MITE BE SMART: NECTAR VOLUME AND ABUNDANCE OF *RHINOSEIUS COLWELLI* IN *CENTROPOGON TALAMANCENSIS*

EMILY L. SHARP, JENNY E. JUN AND MELISSA A. BARGER

Abstract: The mite, *R. colwelli,* resides in *C. talamancensis* flowers and is dependent on hummingbirds for dispersal between flowers. Mite abundance in flowers is positively correlated with number of hummingbird visits, but variation within flowers with equal numbers of hummingbird visits could be attributed to differences in nectar volume. We hypothesized that mites preferentially choose to jump onto flowers with more nectar. We simulated hummingbird visits to flowers with manipulated nectar volume and then quantified mite abundance. We found that flowers with more nectar had more mites. This suggests that mites are able to choose which flowers to inhabit. This may be important because nectar is a food resource and possibly an indicator of a senescing flower.

Key Words: dispersal, hummingbirds

INTRODUCTION

The mite, *Rhinoseius colwelli,* resides in the flowers of *Centropogon talamancensis* (Campanulaceae), which are pollinated by *Eugenes fulgens* hummingbirds. Both mites and hummingbirds consume the *C. talamancensis* nectar. The mites are dependent on the hummingbirds for dispersal between flowers, as they climb onto the bird's beak during a hummingbird visit (Colwell 1973).

Mite abundance in *C. talamancensis* is positively correlated with number of hummingbird visits (Colwell et al. 1974). However, our preliminary data showed that there was still variation in mite abundance between flowers that receive equal pollinator visitation. We hypothesized that this variation might be due to differences in nectar volume, with more mites in flowers with more nectar. If so, this suggests that mites will choose to leave the hummingbird's bill in flowers that contain more nectar. We tested this prediction experimentally in a montane forest in Costa Rica.

METHODS

We created 17 artificial patches of *C. talamancensis* flowers at Estacion Biologica Cuerici, Cerro de la Muerte. Each patch consisted of six randomly selected flowers that we had removed from various *C. talamancensis* plants from around the station. We removed all nectar from each flower using capillary tubes, and then added 8 μL of 30% sugar water to three of the six flowers; thus creating no-nectar and nectar treatments in each patch. Mites were larger than the capillary tube opening; therefore, we assumed they were not disturbed during nectar removal or addition, thus maintaining their original distribution among flowers. The simulated nectar was 50% higher in sugar concentration and three times higher in volume than occurred in flowers in the field. This was done to

exaggerate the difference between no-nectar and nectar treatments.

We created an artificial hummingbird beak using a black toothpick. We inserted the artificial beak into each flower for 2 s to simulate a hummingbird visit. Each flower was visited 10 times in a random order. After these simulated visitations, we dissected each flower and counted mites. We analyzed data with a two-way ANOVA with patch as a random effect and nectar as a fixed effect using JMP 5.0.1. We confirmed that data met the assumptions of normality and homogeneity of variances.

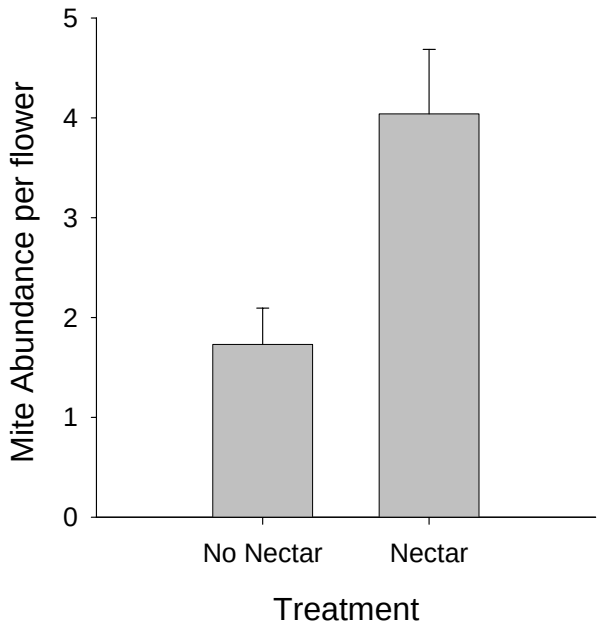

Figure 1. Average mite abundance per flower was higher in the nectar treatment than in the no-nectar treatment.

RESULTS

Total mite abundance in patches ranged from 2 to 39 individuals. Mite abundance was higher in flowers in the nectar treatment (mean = 4.04 $\pm$ 0.65 SE) than in the no-nectar treatment (mean = 1.73 $\pm$ 0.36 SE; $F = 10.50$, df = 1, 79, $P < 0.0025$, Fig 1). One patch was excluded from analysis because of extremely high mite abundance within the patch; however, nectar was still a significant factor when these data were included. Variance in mite abundance between patches was not significant ($F = 1.46$, df = 1, 15, $P > 0.20$).

DISCUSSION

The higher mite abundance in flowers with nectar supports our hypothesis that *R. colwelli* may choose to leave their hummingbird carrier at flowers with greater nectar. This is important to mites because nectar is a food resource. Additionally, increased mite abundance at high-nectar flowers may provide greater access to genetically different mates.

It appears that mites also choose to leave flowers with decreased or low nectar volume, which may be indicative of a senescing flower. Hummingbirds may visit senescing flowers less, thus decreasing the mites' opportunities for dispersal away from diminishing resources to nectar-rich resources. Therefore, the ability to leave a flower with decreased or low nectar may be important for mite survival.

Our experiment did not test the specific cue that mites use to determine nectar abundance. An additional experiment could examine whether sugar concentration, moisture levels, or both act as the cue. Our experiment also exaggerated factors involved in mite dispersal such as nectar

abundance and sugar concentration, and pollinator visits. It would be interesting to examine mite dispersal patterns under realistic conditions to see if this pattern persists.

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Colwell, R. K., et al. 1974. Competition for the nectar of *Centropogon valerii* by the hummingbird *Colibri thalossinus* and the flower piercer *Diglossa plumbea*, and its evolutionary significance. Condor, 76: 447-489.

DISTRIBUTION AND ABUNDANCE OF LIANAS IN PRIMARY AND SECONDARY FORESTS AT CERRO DE LA MUERTE

GABRIEL H. CALVI, TIMOTHY R. MATSUURA AND CHAD M. VALDERRAMA

Abstract: To evaluate the effect of forest structure on liana distribution and abundance, we compared the abundance and cross-sectional area at breast height of lianas between primary forest and secondary montane forests. Primary forest had a higher density of lianas and trees than secondary forest. The mean cross-sectional area of each liana and the number of lianas per tree were not significantly different for the two forest types. The number of lianas per tree was positively related to tree cross-sectional area, possibly because larger trees provide more surface area upon which lianas can climb. Lianas likely colonize and attain greater canopy cover in primary forests than secondary forests, though the species of lianas in each forest type may differ.

Key Words: cross-sectional area, montane forest, structural parasite

INTRODUCTION

Lianas are an important component of tropical forest structure, contributing significantly to total leaf production, woody biomass, and species diversity (Bullock 1990). As photosynthetic structural parasites on trees, liana success is affected by forest structure. Previous work by Laurance (2001) showed that liana abundance was greater near forest edges and in disturbed areas and decreased with tree biomass (Laurance 2001).

Over time, forest structure develops and changes through successional processes. To test changes in liana community with changing forest structure, we examined the difference in liana abundance and size between primary and secondary montane forests in the Talamanca Range, Costa Rica. Similar to disturbed areas, secondary forests have higher light availability and a greater height-stratified network of small branches and stems than primary forests

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(Begon et al. 1990). The lack of structural variability and light, characteristic of primary forests, may limit lianas in these environments. For these reasons, we predicted that secondary forests would have greater numbers of lianas and larger lianas, as measured by total liana cross-sectional area at breast height, than would primary forests.

METHODS

We selected six 10 m x 10 m plots, three in primary forest and three in the adjacent secondary forest along the western part of the lookout loop trail north of the Estacion Biologica Cuerici at Cerro de la Muerte, Costa Rica. Primary forest plots were located approximately half way between the Estacion Biologica Cuerici and the Mirador in old growth forest. Secondary forest plots were located adjacent to the Estacion Biologica Cuerici in an area disturbed by farming approximately 50 years ago (Bellow and Piluk 1998). We quantified abundance and diameter at breast height (DBH) of all trees and lianas in each plot. Diameter at breast height was used to calculate cross-sectional area of trees and lianas. We also noted whether each liana was associated (in contact) with a tree at breast height.

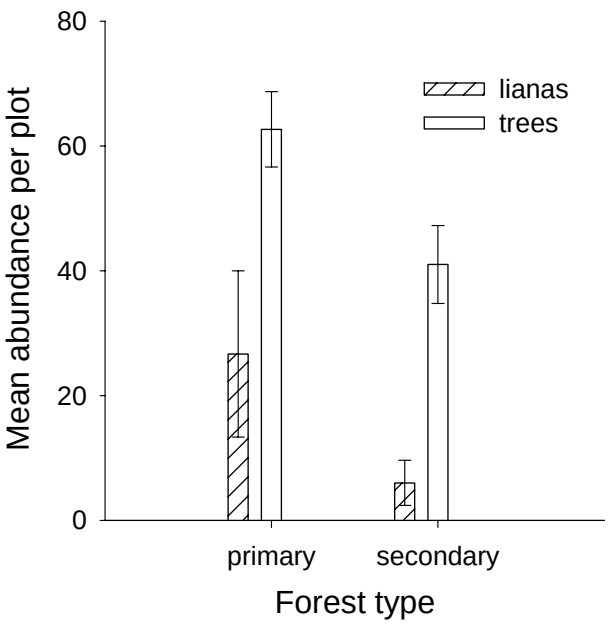

Figure 1. Mean abundance (± 1 SE) of lianas and trees in 10 m x 10 m plot in primary and secondary forests. Primary forest had a greater abundance of lianas and trees (analysis performed on ln transformed data; see text).

Abundance and cross-sectional area at breast height of trees and lianas were compared between forest types using one-way ANOVAs. Because our sample size was small, we were unable to evaluate the assumptions of normality and homogeneity of variances. As a conservative approach, we transformed the data using natural log. Because we had a balanced experimental design we felt justified in using parametric tests (Box 1954). A linear regression was used to examine the relationship between the number of lianas per tree and tree DBH. All analyses were performed using JMP 5.0.1.

RESULTS

More lianas and trees occurred in primary forest than secondary forest ($F = 9.23$, $df = 1, 4$, $P = 0.04$; $F = 17.99$, $df = 1, 4$, $P = 0.01$, respectively; Fig. 1). Total cross-sectional area of lianas at breast height was greater in primary forest (mean ± SE, 92.2 ± 17.7 cm^2) than in secondary forest plots (18.9 ± 17.7 cm^2; $F = 11.10$, $df = 1, 4$, $P = 0.03$). The same result was found for total tree cross-sectional area at breast height

(3.35 ± 1.16 m^2 and 0.24 ± 1.16 m^2, respectively; F = 8.68, df = 1, 4, P = 0.04). Mean tree cross-sectional area was marginally greater in primary forest plots than secondary forest plots, 563.5 ± 207.4 cm^2 and 60.1 ± 207.4 cm^2 respectively (F = 4.98, df = 1, 4, P = 0.09). The number of lianas per tree increased with tree diameter in primary forests plots (r^2 = 0.41, df = 22, P = 0.0008), but the relationship did not exist in the secondary forest plots because no tree was host to more than one liana (Fig. 2).

There was no difference between mean cross-sectional area of each liana in primary forest (4.0 ± 0.86 cm^2) and secondary forest plots (2.9 ± 0.86 cm^2; F = 0.50, df = 1, 4; P = 0.52). Likewise, the ratio of total liana cross-sectional area to total tree cross-sectional area was not different between forest types (0.0060 ± 0.0029 and 0.0069 ± 0.0029, respectively; F = 2.98, df = 1, 4, P = 0.16).

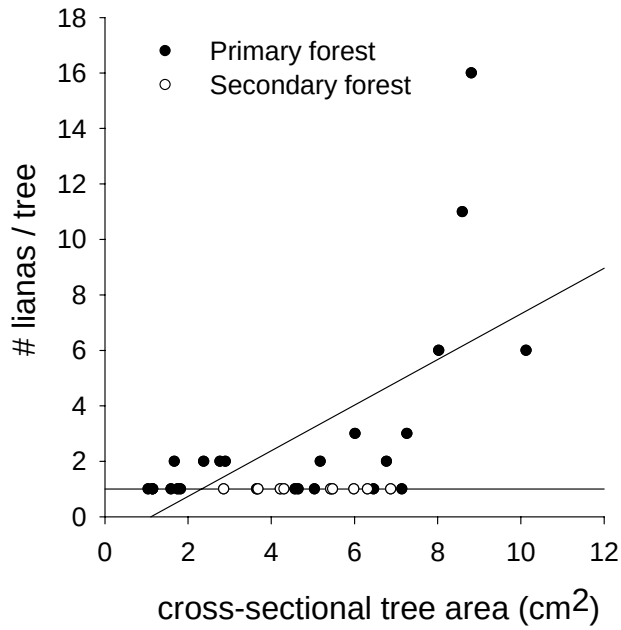

Figure 2. Number of lianas per tree by tree cross-sectional area at breast height in primary and secondary forest. Primary forest had a greater range of tree cross-sectional areas at breast height. The number of lianas per tree was positively related to the tree cross-sectional at breast height in primary forest (y = 0.82x - 0.91). No relationship existed for the secondary forest data. No trees in the secondary forest had more than one liana (tree cross-sectional area ranged from 17.3 to 962.1 cm^2). Line through secondary forest data (open dots) shows mean number of lianas per tree. The slope of the relationship was not significantly different from zero.more than one liana (tree cross-sectional area ranged from 17.3 to 962.1 cm^2). Line through secondary forest data (open dots) shows mean number of lianas per tree. The slope of the relationship was not significantly different from zero.

Discussion

We found that the primary forest had more trees and supported more lianas than the secondary forest. Our prediction that a secondary forest would have more lianas than a primary forest was based on the probably false assumption that a secondary forest would have a greater density of small branches and trees than a primary forest that would provide physical support for young lianas.

We did not measure the canopy cover of lianas or trees. This information is necessary to definitively compare the structural advantage (ratio of leaf biomass to woody biomass) of lianas over trees between primary and secondary forests. However, liana leaf biomass can be inferred based on the cross-sectional area of each liana, with lianas of greater cross-sectional area having more leaves. The mean total cross-sectional area of lianas was higher in primary forest, implying that the primary forest probably had more liana canopy cover than the secondary forest. Further, because lianas are structural para-

sites, their investment in woody biomass per unit area leaf is relatively smaller than for trees. It follows that as a tree grows larger, the ratio of liana cross-sectional area to that of the tree would decrease even if the ratio of canopy cover between the liana and tree remained constant. The ratio of total liana cross-sectional area to that of trees did not differ between the primary and secondary forests we studied. Thus, canopy cover due to lianas is probably proportionally greater in primary forests than secondary forests than implied by liana cross-sectional area alone.

There were no trees in the secondary forest supporting more than one liana at breast height. In the primary forest, the number of lianas per tree, ranging from 1 to 16, was positively related to tree cross-sectional area, possibly because larger trees have more surface area for the lianas to colonize.

Mean area per liana did not change between primary and secondary forests, likely due to the prevalence of small lianas in both forest types. Their presence implies that lianas are able to colonize in primary forests as readily as secondary forests, which we predicted would be difficult in the poorly lit understory. Primary forests may not have low light levels, as we assumed, or lianas may not be strongly affected by the variation in light conditions between primary and secondary forests.

Though we collected no quantitative data on the species of lianas in our primary and secondary forest plots, there appeared to be no overlap between forest types. It is possible that different liana species that require different environmental conditions are colonizing the different forests. Studying the distribution of liana species will be a key to understanding how forest succession changes liana communities.

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PATTERNS IN NECTAR PRODUCTION AMONG PATCHES OF HUMMINGBIRD-POLLINATED FLOWERS

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RICHARD W. TRIERWEILER AND CHELSEA L. WOOD

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

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

INTRODUCTION

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

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

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

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

METHODS

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

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

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

RESULTS

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

DISCUSSION

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

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

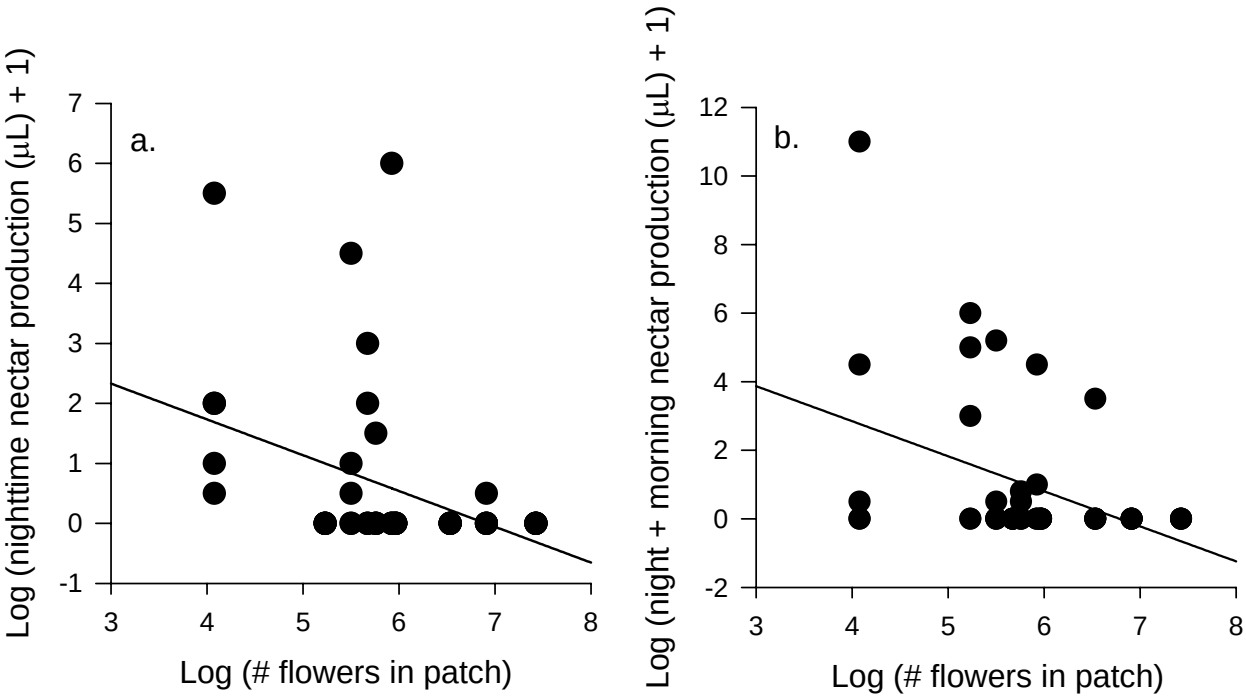

Figure 1. (a) Average night-time nectar production per flower and (b) average night and morning nectar production per flower decreased with increasing number of flowers in a patch (a: y = -0.0004x + 0.47, b: y = -0.0005x + 0.56). The x-axis was log-transformed to linearize the relationships. Lines were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

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

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

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

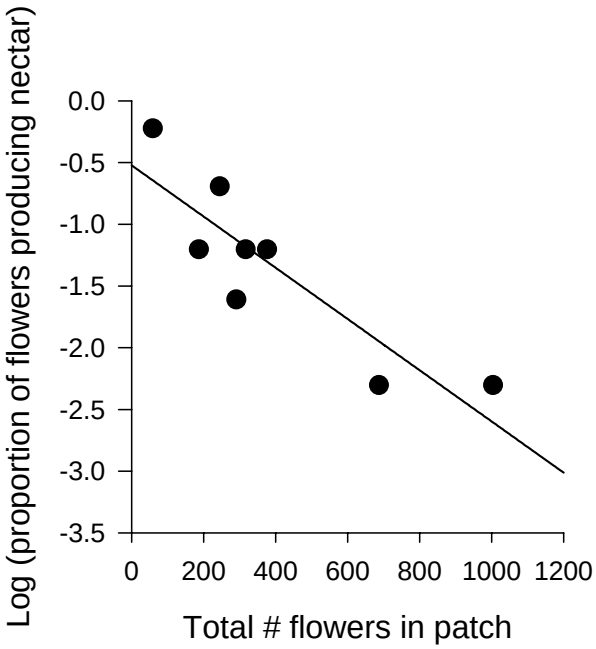

Figure 3. Proportion of nectar-producing flowers decreased with increasing number of flowers in a patch (y = -0.002x – 0.52). Line was fit by least squares regression.

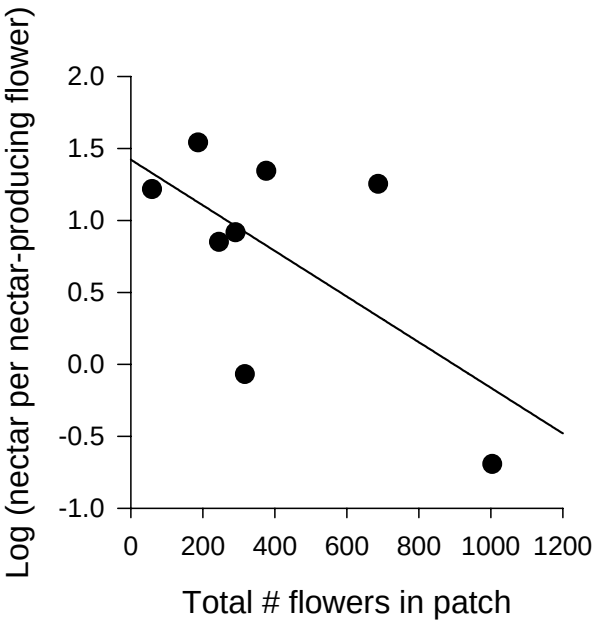

Figure 2. Average amount of nectar produced per nectar-producing flower decreased with increasing number of flowers in a patch (y = -0.002x + 1.42). Line was fit by least squares regression.

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EFFECT OF LEAF TEXTURE ON EPIPHYLL COVER IN A HIGH-ELEVATION FOREST

ANNA R. NOWOGRODZKI AND CAYELAN C. CAREY

Abstract: The distribution of epiphylls is affected by various environmental factors, especially leaf surface characteristics. We examined the relationship between epiphyll cover of leaves and three indices of texture (pubescence, waxiness, and roughness) in the Talmanca Mountains of Costa Rica. We found that epiphyll cover decreased with pubescence, increased with waxiness, and was not related to roughness. Our findings conflict with previous studies performed at lower elevation cloud forests, which suggests that epiphyll species composition or ability to adhere to leaves may vary between habitats.

Key Words: Cerro de la Muerte, leaf pubescence, leaf roughness, leaf waxiness

INTRODUCTION

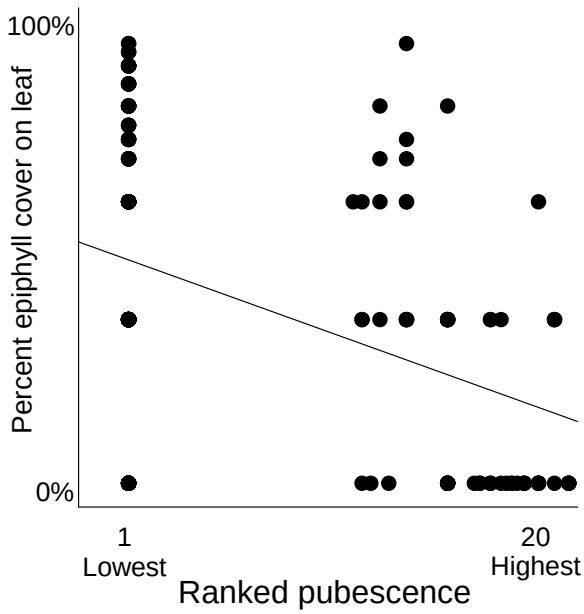
Epiphylls, small epiphytes that grow on leaves, are prevalent and well-researched in tropical cloud forests (Bykowski and Liebert 1994, Ginsburg et al. 1995, Morales 2000). In cooler and drier high-elevation forests, however, epiphylls have a limited distribution due to reduced precipitation (Hartshorn 1983). With limited moisture, leaf morphology may be more important in determining epiphyll distribution at high elevations compared to low elevations. Past studies have found conflicting evidence concerning the effect of leaf morphology on epiphyll cover: Ginsburg et al. (1995) found that rough leaves had relatively high epiphyll cover, while Morales (2000) reported more epiphyll growth on smooth leaves.

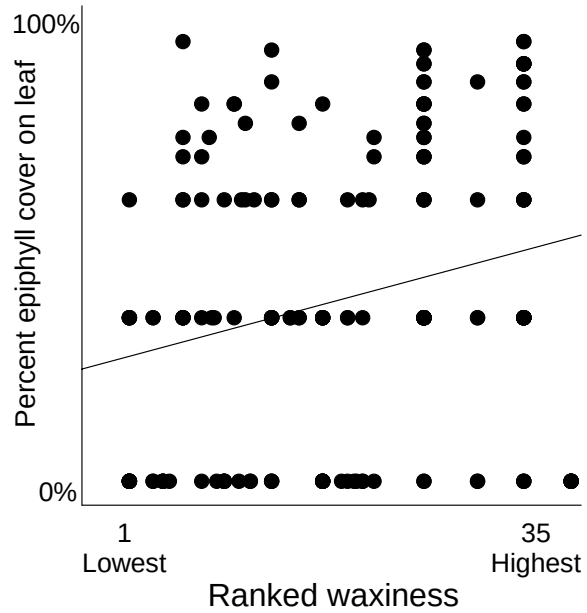
We hypothesized that leaf texture affects epiphyll distribution in the high-elevation oak-dominated forest at Cerro de la Muerte, Costa Rica. Using three indices of texture (pubescence, waxiness, and roughness), we quantified the effect of leaf texture on leaf epiphyll cover. We predicted that epiphyll cover would be highest on leaves with low pubescence, low waxiness, and low roughness.

METHODS

Our study was conducted on 28 January 2005 in primary oak-dominated forest north of Estacion Biologica Cuerici at Cerro de la Muerte. We selected 10 plots (1 m^2) between elevations of 2800 and 2890 m in which epiphylls were found on at least one leaf in 50% or more of individual plants. All plots had similar canopy cover (75 - 100% by visual estimate) and vegetative structure (understory shrubs and herbs). For every shrub and herbaceous plant in a plot, whether it had epiphylls or not, we collected one median-aged leaf, defined as the leaf at the middle node on the main stem. Leaves were omitted if they were less than 3 cm long.

We visually estimated leaf epiphyll cover to the nearest 10% on all leaves ranging from 0 - 100% (11 categories total). We





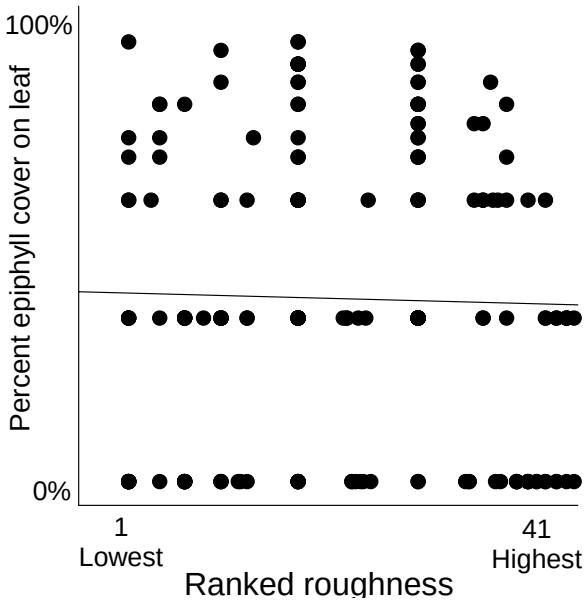


Figure 1. The relationship between percent epiphyll cover and three measures of leaf texture: pubescence, waxiness, and roughness. Percent epiphyll cover decreases with pubescence, increases with waxiness, and is independent of roughness (Spearman's Rho correlations on ranked averaged data).

ranked these categories of percent epiphyll cover, with 1 being the lowest value (0% epiphyll cover) and 11 the highest (100% epiphyll cover). Based on plant and leaf morphologies (shape, venation, thickness, color, and texture), we sorted leaves into morphotypes that corresponded to individual plant species.

Each morphotype was then assessed for degree of pubescence, waxiness, and roughness, and ranked from lowest to highest. When morphotypes had tied ranks, we assigned them the average of the ranks they would have received if they had not been tied (Zar 1999). This resulted in ranked categories of 1-20 for pubescence, 1-35 for waxiness, and 1-41 for roughness, with 1 being the lowest rank for each trait. We then used JMP 5.0.1 to perform a non-parametric Spearman's Rho correlation for ranked values of epiphyll cover, pubescence, waxiness, and roughness.

RESULTS

We collected 188 leaves from 45 distinct leaf morphotypes from the 10 plots. Epiphylls on the leaves we collected were

predominantly liverworts. Epiphyll cover was negatively correlated with pubescence (non-parametric Spearman's Rho correlation, $\rho = -0.40$, $P < 0.0001$, $n = 188$; Fig. 1) and positively correlated with waxiness ($\rho = 0.25$, $P = 0.0006$, $n = 188$). There was no significant relationship between epiphyll cover and roughness ($\rho = -0.02$, $P = 0.74$, $n = 188$).

Discussion

High pubescence may prevent epiphylls from adhering to the leaf surface. Our finding that more epiphylls are found on waxier leaves suggests that epiphylls are more likely to attach, germinate, and grow on waxy leaves. It is possible that waxy leaves last longer, so epiphylls have more opportunities to colonize them or more time to grow once established (Coley 1988). Also, epiphyll reproductive structures, such as gemmae, may adhere more easily to waxy surfaces (Morales 2000).

Roughness apparently had no effect on the likelihood of epiphyll germination or growth. This could be because our scale of roughness was too crude, or because the range of variation in roughness that we found was not large enough to produce an effect.

The high elevation forest at Cerro de la Muerte is subject to extreme seasonality and fluctuations in light conditions, temperature, and moisture regimes. Therefore, it is not surprising that our results conflict with a study conducted in the cloud forest at Monteverde, which found that waxy leaves had decreased epiphyll cover and rough leaves had increased epiphyll cover (Ginsburg et al. 1995). It is possible that epiphylls at Cerro de la Muerte have a greater ability to adhere to leaf surfaces than at Monteverde, or that different species of epiphylls exist in the two habitats. We recommend further study on how the distribution of epiphylls on different leaf morphologies varies between different ecosystems, to elucidate how environmental conditions affect epiphyll attachment.

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ABUNDANCE OF PHORETIC MITES ON PASSALID BEETLES

S. ALLIE HUNTER, JONATHON C. RAFFENSPERGER AND ELVINA C. CHOW

Abstract: Two species of passalid beetles coexist within decomposing oak logs in Costa Rican montane forests. Both beetle species are infested by two species of phoretic mites, whose relationship to their host organism (parasitism, commensalism or mutualism) is unknown. The larger mite species was found to be more abundant on the larger beetle species, while smaller mites were more abundant on the smaller passalid species. We also quantified approximate volume and mass of beetle individuals, regressed mass on volume, and calculated residuals in an attempt to remove volume effects on mass. We then correlated residual mass with mite abundances, to explore patterns that may result from mite-beetle interactions. However, we recognize that a rigorous analysis would include examination of allometric relations, which typically cause changing relationships among size metrics, and also between size and mass metrics, as animals increase in size.

Key Words: montane tropical forest, mutualism, parasitism, passalid beetles, phoretic mites

INTRODUCTION

Two species of passalid beetles (Coleoptera: Passalidae) co-exist under decomposing oak logs in the high elevation montane forests of Costa Rica. The species are similar in all aspects of their appearance except size; one is larger (~4.6 cm in length, henceforth referred to as beetle species A), and the other smaller (~2.5 cm, beetle species B). There are at least two species of phoretic mites found on these beetles (mite species 1: smaller, more mobile, tan, with longer legs and antennae, and mite species 2: larger, rounder, reddish with short appendages). There are more mites on larger beetles (Baptista et al. 1998), but little is known about whether the relationship between the mites and the beetles is parasitic, mutualistic or commensal. In this exploratory study, we collected data on several metrics (size and weight) on both beetle species, and correlated these with counts of mites on individual beetles. Our motivation was to expose patterns and trends that could conceivably result from effects of the mites on the beetles (e.g. beetles that have low weight/volume ratios may be in poor health due to parasitism by mites).

METHODS

On 28 January 2005, we collected beetles from under fallen trees on the eastern part of the Loop trail from the lookout to the "flat bench" area in the predominantly oak forest north of Cuerici Biological Station, Cerro, Costa Rica. We haphazardly sampled under 28 logs, and collected all beetles encountered (between one and four per log). We quantified the abundance of each mite species on each beetle, using a hand lens and a white surface to increase contrast. For each beetle, we measured the length from tip of mandibles to end of abdomen, width at widest point, and depth from dorsal to ventral surface.

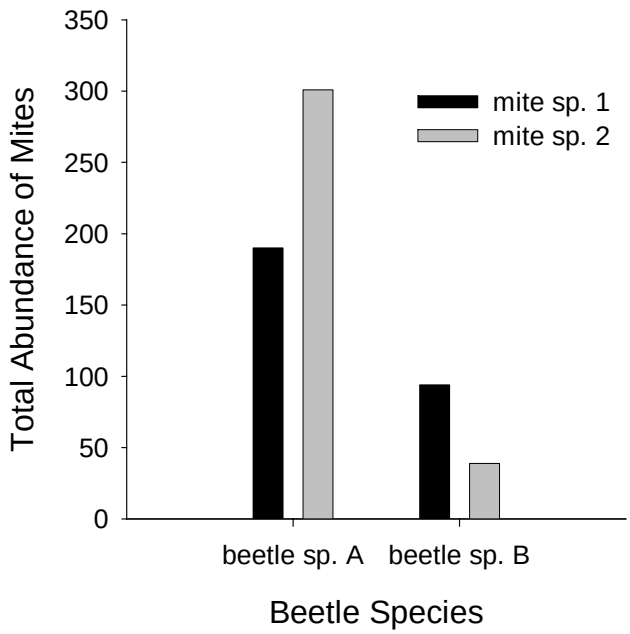

Figure 1. The abundance of mite species 1 and 2 on beetle species A (n = 13) and B (n = 33) (X2 = 41.9, df = 1, P = 0.05).

We then weighed the beetles using a 5 g spring scale for beetle B and a 60 g spring scale for beetle A. Each beetle was released near the log from which it was collected.

To analyze the data we used linear regressions in JMP 5.0.1, using the residuals of a mass to volume regression to remove the effects of volume on mass. (Note, however, that non-linear allometric relations, which are common in animals, can confound this "removal" of effects. We did not check for non-linear relations). We also performed a Chi Square test of homogeneity to identify the proportional differences in abundance of the two mite species on the two host beetles. Expected values were determined using the formula [(mite sp. on beetle sp.)/(total mites on beetle sp.) x total mites]. Our data met the assumptions for parametric tests.

RESULTS

We found 47 beetles total, 13 of the larger beetle (sp. A) and 33 of the smaller beetle (sp. B). There was a significantly greater proportion of mite sp. 1 on beetle sp. B, and of mite sp. 2 on beetle sp. A (Fig. 1). Mite sp. 1 was more abundant than mite sp. 2 on beetle sp. B, while this relationship was reversed on beetle sp. A. The mean number of mites of both species was greater on beetle sp. A than beetle sp. B (Table 1).

We found no relationship between residual mass of beetles (including both species in the analysis) and total abundance of mites ($r^2 = 0.0001$, df = 1, P = 0.94). After separating the data by beetle species, there was still no significant relationship (beetle A: $r^2 = 0.06$, df = 1, P = 0.40, beetle B: $r^2 = 0.06$, df = 1, P = 0.29). These results indicate that there was no effect of total mite abundance on residual beetle mass.

For beetle sp. B, however, there was a positive relationship between abundance

Table 1. Mean mass of each passalid beetle species, and mean mite abundances of each beetle species.

	Mass (g)(±SE(n))	Mite sp. 1/ beetle	Mite sp. 2 / beetle
Beetle sp. A	4.45 ± 0.09 (14)	14.6 ± 1.4	23.2 ± 2.0
Beetle sp. B	0.8 ± 0.05 (33)	3.1 ± 0.9	1.3 ± 1.3

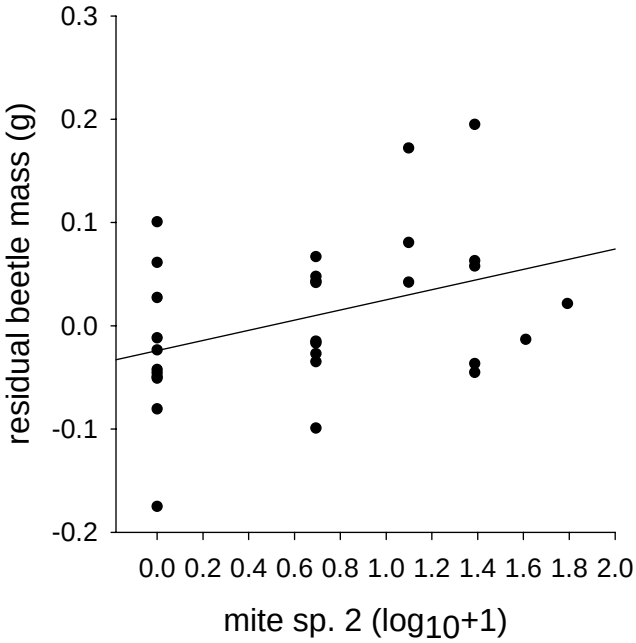

Figure 2. The relationship between residual mass of beetle sp. B and number of mite sp. 2 (r2 = 0.15, df = 1, P = 0.04).

of mite sp. 2 and residual mass (Fig. 2) and a negative relationship between abundance of mite sp. 1 and residual mass (Fig. 3). No relationship was found between mite abundance and residual mass of beetle sp. A. All analyses on residual mass assume, as noted above, that relations between volume and mass were linear.

DISCUSSION

While there was no general effect of mite abundance on residual mass, abundance of mite sp. 1 and mite sp. 2 individually seemed to have opposing effects on the residual mass of the smaller passalid beetle species.

The higher proportional abundance of mite sp. 1 on beetle sp. B and of mite sp. 2 on beetle sp. A (Fig. 1) could result from size differences between the mite species. The larger, more rotund mites of sp. 2 may require large gaps in the exoskeleton of their host in which to attach, which would be scarce on small beetles but more plentiful on larger passalids. Small mites of sp. 1, which could occupy tight spaces in the carapace of a small beetle, might be excluded from many of the corresponding areas on the large beetle species by larger mites. Our study was limited by sample size, imprecise weighing techniques and a lack of attention to allometric relations which can strongly affect the relations among metrics as animals increase in size. Even if mite-beetle interactions do influence the relations between beetle volume and residual mass, one must consider carefully when the effects of mites on a beetle may have occurred, relative to the timing of molting events. For all these reasons, we do not attempt to interpret the patterns (or, in some cases, lack of patterns) in the rela-

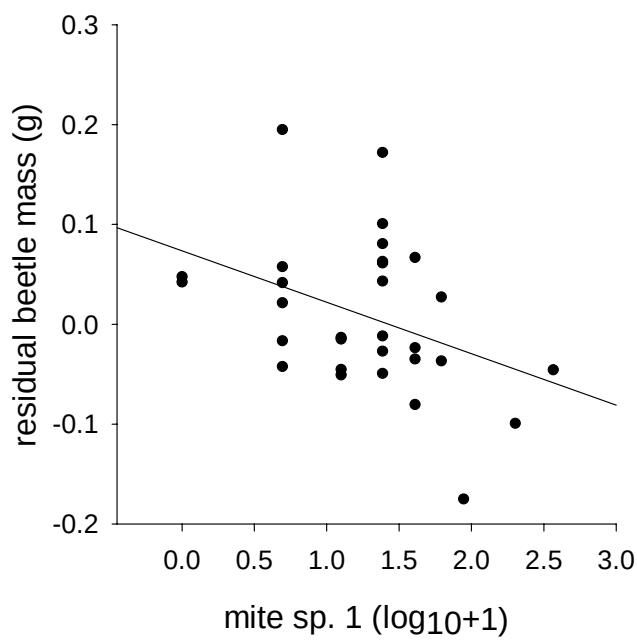

Figure 3. The relationship between residual mass of beetle sp. B and number of mite sp. 1 (r2 = 0.15, df = 1, P = 0.03).

tions between beetle volume and mass. We include those results for the benefit of other researchers who may be interested in a more complete analysis of those relations.

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EFFECTS OF TIDE ON THE PATTERNS OF FISHING ACTIVITY IN *NOCTILIO LEPORINUS*

DANIEL J. MADIGAN AND CHAD M. VALDERRAMA

Abstract: The greater bulldog bat, *Noctilio leporinus*, forages for fish mostly at high tide, and displays two types of fishing behavior depending upon the presence or absence of jumping fish. Using infrared binoculars, we observed bat hunting behavior to assess differences in fishing patterns between high and low tides. We followed individual bats and recorded hunting patterns, time fishing, and number of fishing attempts. Bats showed target-orientated circular-flight hunting behavior during high tide and linear-flight hunting behavior during low tide, probably as a response to fish abundance. This suggests that bats alter their hunting modes with resource availability, probably to maximize foraging efficiency.

Key Words: bulldog fishing bat, foraging efficiency

INTRODUCTION

Noctilio leporinus, the greater bulldog bat, is a nocturnal fishing bat that relies on echolocation to find its prey. After it locates a fish, it dips into the water attempting to spear fish with its claws or scoop fish into the pouch between its legs (Brandon 1983). The bat is only successful in catching fish once every 50-200 passes through a hunting area (Schnitzler et al. 1994). The bat has two main hunting modes. When there are fish jumping, the bat performs circular high flight searches, dipping when it detects a fish. When fish jumping is absent, the bat flies low, sweeping in a linear, trawl-like fashion through areas where it has fished successfully in the past (Schnitzler et al. 1994).

We studied bat hunting activity at the Rio Sirena Lagoon at Corcovado National Park, Costa Rica, in which the greater bulldog bat fishes predominantly at high tide (Yale et al. 1998, Veysey et al. 2000). There are higher fish abundances at high tide in the lagoon (Leslie et al. 2001). We hypothesized that the hunting patterns of the greater bulldog bat would change with tide, and that the bats would prefer high flying circular patterns at high tide when there are more fish and low flying linear patterns at low tide when there are fewer fish.

METHODS

Our study was conducted in the Rio Sirena Lagoon in Corcovado National Park. We observed *N. leporinus* fishing behavior for 4 h on two nights on 2-3 February 2005. These two sessions occurred during a high tide and a low tide on each night, beginning at 2100 and 0400 the first night and at 1730 and 2330 the second night. Using infrared night vision binoculars, we followed individual bats, recording time spent fishing (run time), fishing pattern (circular or linear), and number of dips into the water (attempted fish captures), until the individual was no longer

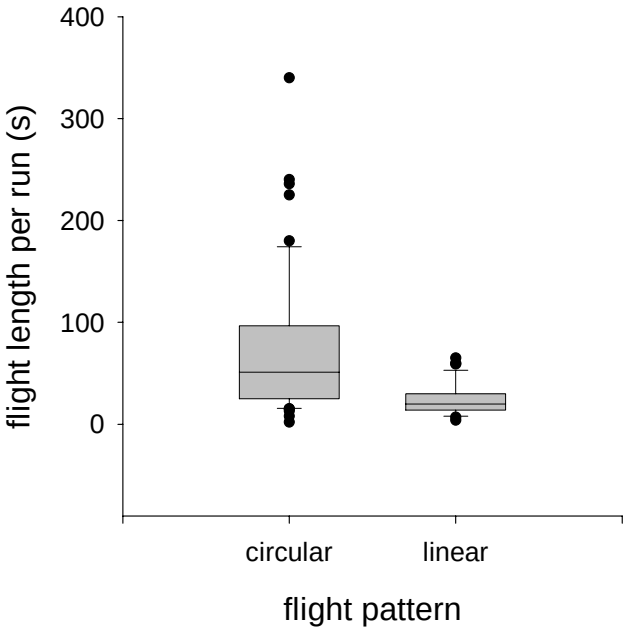

Figure 1. Flight length per run (s) of bulldog bats with respect to flight pattern. Circular flight patterns were significantly longer than linear flight patterns (n = 89, P < 0.001). Mean flight length and quartiles ± SE are shown for each flight pattern. Dots indicate observations >2 SE from the mean.

visible. Number of dips and flight time were used to estimate fishing efficiency for each observed bat. Bat patterns over the water were assessed as linear or circular. In circular mode, the bat cycled over a given region of the lagoon at least twice; in linear mode, the bat swept low over the lagoon once, sometimes dragging its feet in the water, and flew out of sight. Water velocity was assessed every 30 min by recording the travel time of a floating stick over 10 m, and relative tide was assessed by observing water level.

A contingency analysis was performed to assess differences in hunting patterns between different tides. Differences in bat fishing patterns with respect to run length, number of dips, and dips/run were analyzed with multiple ANOVAs. We analyzed these data using JMP 5.0.1 and verified assumptions of parametric tests before conducting analyses of variance.

RESULTS

Bat fishing patterns differed between tides, with more circular patterns at high tide and greater occurrences of linear, low flying patterns at low tide (X^2 = 47.08, df = 81, P < 0.0001, Table 1). Circular fishing runs lasted significantly longer (73.9 ± 10.1) than linear fishing runs (22.1 ± 2.6; F = 15.92, df =1, 85, P < 0.001, Fig. 1) and resulted in more dips/run (7.5 ± 1.2) than did linear pattern fishing (3.1 ± 0.5; F = 7.61, df =1, 87, P < 0.01, Fig. 2). However, the number of dips/minute did not differ between circular (7.9 ±1.1) and linear (8.7 ± 1.1) fish-

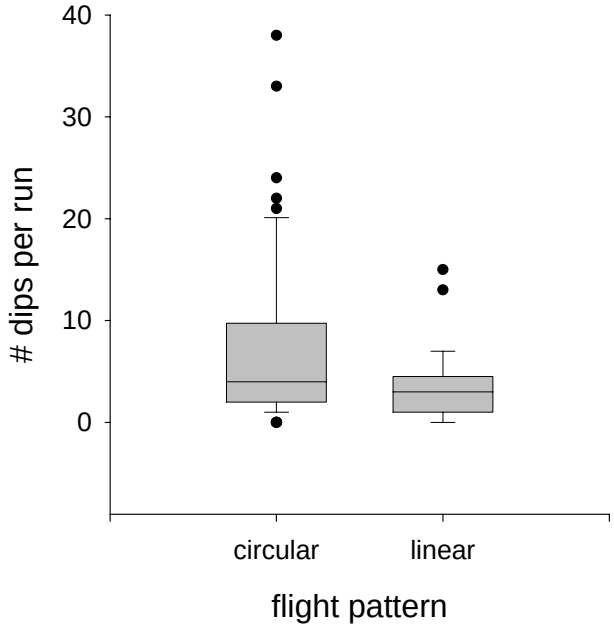

Figure 2. Number of dips per run of bulldog bats with respect to flight pattern. Circular flights had a greater number of dips per run than linear flights (n = 89, P < 0.001). Mean dips/run and quartiles ± SE are shown for each flight pattern. Dots indicate observations >2 SE from the mean.

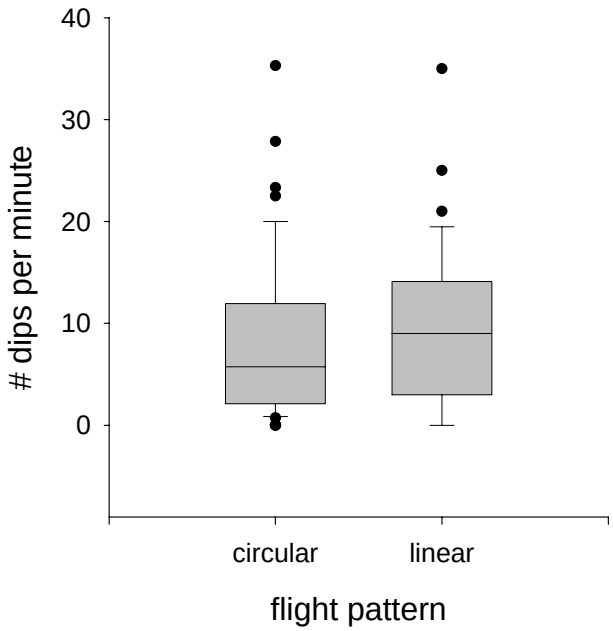

Figure 3. The number of bulldog bat dips per minute during one run with respect to flight pattern. The number of dips per minute during a circular run is not significantly different from the number of dips per minute during a linear run (n = 89, P = 0.96). Mean dips/minute and quartiles ± SE are shown for each flight pattern. Dots indicate observations >2 SE from the mean.

ing patterns (F = 0.64, df =1, 85, P = 0.43, Fig. 3).

DISCUSSION

As expected, the bats used high flying circular fishing patterns during high tide, when fish were more available. During low tide, when fish are scarce (Leslie et al. 2001), bats used low flying linear fishing patterns, probably where they have previously been successful in obtaining fish.

Greater run length in circular fishing patterns may indicate that runs in this hunting mode are generally longer, or that the fishing bat performs longer runs during high tide. Greater dips/run in the circular fishing mode suggest that bats make more attempts at catching fish during circular runs than in linear runs. However, bats were much easier to follow for longer periods of time during circular flight, and both of these relationships may have been results of this sampling bias.

We were unable to determine the success of bat fishing attempts, as after catching a fish the bats either transferred the fish to their mouths while in flight or flew off to roost and eat (Brandon 1983). Dips/min was the only indicator we had of fishing efficiency. Based on this measure, our results suggest that though the two fishing methods differ in flight patterns and fish-targeting, neither is more efficient with respect to dips per unit time.

This study showed a significant difference in fishing patterns of the greater bulldog bat at high and low tide. The use of infrared binoculars allowed us to follow individuals, allowing the opportunity to observe runs by individual bats, an important first step in assessing the foraging efficiency of this bat. The two fishing types probably differ in energy expenditure per unit time and fish-capturing efficiency. Further studies could quantify these unknown variables to better understand the tradeoffs between circular and linear fishing in greater bulldog bats.

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Table 1. Contingency analysis for observations of circular (n = 52) and linear (n = 37) fishing patterns during high and low tides. Column percentages represent the proportion of observations for the column patterns during the row tide; row percentages represent the relative proportions of circular and linear patterns observed during that tide.

Count	Circular	Linear	Total
High tide	20	1	21
High tide (incoming)	10	5	15
High tide (outgoing)	13	1	14
Low tide (incoming)	9	21	30
Low tide (outgoing)	0	9	9
Total	52	37	89