plots. However, this should be determined by a more thorough examination of the arthropod community. We only observed aerial insects, which may be more mobile than others, so perhaps other insect communities would show more distinctive trends in abundance and richness. Also, since there is much more height to the forest structure of late successional growth we may

not have sampled the entire arthropod community. Future studies could sample at a wider range of levels in the different successional stages, to see how insect abundance and richness varies with height.

Since bat richness did not change with successional stage, it seems that forests of different types support the same overall richness, even though individual species may differ. The lack of a difference in insect abundance between successional stages may explain the lack of change in bat foraging minutes/sample. There are also other factors that may have influenced our measurements of bat foraging; the range with the Petterson D240X ultrasound detector is limited to a 10 m radius, and perhaps bat activity is high up in the forest canopy, but we could not sample it. Additionally, we experienced scattered periods of rainfall throughout our sampling effort. Rain seemed to diminish the insect activity, which may have thus influenced bat feeding activity. Future studies could examine how weather influences bat and insect activity by observing feeding activity through a variety of weather patterns.

Differences in successional stage do influence the composition of faunal communities. Therefore the increasing rate of human-influenced change of forest structure and age may likely also increase the rate of change of resident species. Richness and abundance may not be influenced, but the alterations in species composition should be taken into consideration as humans alter land use and continuously diminish old forest growth.

Appendix 1.



The directions on how to use the Sonobat 2.0 program are excellent in explaining how to analyze recordings of bat calls on a computer. Their directions on using the Petterson ultrasonic recorder, however, are somewhat lacking. The diagram above shows the settings we used to record bat calls.

What you hear:

When the detector is turned on, bat calls sounds like clicks that change in volume and speed as bats fly and hunt. These clicks are changed into tonal chirps by the computer.

Modes:

There are two modes to this detector: **AUTO** and **MAN**ual. In **AUTO** mode the machine is supposed to be able to be triggered by the presence of a bat call, and automatically record calls continuously to the computer. We were unable to get this mode to work, as bat calls never actually triggered recording. A less finicky mode is **MAN**ual, which makes use of the **MANUAL START/STOP** button on the back.

*How to setup **MAN**ual mode:*

When the back TRIG is on **MAN**, the detector is in manual mode. In order to continuously hear any bat clicks, keep the front switch on **NORMAL.** In **TE-HET** the detector records in a way that we cannot hear, making it difficult to determine when a bat was actually present. More work should be done to determine exactly what happens in **TE-HET** mode, but keeping it on **NORMAL** works fine. The switch below, with **HET** and **TIME-EXP,** is interesting. You can listen in **TIME-EXP** (time expansion) to bat calls that are lengthened as they would be on the computer, so actual tones can be heard. However, we were unable to obtain recordings this way, nor could we tell how long bats were in our detection area. Therefore we kept the switch on **HET**.

*How to record calls in **MAN**ual mode:*

When turned on the detector immediately starts playing picked up sounds through the speaker. When the **START/STOP** button on back is pressed, the red light should turn on. This means that the detector is continuously re-

cording. When the button is pressed again, the light turns off and the machine replays the last 3.4 sec (or 1.7, depending on which **MEM SIZE** is preferred) onto the computer (which records at a slower speed for analysis, so at 10x speed it takes 34 sec to get the entire replay). At the same time, the speaker plays all current sounds. Therefore you can record a call and still note whether bats are in the area.

Some issues:

Cicadas, breaking sticks, and water can also be picked up by the detector, which may hinder recording. Interference can be minimized by switching the **GAIN** to **HIGH**. Quieter bat calls will not be recorded this way, but it prevents cicadas from overloading the recorder (indicated when the red **OVERLOAD** light is on). We're also not sure what the **TRIGGER LEVEL SOURCE** switches do on the back, but the settings shown worked.

Frequency setting:

We listened and recorded at a **FREQUENCY** of 45kHz because other studies determined that many bat calls are picked up +/- 5kHz of this level. However, bats have a range of calls that can reach up to and above 100kHz, so it may be beneficial to experiment with recording at different ranges.

Final thoughts:

Whenever the red light next to **FREQUENCY** is lit, the detector is recording, and whenever the red light is unlit it is replaying. Any experimentation with switch combinations should be done with this in mind. It was unwieldy to need a computer in order to record calls in the field. It is possible to record calls from the detector onto a tape recorder that can then be dumped on a computer later. This should be looked into.

SOIL CARBON DYNAMICS IN DIFFERENT SUCCESSIONAL STAGES OF TROPICAL FORESTS

R. QUINN THOMAS AND PETER N. CHALMERS

Abstract: The rates of ecological processes change with successional patterns and disturbances. Soil respiration rates are influenced by many abiotic factors, but how forest age influences soil respiration rates is poorly understood. We examined the effects of soil temperature, soil moisture, and litter quantity on soil respiration rate between forests of different successional stages and their effects. Soil respiration rate tended to increase from early successional stages to secondary growth, but decreased from secondary growth to primary growth; this could be due to differences in the quality and/or quantity of litter input. Soil respiration rates and soil moisture did not differ between successional stages but soil temperatures averaged 1.6°C warmer in early successional plots. As the relative proportion of young forests increases from anthropogenic effects, understanding the resulting effects on pools and fluxes of soil carbon will become more important.

Key words: carbon content, decomposition, litter quality, litter quantity, soil respiration rate, temperature, water content

INTRODUCTION

Tropical forests are a mosaic of different successional stages, ranging from new gaps to stands with old trees and no recent tree falls. Abiotic and biotic forest characteristics such as temperature, litter quantity, litter quality and moisture levels probably change with successional stage. Temperature may be lower in late successional stages because of increased canopy cover. Litter quantity may be higher in late successional stages because of a higher standing biomass available to input litter. Litter quality may be lower in late successional stages because of increased secondary metabolites. Moisture levels may increase with forest age because soil evaporation rates decrease with decreased soil temperature, or because moisture levels may decrease with forest age because higher canopy cover reduces the amount of rainfall reaching the soil.

Abiotic and biotic differences between successional stages may affect effluxes and influxes associated with the pool of carbon in the soil. The main influx to this carbon pool is leaf litter, and the main efflux is respiration from the soil. We expected that soil respiration rates may be affected by forest characteristics associated with different successional stages.

We predicted that soil temperatures would be higher in early successional forests, and that soil respiration rates would also be higher than in older forests. Older forests may produce more leaf litter that leads to higher total respiration, but the rate of soil respiration per gram litter will not increase. Higher litter quality, associated with early successional forests, may lead to higher soil respiration rates in those forests. Higher soil moisture content may lead to higher soil respiration rates, so if soil moisture content increases with successional stage due to decreased soil evaporation, soil respiration rates may increase.

The influxes and effluxes of carbon pools in the soil determine the amount of carbon held in this pool. As soil respiration rates increase, the size of the soil carbon pool will decrease. Therefore, if soil respiration rates decrease with temperature and temperature decreases with successional stage, the size of the carbon pool stored in the soil will increase with successional stage. Similarly, if soil respiration rates decrease with litter quality and litter quality decreases with successional stage, pool sizes will increase with successional stage. Alternatively, if total soil respiration increases with litter

quantity but soil respiration rates do not increase with litter quantity, pool sizes will not change with successional stage even though total soil respiration would increase.

To examine the affect of successional stage on carbon size and soil respiration rates, we measured soil respiration rates, litter input rates, soil temperature, and soil moisture content in addition to the size of the soil carbon pool in three forests in different successional stages.

METHODS

We took all measurements on 15 - 17 February 2004 at La Selva Biological Reserve, Puerto Viejo, Costa Rica. We measured litter fall for two days with 1.0 m x 1.7 m plastic sheets suspended approximately 1 m from the ground. We set up triplicate traps in primary, secondary (19 - 25 year old), and early successional forests (2 - 5 year old) with similar alluvial soil. From dry mass of the litter that collected in these traps, we calculated the grams of carbon per square meter per hour (g C m^{-2} hr^{-1}) that is added to the soil.

We measured moisture content, carbon content, and mineral content for the organic horizon of these same forests by weighing samples from each forest, drying them at 100°C for 4 hours, weighing them again, burning them at 750°C overnight, and weighing them again. The difference between wet and dry weight is water content and the difference between dry and burned weight represents the size of the carbon pool. Unfortunately, our burning procedure melted the aluminum foil containers so the data could not be collected and carbon contents were not calculated.

We took three measures of soil respiration rates in each of the three forest ages using volumetric soil respirometers. All measurements were conducted in the laboratory at a relatively constant temperature of 25.6°C. We used the soil respiration methods described by Eaton et al. (1998). From these data, organic layer depths and bulk densities garnered from Sollins et al. (1994), and the ideal gas law we expressed soil respiration rates as grams of carbon released per square meter of soil per hour (g C m^{-2} hr^{-1}) so as to compare with litter fall rates.

RESULTS

Litter fall rates varied widely (0.74 - 15.81 g of dried leaves collected) as did soil respiration rates (0.43 - 2.20 mL of O_2 dry soil g^{-1} hr^{-1}). Temperature differed significantly between primary, secondary, and early successional forests, rising as age decreased ($F_{2,7}$ = 23.48, P = 0.003; Table 1, Fig. 1). Percent water content did not differ significantly with successional stage ($F_{2,7}$ = 3.15, P = 0.13), so we did not examine any further correlations with water content. Leaf litter input did not differ significantly between primary, secondary and early successional forest

Table 1. Temperature, soil respiration rate, and litter fall rates (means ± SD) differ between forest types.

Forest type	Temperature (°C)	Soil respiration (g C m^{-2} hr^{-1})	Litter fall (g C m^{-2} hr^{-1})	Percent water content
Early successional	25.6 ± 0.3	0.030 ± 0.023	0.060 ± 0.050	53.4 ± 1.3
Secondary	24.6 ± 0.4	0.063 ± 0.011	0.015 ± 0.012	61.8 ± 5.1
Primary	24.0 ± 0.2	0.029 ± 0.017	0.024 ± 0.016	62.1 ± 6.3

($F_{2,7}$ = 1.64, P = 0.28) but the lowest amount of leaf litter fell in the secondary forest (Table 1, Fig. 1). Soil respiration rate did not differ significantly between primary, secondary, and early successional forest ($F_{2,7}$ = 2.34, P = 0.19), but soil respiration rate was highest in secondary forest (Table 1, Fig. 1). We were unable to estimate pool sizes because of our difficulties with the Muffle furnace.

DISCUSSION

Soil respiration rate does not have a linear relationship with forest age, but appears to have a more complex pattern. While we expected to see soil moisture content differ between successional stages, we found no such pattern. The range of soil moisture that we found was very small, and seemed unlikely to influence soil respiration rates. Assuming a typical temperature response (Q_{10} = 2), mean temperature difference between early successional and primary forest (1.6°C) would roughly correspond to an 11% increase in soil respiration rate.

If there are real differences between successional stages in temperature controlled soil respiration rate, it could arise from the effects of litter quantity and/or litter quality. This could be tested by more thorough measurements of litter input rates and litter quality for microbes in stands of different ages. The relative importance could be examined by studying the size of the carbon pool. We would expect to see a decrease in the soil carbon pool with increasing forest age if the litter quality is the driving factor, while we would expect little or no change in the soil carbon pool with increasing forest age if the litter quantity is the driving factor. Future

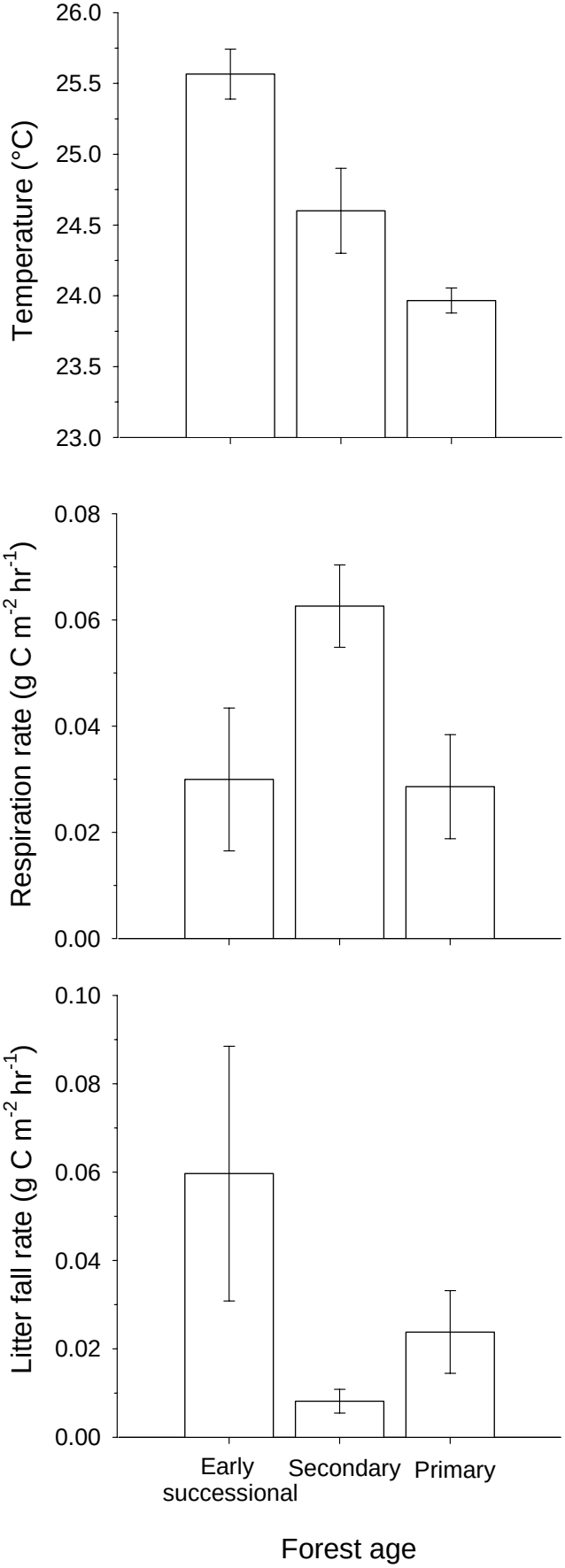


Figure 1. Comparison of mean temperature, respiration rate, and litter fall rate (± SE) between early successional, secondary, and primary tropical forests.

studies should examine the size of soil carbon pools in forests of different successional stages, as well as following the change in soil respiration rates and pool size for the same plot over time.

Our study suggests that the carbon stored in the forest soils and the rates of carbon efflux can change with forest age. Many more factors influence these rates, but according to the trend found here, increasing the proportion of forest in an early successional stage may not increase carbon efflux until the forests reach maturity. As deforestation increases, the proportion of forests in early successional stages has increased. Carbon dioxide concentrations are increasing globally, so the effect of the change in proportion of early successional to primary forest on carbon levels is important to understand.

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EVIDENCE OF INDIRECT PLANT DEFENSES IN TWO TROPICAL PLANT FAMILIES

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Abstract: Plants may use herbivore-induced chemicals to attract herbivore predators. The number and type of herbivore predators attracted may differ depending on plant family, time of day, amount of herbivory on leaf, and leaf age. We found no evidence of higher predation risk, either in the Melastomataceae or Arecaceae, for caterpillars on recently wounded leaves. Plants either were not producing volatiles that attracted predators, or we were unable to induce a response by our simulated herbivory. The type of predation on herbivores varied between night and day. In Arecaceae, the number of predators attracted decreased with leaf age. Perhaps the degree of herbivore-induced chemical production in plants is greater during seasons of high growth or herbivore pressure.

Key words: Arecaceae, clay caterpillars, La Selva, Melastomataceae, plant-induced herbivore predation, volatile chemicals

INTRODUCTION

Plants have a variety of methods of defending themselves against herbivores, including delayed greening, increased leaf toughness, rapid leaf expansion, synchronous leaf production, and secondary metabolites (Coley and Kursar 1988). An additional defense against herbivory is the release of volatile compounds in response to herbivory (Kessler and Baldwin 2001). These compounds attract herbivore predators including parasitoid wasps (De Moraes et al. 1998), ants, and rodents (Loiselle and Farji-Brener 2002) as a means of indirect defense.

By simulating herbivory on leaves from plants representing two tropical lowland rainforest families, we tested for evidence of indirect defenses of plants. Because plants often have diurnal patterns of volatile chemical production (Ryan 2001), we tested plants during both the day and night. Herbivory is more intense on young leaves, so plants may have patterns of induced responses based on leaf age. Conversely, when leaves are young, they may be physiologically incapable of synthesizing defense compounds. To evaluate these alternative possibilities, we included tests on both young and old leaves.

We predicted that predation on herbivores would be lower on Arecaceae than Melastomataceae because palms produce fewer secondary metabolites and have tougher leaves (Coley 2003). We predicted that type and amount of predation on herbivores would vary between night and day. Additionally, volatile chemical defense may be more prevalent in young leaves that lack lignification than in older leaves that are more difficult to damage (Coley and Aide 1991), thus we predicted that more predators would be attracted to herbivores on young leaves.

METHODS

On 14 February 2004, we conducted an overnight pilot study to determine if predators would attack clay caterpillars; for this, we damaged ten leaves with ~ twenty 1 mm puncture wounds (using forceps) in an assortment of plant families. We glued one clay caterpillar to each wounded leaf at dusk. Nine were recovered the next morning. Seven showed noticeable predation, usually consisting of the removal of large pieces of clay from the caterpillar body. Two caterpillars appeared untouched.

We then conducted an experiment to test for effects of previous leaf damage on caterpillar

predation risk. On 15 February 2004, we simulated herbivory on plants in the Arecaceae and Melastomataceae families at La Selva Biological Station, Costa Rica. We used previously undamaged leaves on 28 plants of each family. Trial plants were located at least 10 m apart along the Camino Circular Cercano and Camino Circular Lejano and chosen randomly. There were three morphospecies of Arecaceae and four morphospecies of Melastomataceae represented in our samples. We used young leaves on half the plants and old leaves on the other half. Half of the leaves in each age category (7) were controls, and on half we simulated herbivory by using scissors to remove four small sections of leaf. We estimated leaf age based on leaf size, color, and location on the plant. We made clay caterpillars simulating Sphingidae larvae and glued them on the center of each leaf in our study. Model caterpillars were 4 x 20 mm with painted yellow heads and green bodies (as described in Loiselle and Farji-Brener 2002).

We left caterpillar models out for 8 hours during the day, and repeated the experiment for 14 hours at night. Caterpillars were scored as depredated if they exhibited nicks or marks that appeared to come from mandibles, stingers, or bills. We performed a logistic contingency analysis using predation as the dependent variable comparing all main effects (time of day, family, age of leaf, and damaged treatment) and two-way interactions. We also collapsed types of predation into three categories based on the types of marks left on model caterpillars (Appendix 2) and tested for relationships with main effects.

Results

Model caterpillars did not suffer higher predation depending on time of day (55% vs. 48% for day vs. night), age of leaves (47% vs. 57% for old vs. young leaves), or control vs. experimental leaf damage (50% predations for both control and damaged leaves) (Table 1). Predation tended to be more probable for model caterpillars on Melastomataceae than on Arecaceae (59% vs. 44% predation), although the difference was not significant (Table 1).

No interactions were significant except family x age (Table 1). Among Melastomataceae, predation was highest for caterpillars on old leaves (56%), while among Arecaceae, predation was highest for caterpillars on young leaves (67%).

Table 1. Summary of results of logistic contingency analysis for predation. Summary includes all main effects and two-way interactions.

Effect	DF	Wald χ^2	P
Time of day	1	0.75	0.39
Family	1	2.60	0.11
Age	1	1.02	0.31
Damage	1	0.03	0.86
Time of day x family	1	1.59	0.21
Time of day x age	1	0.00	0.96
Time of day x damage	1	1.56	0.21
Family x age	1	6.41	0.01
Family x damage	1	2.77	0.10
Age x damage	1	0.39	0.53

Table 2. Summary of results for logistic contingency analysis of main effects for three functional categories of types of predation on caterpillars.

Effect	DF	Wald χ^2	P
Time of day	2	23.68	< 0.0001
Family	2	3.12	0.21
Age	2	2.92	0.23
Damage	2	0.51	0.77

The type of predation on caterpillars did not differ between plant families, age of leaves, or treatment (Table 2). However, type 2 predation occurred only at night, while type 1 and other types of predation occurred primarily during the day (Table 2, Appendix 2).

Discussion

Surprisingly, damaged leaves did not show higher predation rates on caterpillars than control leaves. This suggests that either leaves were not producing volatile chemicals that attract predators, or that they were producing the same amount of volatile chemicals prior to and independent of our treatments. It is also possible that our method of simulated herbivory did not induce a large enough plant response to create a difference in volatile chemical production between treatments. In our pilot study, we aggressively punctured and ripped leaf tissue to simulate herbivory, while in our experiment, we attempted to simulate herbivory more realistically by cutting small "bites" of leaf in our experiment. Additionally, torrential rain during the night portion of our study may have had an impact. Volatile chemical cues may be less effective when it is raining, and the number and type of caterpillar predators may also change with precipitation.

The trend towards higher predation on the Melastomataceae than the Arecaceae was in accordance with our prediction, but requires further sampling to confirm or reject. The frequency of predation did not differ with time of day, but the types of predation did, suggesting that plants produce different volatile chemicals during the day than at night, or that there is a temporal shift in the type of predators responding. While there was not an overall pattern of predation based on leaf age, there was a strong pattern within plant families. Young Arecaceae leaves attracted more predators than old leaves, while the highest amount of predation occurred on old Melastomataceae leaves. Arecaceae may produce fewer volatile chemicals as they age, allocating increased levels of resources to young leaves. Melastomataceae do not appear to allocate more resources to the defense of young leaves. They could be allocating more resources to growth, or the plants may be physiologically constrained, with only older leaves capable of synthesizing volatile chemicals.

Herbivore-induced plant chemical responses may differ between plant families and in the type of predators they attract. The magnitude of volatile chemical production in plants may be synchronized to peak during periods of rapid plant growth or higher herbivore pressure. Future studies may utilize similar methodology to examine indirect plant defenses in other plant families and with respect to other plant defense strategies.

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Appendix 1. Number of clay caterpillars depredated and not depredated in each treatment group.

Time of day	Family	Age	Damage	Predation	Number of occurrences
Day	Arecaceae	old	no	no	4
				yes	3
Day	Arecaceae	old	yes	no	4
				yes	3
Day	Arecaceae	young	no	no	3
				yes	4
Day	Arecaceae	young	yes	no	2
				yes	5
Day	Melastomataceae	old	no	no	4
				yes	3
Day	Melastomataceae	old	yes	no	2
				yes	5
Day	Melastomataceae	young	no	no	3
				yes	4
Day	Melastomataceae	young	yes	no	3
				yes	4
Night	Arecaceae	old	no	no	5
				yes	2
Night	Arecaceae	old	yes	no	7
				yes	0
Night	Arecaceae	young	no	no	1
				yes	5

Appendix 1 (Continued).

Time of day	Family	Age	Damage	Predation	Number of occurrences
Night	Arecaceae	young	yes	no	4
				yes	2
Night	Melastomataceae	old	no	no	1
				yes	6
Night	Melastomataceae	old	yes	no	2
				yes	4
Night	Melastomataceae	young	no	no	5
				yes	1
Night	Melastomataceae	young	yes	no	2
				yes	5

APPENDIX 2. Number of clay caterpillars suffering each predation type at day and night.

Predation type	Description	Number of occurrences	
		Day	Night
1	scratches, dents, or grooves	26	10
2	pairs of deep incisions	0	15
Other	includes flakes, gouges, or punctures	9	4