Distribution and abundance of Tipulid larvae in bamboo litter clumps in a high-elevation Costa Rican forest

Matthew T. Kemp and R. Quinn Thomas

Abstract: We investigated factors influencing the distribution and abundance of Tipulid larvae living in a unique microhabitat: clusters of organic matter trapped in stem nodes of *Chusquea longifolia* bamboo. We hypothesized that nodes with high amounts of organic matter would contain high densities of tipulids, and that tipulid abundance would be higher in the understory of primary forest than in secondary habitat. We sampled bamboo plants in each habitat and found that tipulid abundance was positively related to organic matter content, but was unaffected by habitat type. The community of invertebrates and microorganisms in bamboo litter clumps remains a largely unstudied system, though this abundant microhabitat may be important to numerous populations within the fauna of high-elevation forest.

Key words: Chusquea longifolia*, cranefly, litter trap, Tipulidae*

Introduction

The shoots of *Chusquea longifolia,* a common understory bamboo species on Cerro de la Muerte (Janzen 1989), contain a series of cuplike nodes (dense groups of leaf stems emanating from a single point on the main stem) which catch leaves and other debris and often hold a small amount of fine particulate organic matter. On 27 January 2004 at Cuerici Biological Station, we observed several cranefly (Tipulidae) larvae embedded in these organic matter traps. Tipulid larvae have not previously been noted in this unique microhabitat; their more common larval habitat is aquatic, although some are known to inhabitat terrestrial plants and fungi (Borror and Delong 1964, M. Ayres pers. comm.).

We examined the effects of organic matter accumulation and habitat type on the distribution and abundance of these bamboo-living tipulids. Because tipulids generally feed on decaying plant material (Borror and Delong 1964), we hypothesized that the number and biomass of tipulids in a particular node would be related to the amount of organic matter trapped in that node, with more organic matter supporting more tipulids. We also tested differences in tipulid number between secondary growth and the understory of primary forest, predicting that greater litter fall into the nodes of understory bamboo would lead to greater tipulid abundance and biomass in this habitat.

Methods

Our study site was Cuerici Biological Station (elev. 2580 m), near Cerro de la Muerte, Costa Rica. On 29 January 2004, we sampled tipulids inhabiting bamboo along trail transects in two habitats, secondary growth and primary forest understory. Transects (one in each habitat) were at similar elevations and consisted of eight points 10 m apart. At each point, we alternated sampling on the right and left side of the trail and located the nearest stand of bamboo shoots at least 2 m off the trail. Stands were defined as a tight cluster of individual bamboo shoots (usually 10 - 20) that formed a group distinctly separated from other bamboo. Within the stand we selected two shoots; the one with the most organic matter (high OM) and the one with the least (low OM) to ensure an adequate range in our measures. Organic matter was defined as matter collected in the crotch of the node. At each shoot, we clipped off and bagged

the node with the most organic matter, along with the node above it. We then sorted each sample for tipulids and organic matter and measured the mass of each tipulid. The organic matter was filtered through a 0.5 mm mesh to eliminate coarse material, leaving only FPOM which is the size of OM used by tipulid larvae, then weighed. We evaluated tipuloid abundance with a general linear model that included habitat type (primary forest vs. secondary growth), stand nested within habitat type (defined as a random effect), OM mass (continuous variable), and the interaction between OM mass and habitat.

RESULTS

We found a total of 29 tipulid larvae, 19 on understory bamboo plants and 10 on secondary bamboo plants. All nodes on which tipulids were found contained some amount of organic matter, although a few tipulids were found in nodes with very low amounts. There was a strong correlation between tipulid number and tipulid biomass per node ($r = 0.90$), so we only report statistical results for tipulid number.

There was a significant effect of OM mass on tipulid number ($F_{1,17} = 20.67$, $P < 0.0001$). Effects of habitat ($F_{1,17} = 0.95$, $P = 0.35$), stand ($F_{14,17} = 1.16$, $P = 0.33$), and the interaction of OM mass and habitat ($F_{1,17} = 2.75$, $P = 0.10$) were not significant (Fig. 1).

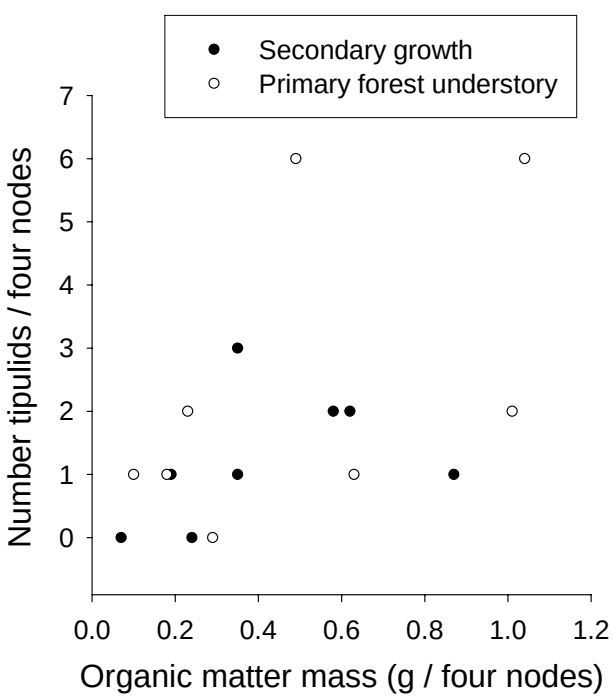

Figure 1. Abundance of tipulid larvae associated with bamboo vs. organic matter captured within bamboo branching nodes. Each point represents one bamboo stand within one of two habitat types.

DISCUSSION

Our results supported the hypothesis that greater organic matter accumulation in bamboo nodes leads to greater numbers and biomass of tipulid larvae. However, our second hypothesis, that tipulids would be more abundant in understory than secondary habitat, was not supported. Contrary to our expectations, the amount of organic matter within bamboo nodes did not differ between habitat. Nevertheless, we cannot entirely discount the possibility that habitat type influences tipulid larvae abundance, because we did find nearly twice as many tipulids in understory bamboo than in secondary growth. Future studies should further investigate this trend, as well as other potential mechanisms influencing tipulid distribution and abundance, such as age and density of bamboo stands, sunlight, temperature, and preferred habitat of adult craneflies.

If the tipulids we investigated are bamboo node specialists, it is likely that the local population dynamics of tipulids are closely linked with the occurrence of *C. longifolia* bamboo. Because *C. longifolia* populations in this region have a synchronized, semelparous life history (fruiting and dying at approximately 25 - 30 year intervals; Carlos Solano, pers. comm.), the bamboo-node microhabitat must sometimes disappear over large areas, depriving the tipulids

of their larval environment. The degree of specialization of tipulids on this microhabitat should be examined to understand the effects of bamboo life history on tipulid population dynamics.

Also, another species of bamboo, *Chusquea subtessalata,* occurs at slightly higher elevations at Cuerici, and studies of the differences in tipulid habitat quality between these two species would be valuable. Casual searches revealed some tipulids in *C. subtessalata* nodes but densities appeared to be much lower than on *C. longifolia* (M. Kemp, pers. obs.), perhaps because the high-elevation bamboo species does not have dense, litter-collecting nodes.

Litter clumps on bamboo shoots constitute an unexplored microhabitat that presents exciting opportunities for novel natural history and in-depth ecological investigation, especially given the prevalence of *Chusquea* species in high-elevation forests. Although tipulid larvae were the most common and obvious members of this "bamboo node fauna," we observed a surprising diversity of other arthropods, including members of Aranea, Coleoptera, Diplura, Hemiptera and Lepidoptera; a wealth of microorganisms, fungi, and mites must also be present as well. We hope that our basic findings will stimulate further studies of this unique community.

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NECTAR VOLUME DISTRIBUTION AND CHARACTERISTICS OF THE HUMMINGBIRD-POLLINATED FLOWER *CENTROPOGON TALAMANCENSIS*

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Abstract: Centropogon talamancensis is a flower pollinated by the hummingbird *Eugenes fulgens*, and is susceptible to nectar robbing by *Diglossa plumbea*. Feinsinger (1978) found that nectar volume in hummingbird-pollinated flowers at Monteverde was unevenly distributed within plants, with most flowers containing no nectar. The benefits to plants of this bonanza reward system may be a feature of pre-montane cloud forests, or may be ubiquitous among hummingbird pollinated flowers. To test these alternatives, we measured nectar distributions in *C. talamancensis* at Cerro de la Muerte. We found that *C. talamancensis* in montane forests also provide highly variable nectar rewards. Additionally, we hypothesized that pollinators would be unable to predict nectar reward from external characteristics; as predicted, neither corolla length nor the number of scars from nectar robbers were correlated with nectar volume. Apparently, the bonanza reward system is not restricted to pre-montane cloud forests, and may be a common component of hummingbird - flower interactions.

Key words: Bonanza!, Cerro de la Muerte, corolla length, Diglossa plumbea, Eugenes fulgens, *flowerpiercer, pollination*

INTRODUCTION

Centropogon talamancensis, a pink flower with a long, curved corolla, supplies a nectar reward to the magnificent hummingbird, *Eugenes fulgens*, a specialist pollinator. The nectar of *C. talamancensis* may also be stolen by *Diglossa plumbea*, the slaty flowerpiercer, a specialist nectar robber. In a study of ten species of hummingbird-pollinated plants in Monteverde, Costa Rica, Feinsinger (1978) found that nectar volume was unevenly distributed within plants, with most flowers containing no nectar and a few containing copious nectar. Feinsinger (1978) proposed that this pattern of distributing nectar among flowers was adaptive because it maximized the duration of hummingbird visits while minimizing energy expenditure on nectar production. The "bonanza" reward system might be ubiquitous among hummingbird pollinated flowers on flowers, or might be restricted to pre-montane cloud forests. For example, hummingbirds in higher, cooler montane forests might select for more predictable rewards because their energetic demands for thermoregulation are greater. We tested these alternatives by evaluating the nectar reward system in *C. talamancensis* at Cerro de la Muerte.

We also evaluated some more specific details of the reward system. We examined the relations among nectar volume, corolla length, number of flowers per plant, and frequency of nectar robbing for *C. talamancensis*. Under Feinsinger's adaptive model, pollinators should be unable to predict nectar reward from external characteristics. So we predicted that corolla length would be unrelated to nectar volume, as any correlation would result in selective pollination. Similarly, we predicted that nectar-robber scars would not vary with nectar volume, as nectar-robber birds should not be able to determine nectar volume before puncturing flowers.

METHODS

We placed individual cloth bags (to preclude nectar consumption) over 42 open *C. talamancensis* flowers on 17 plants along the west end of the loop trail north of the Cuerici Biological Station, Cerro de la Muerte, Costa Rica, be-

tween 0745 and 0900 on 29 January 2004. "Plants" were defined based on aboveground connections of stems and/or vines. We removed the bags 24 h later and measured nectar volume of each flower with a 20 µl capillary tube. We also measured the corolla length of each flower from the base of the bud to the tip of the longest petal and counted the number of open flowers per plant and number of nectar-robber scars. We used a one-way ANOVA model to test for variation among plants in nectar volume and corolla length. Prior to analyses, we log-transformed nectar volume + 1 to improve normality.

RESULTS

The distribution of nectar volume in *C. talamancensis* was highly variable, with 55% of flowers offering no nectar reward to pollinators (Fig. 1). Of open flowers, 29% had one or more nectar-robber scars (range = 0 - 57% among plots with ≥ 5 flowers). There were between 1 and 16 open flowers per plant. The mean corolla length ± 1 SE was 4.55 ± 0.05 cm. Corolla length differed significantly between plants ($F_{16,25}$ = 3.83, P = 0.001).

A correlation matrix revealed no significant relationships among corolla length, number of flowerpiercer scars, number of flowers per plant, and nectar volume (Table 1). Also, evaluation of all possible multiple linear regression models showed that no combination of variables (paired or all three combined) could explain a significant fraction of the variation in nectar volume.

DISCUSSION

C. talamancensis at Cerro de la Muerte displays the uneven nectar distribution reported by Feinsinger (1978) from a different ecosystem. This could be an adaptation of plants to manipulate the visitation behavior of hummingbirds. Results supported some predictions de-

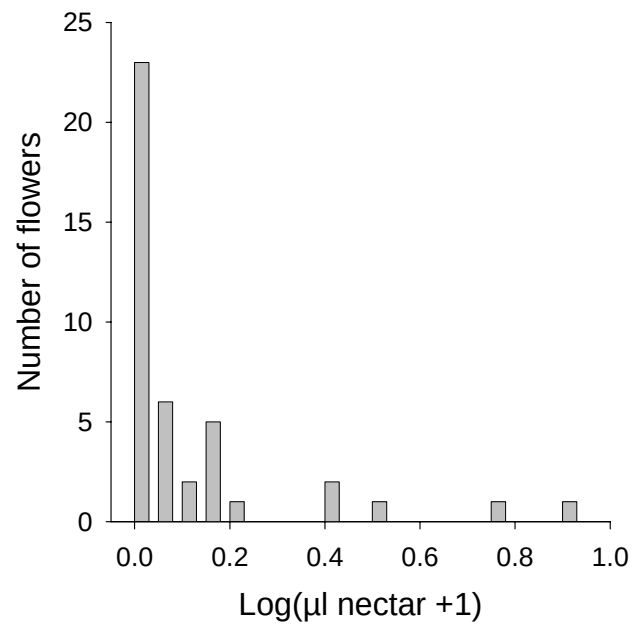

Figure 1. Frequency distribution of nectar secretion per flower in *C. talamancensis* at Cerro de La Muerte, Costa Rica. Values represent log-transformed nectar volumes per flower (n = 42).

Table 1. Correlation matrix of *C. talamancensis* flower characteristics measured at Cerro de la Muerte (n = 42 flowers). No correlations were statistically significant.

	Corolla length (cm)	Nectar-robber scars	Flowers per plant	Nectar volume (µl)
Corolla length (cm)	-	0.05	-0.24	-0.18
Nectar-robber scars	-	-	-0.18	-0.04
Flowers per plant	-	-	-	-0.16
Nectar volume (µl)	-	-	-	-

rived from this adaptive explanation. Specifically, there was no correlation between corolla length and nectar volume, which might be expected if nectar volume was just an artifact of variation among plants short in carbohydrate supplies for flower expansion and nectar production. If hummingbirds could determine nectar volume through external characteristics, such as corolla length, then hummingbirds would likely only visit flowers that offered high rewards. Similarly, nectar-robber scars were also unable to predict which flowers contain the most nectar, as the number of previous nectar-robber scars and nectar volume of a flower were uncorrelated. In addition, individual plants varied significantly in the corolla length of their flowers but not in their nectar distributions. Flowers of *C. talamancensis* apparently provide variable nectar volume without providing obvious external characteristics, which presumably compels hummingbirds to visit more flowers.

Bonanza reward systems may be a rather general feature of hummingbird pollinated plants even across climatic zones that must create quite different energetic challenges for the hummingbirds. To our knowledge, it remains unknown whether insect pollinated plants in these same systems also tend to create bonanza reward systems. It might work for the same reasons as it does with hummingbirds, or it might not because insects learn differently or have different innate responses to variable reward systems.

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EFFECT OF POLLINATOR TYPE ON PLANT DENSITY AND MORPHOLOGY

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Abstract: Animal pollinated plants face challenges that include attracting pollinators as well as maximizing the probability of genetic outcrossing. Plant density can affect the reproductive success of insect pollinated plants differently from that of hummingbird pollinated plants. We hypothesized that there would be a difference in the number of flowers per plant because hummingbird pollinated plants must attract pollinators from a distance, while insect pollinated plants must maximize cross-pollination. We also predicted differential success in seed set would influence the size of conspecific patches of plants. However, pollinator type was unrelated to flowers per plant or plants per patch. Instead there were strong differences among plant species within pollinator guilds.

Key words: flowers, hummingbirds, insects, pollination, pollinator guilds

INTRODUCTION

The agents of plant pollination are primarily wind or animals. Plants that exploit animal pollinators must both attract pollinators and maximize the probability of genetic outcrossing via that pollinator. These challenges have led to a variety of strategies, especially involving flower morphology and nectar reward systems. Some plants are generalists, trading off wasted nectar and pollen to take advantage of many visitors; many others have specialized on a particular pollinator species to increase cross-pollination events, although they then become dependent on the existence of that pollinator (Begon et al. 1990).

In the tropics, where a majority of flowering plants use animal pollinators, two particularly important subsets of pollinators are hummingbirds and insects. Bird and Canny (1996) showed that insect-pollinated plants in patches have a higher reproductive success than solitary individuals, but that solitary hummingbird-pollinated plants have a reproductive success that is equal to or higher than individuals in patches. They suggested that this was because an insect expends proportionally more energy to travel the same distance as a larger hummingbird. Thus, insects tend to pollinate plants that are close together, so small isolated patches of insect pollinated plants should grow smaller while high density patches grow larger (assuming that seeds frequently fall close to the parent). On the other hand, plant species that are pollinated by hummingbirds, which can easily travel longer distances, may have a higher reproductive success in isolation where their chances of self-pollination are decreased. Plants that are aggregated in a way that matches pollinator behavior might leave relatively more offspring than plants that are not.

Plant morphology also contributes to the success of a plant. Flower density on an individual plant may influence how effectively pollinators of various types are attracted. More flowers may attract visitors from a greater distance, but decrease the chance of exchanging pollen with a conspecific. The optimal number of flowers on a plant may be different for hummingbird-pollinated plants vs. insect-pollinated plants.

Because plants tend to be pollinator limited, pollination success is a strong selective pressure on flowering plants. We hypothesized that plant densities would reflect the influence that pollination success has on flowering plant distributions, predicting that insect pollinated plants would be found in greater densities than hummingbird pollinated plants. We also hypothesized that the type of pollinator would be

related to plant flower density, predicting that insect-pollinated species would have fewer flowers per individual than hummingbird-pollinated species.

METHODS

We sampled six flowering plant species (three presumed to be hummingbird pollinated and three presumed to be insect pollinated) in a 2 ha field north of the biological station in Cerro de la Cuerici on 29 - 30 January 2004. For each species, we sampled all flowering and non-flowering conspecifics within at least five patches. Patches (defined by the presence of at least one flowering individual) were haphazardly selected within the field. Patches were defined by a boundary rule; to be scored as within the patch, a plant had to be within 1 m or 5 m (insect-pollinated vs. hummingbird-pollinated) of another conspecific plant already within the patch. We then estimated the size of each patch (by measuring the area defined by the boundary), and the density within the patch of plants of that species (with "plant" defined based on the presence or absence of above-ground connections).

We determined plant density by dividing the number of plants by the patch area. We standardized for plant size differences by dividing the number of flowers per plant by plant height. We summed these flower values for all plants with at least one flower within each patch to calculate flower density. Both flower density and plant density data were log transformed to correct for non-normality. We tested for patterns in plant density with an ANOVA model that included pollinator guild and species nested within pollinator guild. We tested for patterns in flower density with an ANOVA model that included pollinator guild, species nested in this guild, and patch nested within species (with patch as a random effect); this analysis excluded plants without flowers.

RESULTS

Plant species within guilds varied strongly in plant densities ($F_{5,145} = 25.63$, $P < 0.0001$) and flower densities ($F_{5,142} = 29.31$, $P < 0.0001$; Table 1). Plant density was not related to pollinator guild ($F_{1,98} = 0.08$, $P = 0.94$), but varied among species ($F_{4,98} = 6.25$, $P = 0.0002$). Similarly, flowers per plant was not related to pollinator guild ($F_{1,117} = 1.54$, $P = 0.28$), but varied among species ($F_{4,117} = 7.27$, $P = 0.0002$). Flowers per plant did not vary among patches ($F_{25,117} = 1.15$, $P = 0.09$).

Table 1. Mean (± SE) plant density and flowers per plant for six species, studied at Cerro de la Muerte, Costa Rica.

Plant name	Pollinator guild	Plants per m^2	Mean flowers per plant
Bomeria spp.(Alstroemeriaceae)	hummingbird	23.6 ±19.3	18.2 ±5.8
Uncaria torrentosa? (Rubiaceae)*	hummingbird	0.4 ±0.2	105.2 ±36.8
Centropogon talamancensis (Lobeliaceae)	hummingbird	61.1 ±23.7	36.9 ±13.5
Monnim xalapensis (Polygalaceae)	insect	14.2 ±3.9	40.4 ±1.9
Monochaetum spp.(Melastomataceae)	insect	4.9 ±2.8	20.5 ±5.1
Dahlia spp.(Asteraceae)	insect	3.3 ±1.7	5.1 ±1.5

*known by locals as Uña de gato, but this may be incorrect identification

Discussion

Our results strongly refuted both hypotheses. Plant species, not pollinator guild, was the main determinant of plant density per patch and flowers per plant. Patches within species did not differ, reinforcing the conclusion that species identity explains most of the variation seen in local plant density and flowers per plant. Apparently factors other than pollinator type are important in determining plant density and flowers per plant.

One interpretation is that selection acts at a finer scale than the broad guilds we defined. Each species may have a different subset of insects or hummingbirds with different idiosyncratic preferences for floral patches of different sizes. Future studies could evaluate whether differences in flower morphology relate to pollinator subsets that are more specific than those recognized in this study.

Pollinators, by affecting plant reproductive success, may influence plant density by affecting how many seeds are available for dispersal in different patches. Other factors, such as interspecific competition, microhabitat quality, and dispersal limitation, may however have more influence on plant density than pollinator selection pressure. Future studies could explore the interaction of other factors that may determine flowering plant densities at a larger scale than within individual patches. The relative importance of these mechanisms could be tested by mapping flowering plant distributions and measuring distances between conspecific patches as well as soil quality and light availability for each patch. Despite the selection pressure of pollinators on pollinator-limited plants, other factors are influential and cause species specific variation in plant and flower density. Varying the scale of the study and increasing the number of species tested could help to determine which factors are most influential on these plant characteristics.

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THE EFFECT OF MYCORRHIZAE ON BAMBOO GROWTH

JILL HARRIS AND HEATHER LAPIN

Abstract: In some systems, plant interactions with mycorrhizal fungi can range from mutualism to parasitism depending on the environment. On Cerro de la Muerte two types of bamboo dominate the understory, *Chusquea longifolia* and *Chusquea subtessalata*, and both species are associated with obligate symbiotic mycorrhizal fungi. We tested whether differences in growth rates among bamboo patches could be a function of mycorrhizae symbiosis. We sampled *Chusquea* spp. at Cuerici Estación Biológica and measured bamboo height, density, biomass and mycorrhizal root coverage. All three measures tended to decrease with increasing mycorrhizae coverage. Mycorrhizal fungi could be parasitic in this system, or may just be present in areas of poor soil that lead to low bamboo growth rates.

Key words: C. longifolia, C. subtessalata, Chusquea, *conditional interaction, mycorrhizal fungi, obligate mutualism*

INTRODUCTION

Mycorrhizal fungi are an important part of many forests, particularly in nutrient-poor soils such as those that prevail in many tropical ecosystems (Begon et al. 1990). Depending on conditions, mycorrhizae can be either beneficial or parasitic to the host plant. Mycorrhizae aid in nutrient uptake, enabling plants to grow in areas with poor soil conditions. However, there is a cost to the plant to maintain the mycorrhizal fungi, so if nutrients are readily available without the mycorrhizae, the fungi can become a parasite. Lovelock et al. (1996, as cited in Leigh 1999) found that plants with associated mycorrhizae on roots often have lower growth rates than plants without mycorrhizae.

Two species of bamboo that dominate the understory on Cerro de la Muerte, *Chusquea longifolia* and *Chusquea subtessalata* (McLearn 1999), have an obligate, mutualistic mycorrhizae (Solano and Seely, pers. comm.). Both *C. longifolia* and *C. subtessalata* occur in patches that differ in the size of plants and density of stems. Because *Chusquea* spp. are monocarpic, semelparous, and reproduce synchronously (Janzen 1983), all stems are the same age and differences among patches in plant size must be a result of different growth rates.

We tested whether differences in plant growth rate among *Chusquea* patches could be a function of differences in mycorrhizal relationships. If areas of high *Chusquea* spp. biomass have more mycorrhizae than areas of low *Chusquea* spp. biomass, the implication would be that mycorrhizal fungi are augmenting bamboo growth in this system. However, if areas of low *Chusquea* spp. biomass have more mycorrhizae, the implication would be that mycorrhizae are inhibiting growth.

METHODS

We sampled *C. longifolia and C. subtesselata* along the loop trail at Cuericí Estación Biológica, Cerro de la Muerte, Costa Rica on 29 - 30 January 2004. For each species, we haphazardly chose five areas that appeared to have low bamboo biomass (i.e., low stem density, small plants) and five areas that appeared to have high bamboo biomass (i.e., high stem density, large plants). To quantify bamboo size and density, we recorded the number of shoots of the target species within a 2 m^2 plot and recorded their average height. We calculated an index of biomass per 2 m^2 as number of stems x height (in m).

To estimate mycorrhizal density, we ran-

domly selected three 10 cm lengths of growing, small diameter root from *Chusquea* taken from different points within each 2 m^2 plot. We rinsed the roots with water to remove loose soil and examined them under a dissecting microscope. We ranked mycorrhizae coverage on a scale of zero to five, with zero being no visible fungus and five being a complete fungal sheath.

RESULTS

We observed three or four different mycorrhizae morphotypes on the root samples we examined. The most prevalent were dark, thin hyphae that covered the roots and the root tips. Another morphotype created a clear gelatinous sheath around the roots. In one sample, the mycorrhizae was white and covered the entire root surface.

All three measures of bamboo growth (height, density, and biomass index) tended to decrease as mycorrhizae coverage increased, although results were not significant (Fig. 1). *C. longifolia* height decreased strongly with increasing mycorrhizae coverage (r = -0.57, P = 0.08), and *C. subtesselata* height also decreased with increasing mycorrhizae coverage (r = -0.21, P = 0.55). For both species, density was unrelated to mycorrhizae coverage (*C. longifolia*: r = -0.13, P = 0.72; *C. subtesselata*: r = -0.09, P = 0.81). Biomass of both species tended to decrease as mycorrhizae coverage increased (*C. longifolia*: r = -0.51, P = 0.13; *C. subtesselata*: r = -0.11, P = 0.76).

DISCUSSION

Our results suggest that lower growth rates are associated with high mycorrhizae root

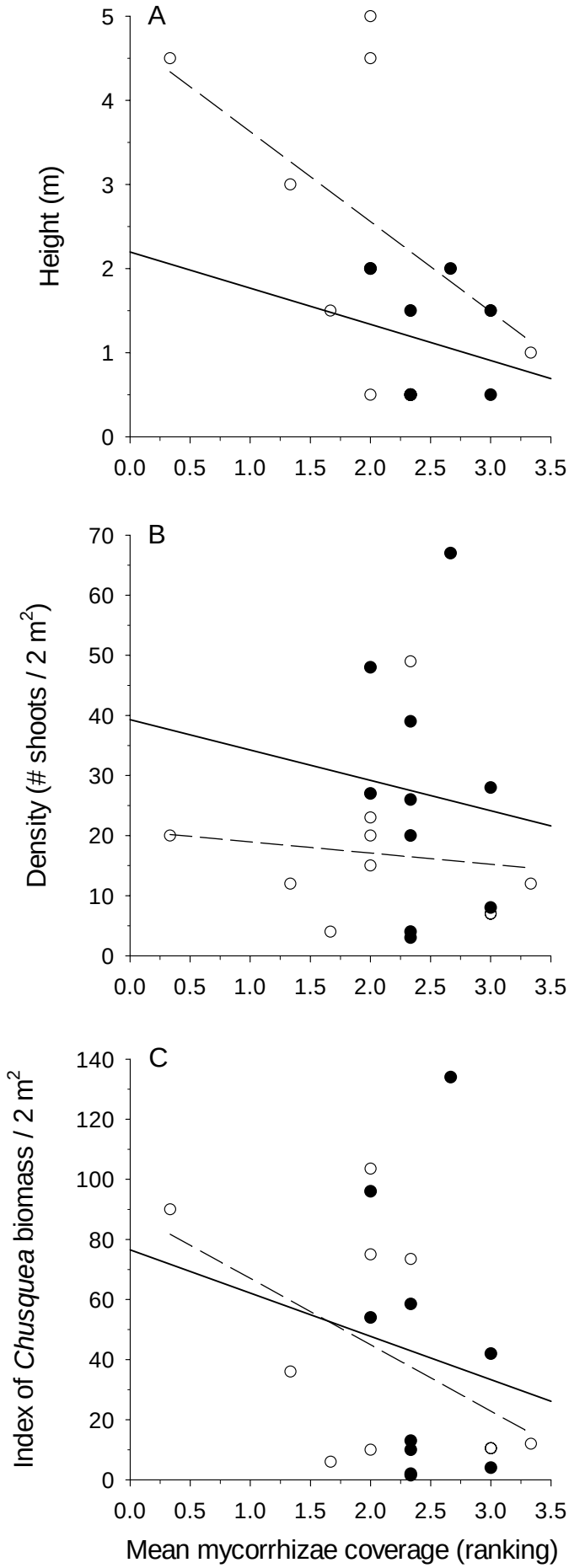

Figure 1. Correlations of height, density, and biomass of *Chusquea* spp. with average mycorrhizae abundance. N = 10 for both species. Open circles, dashed line = *C. longifolia*. Filled circles, solid line = *C. subtesselata*.

coverage. It is possible that in this system, soil nutrients are high therefore mycorrhizal fungi are parasitic on *Chusquea* spp. and decrease bamboo growth rates. Stem density was unrelated to mycorrhizae coverage, suggesting that mycorrhizal fungi do not limit the number of shoots but instead worsen growing conditions for existing plants.

Another explanation for the results could be that bamboo growth rates are low in certain areas because of low soil nutrients. In these areas *Chusquea* may invest heavily in its fungal symbionts, so mycorrhizae are abundant even though they cannot improve growth rates to be equal to rates in nutrient-rich soils. One way to test these two theories would be to manipulate mycorrhizal abundance across different soil types.

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Density dependence of passalid beetles in a high elevation oak forest

Brenda M. Whited, J. Khai Tran, Sarah E. B. Fierce and Paul A. Marino

Abstract: Two species of passalid beetles occur within oak logs of high elevation tropical forests. They form social colonies in which adults feed larvae. On Cerro de la Muerte, the two species tended to co-occur within logs more often than expected by chance, suggesting facilitation, mutualism, or parasitism. Local populations within logs did not appear to be influenced by either positive or negative density dependence, and many apparently suitable logs were unoccupied. It may be that immigration and emigration are the prevailing processes at the level of habitat patches (logs) and that density dependence and population regulation mainly arise at the level of metapopulation. We found no direct evidence of dispersal limitation, but did find that beetles were more likely to occupy relatively larger logs.

Key words: Coleoptera, colony, density dependence, dispersal, oak forest, resource limitation

Introduction

Passalid beetles (Coleoptera: Passalidae) are a unique family of beetles in that they exhibit social behavior. Colonies of mature adults and immature larvae occur in rotting oak logs where adults feed on decaying wood matter, which they partially digest and feed to larvae (White 1983). Two species of passalid beetles are present in the high elevation oak forests of Costa Rica: a smaller species of ~ 2.5 cm length (sp. A) and a larger species of ~ 4.6 cm (sp. B) (M. P. Ayres pers. comm.). Few previous studies have noted the presence of sp. B, and no studies have looked at the pattern of abundance of sp. A relative to sp. B. Because these two species appear to utilize the same resource, the two beetles may separate themselves spatially, either within a log or among different logs. Alternatively, there may be facilitation or even a mutualism, in which case the two species would be expected to co-occur more often than expected by chance. We evaluated the pattern of co-occurrence of these two species.

Passalid beetles lend themselves well to the study of population dynamics. Population fluctuations can be a function of exogenous effects, such as from generalist predators, and/or density dependent (endogenous) effects. Two forms of density dependence seem possible for passalids. Positive density dependence, also known as the Allee effect, is the tendency for per capita reproduction to increase as density increases. If positive density dependence is present, a population exhibits qualities of a positive feedback loop where greater and greater densities beget larger more fecund populations. Hence positive density dependence contributes to unstable population dynamics. Allee effects often occur in populations of social organisms, where larger groups of individuals facilitate reproduction (Begon et al. 1990). Thus, passalid beetles might be subject to Allee effects because of their sociality in feeding larvae.

In contrast, negative density dependence is the tendency for per capita reproduction to decrease as density increases. This can occur when a resource is limiting and conspecifics compete for this resource. It is unknown if passalid colonies within a log are commonly limited by resources (wood material). If negative density dependence does occur in passalid beetles, this would tend to stabilize population dynamics, possibly producing an equilibrium around which local abundance would tend to be regulated (Begon et al. 1990).

Alternatively, per capita reproduction may be largely independent of local density. It

is possible that a subpopulation of passalid beetles within a log is at too small a scale for density dependence to be important. In fact, Baptista et al. (1998) found that not all oak logs were inhabited by passalid colonies, and suggested that passalid distribution is a function of dispersal limitation. In this case, passalid populations would be more appropriately viewed as a metapopulation, in which colonization and extinction influence the occupancy of specific logs and density-dependent feedbacks mainly arise at the level of populations of logs. Baptista et al. predicted a relationship between presence of passalids and the local abundance of potential habitat (logs). We tested this prediction as a means of testing the hypothesis that passalid distribution is dispersal limited.

METHODS

We studied the passalid beetle populations of a *Quercus* dominated forest in Cuerici Biological Station at Cerro de la Muerte, Costa Rica. Colonies were sampled by haphazardly selecting fallen oak logs (maximum weight approximately 30 kg due to logistical constraints), located on or within 30 m of the trail. We overturned logs and counted adults and larvae of both passalid species. We searched for beetles by sifting through the soil under logs and breaking apart degraded parts of logs with an axe and trowel. We measured the height of each log and the area of ground it covered (shadowed area). We also estimated the percent of ground covered by woody debris (potential passalid habitat) within a 5 m radius of each log.

Sp. A, which was most abundant, was examined for evidence of resource limitation and density dependence. To evaluate density dependence, we calculated a per capita reproduction index (natural log (larvae/adult + 1)) in each log to compare to adult abundance. To evaluate resource limitation, we calculated a volume index for each log (shadowed area x log height) to compare to natural log transformed colony size. To examine the effects of dispersal from nearby logs on colonization, we used logistic regression to compare percent habitat cover and an index of log volume to the proportion of colonized logs.

RESULTS

Of the 48 logs we examined, we found 12 logs colonized only by sp. A, two logs colonized only by sp. B, four logs colonized by both species, and 30 logs uncolonized. Although sample sizes were limited, a G-test suggested that the two species tended to co-occur more than expected by chance ($G = 3.21$, $df = 1,46$, $P = 0.07$; Table 1). Colony size of sp. A ranged from one to seven adults and zero to ten larvae, and the volume of occupied logs varied by more than 51 times. However, colony size was unrelated to log volume ($r = 0.084$, $P = 0.31$).

Of the 16 logs colonized by sp. A, eight also contained larvae. In one colony, we found one callow adult and no other life stages. The highest ratios of larvae to adults (index of per capita reproduction) occurred in the smallest colonies, but there was no significant relationship between the reproduction index and adult abundance ($r = 0.00$, $P = 0.97$; Fig. 1); a second-order polynomial was also not significant ($p = 0.71$).

Table 1. Observed frequencies of large (sp. B) and small (sp. A) passalid species. Values in parentheses are expected frequencies under the null hypothesis of no association between species.

		Larger species	
		Present	Absent
Smaller species	Present	4 (2)	12 (14)
	Absent	2 (4)	30 (28)

Percent habitat cover within a 5 m radius did not differ between colonized logs and uncolonized logs (mean ± SE = 23.0 ± 2.4 vs. 22.5 ± 3.3 respectively; t = 0.13, df = 40, P = 0.89). The probability of a log being colonized did not vary with the ground coverage by logs within 5 m (percent habitat cover; $\chi^2 = 0.02$, df = 1, P = 0.89). The probability of a log being colonized did increase with increasing volume of the focal log ($\chi^2 = 4.65$, df = 1, P = 0.03; Fig. 2), but did not increase with increasing shadow area of the focal log ($\chi^2 = 1.11$, df = 1, P = 0.29).

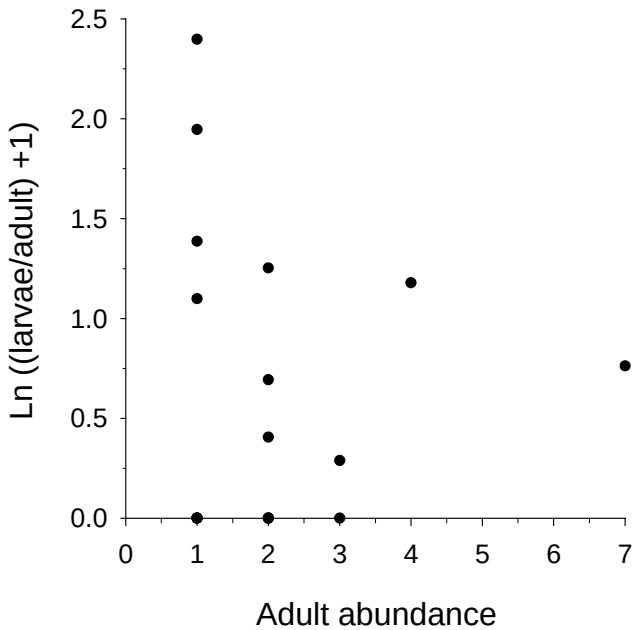

Figure 1. Index of per capita reproduction versus adult abundance in 13 colonies of passalid beetles.

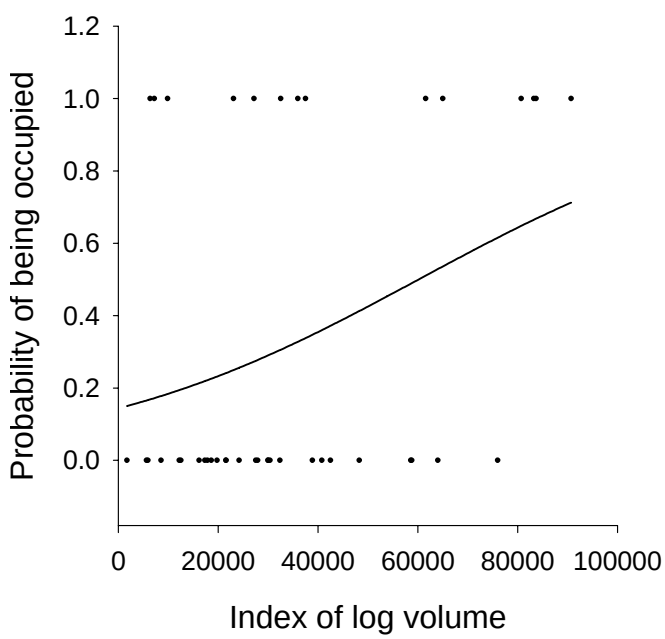

Figure 2. Index of log volume versus probability of being colonized by passalid beetles. Points show observations. Line shows best fit logisitic function.

Discussion

Because both species of passalids occupy the same environment, one might expect them to separate themselves in order to minimize competition. However, the tendency was for them to co-occur. This could be due to a feeding chain commensalism, in which sp. B breaks down wood to a finer particulate, which is then a better resource for sp. A. Alternatively, sp. B may benefit from sp. A. For example, sp. B might prefer logs that have already been colonized (and partly processed) by sp. A. In this case, sp. B might be functioning like a parasite.

Because our index of per capita reproduction did not vary with population density, populations of sp. A within logs appear to lack any density dependent feedbacks (positive or negative) to their population dynamics. The absence of resource limitations (negative feedback) was further supported by the lack of relationship between colony size and log size. One possible explanation is that natural enemies commonly limit populations of passalid beetles to such low abundances that resources are not limiting. The metapopulation structure of passalid beetles suggests an alternative explanation. It is possible that the prevailing processes of population dynamics of the passalids are different at the subpopulation and metapopulation levels. At the level of a log, it may be that local extinction probabilities are high relative to population growth rate, and that immigration and emigration are the prevailing processes. Presumably, negative density dependence and population regulation must arise at some spatial scale, but

maybe this is at the level of the entire metapopulation of passalid beetles on the mountainside, where birth and death rates must become the prevailing processes rather than immigration and emigration.

One limitation of this study was our inability to study large logs (i.e. fallen tree trunks) which may represent a significant portion of suitable habitat for passalid populations.

Contrary to predictions based upon dispersal limitations, the amount of surrounding habitat did not vary between colonized and uncolonized logs. This suggests that dispersal is not a limiting factor in beetle distribution at the scale of a 5 m radius. However, 65% of the logs that we judged to be suitable habitat were uncolonized. Because larger logs had higher probability of being occupied than smaller logs, it seems possible that dispersing beetles prefer larger logs, or that extinction rates are lower in larger logs. We also note that colonization probabilities were related to log volume (Fig. 2) but not to the shadow areas of logs. This suggests that all three dimensions of resource patch size play a role in the probability of colonization and/or local extinction rates.

Overall, our results suggest that examining the demographics of subpopulations may not give an accurate representation of the full population. While passalid reproduction seems to be independent of density within a log, studies of the metapopulation might still reveal density dependent feedbacks.

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NO SLEEP 'TILL BROODIN': FACTORS INFLUENCING THE DAILY ACTIVITY SCHEDULE OF A FEMALE VOLCANO HUMMINGBIRD WITH TWO YOUNG NESTLINGS

R. SCOTT CUSHMAN

Abstract: I looked at a day in the life of a female Volcano Hummingbird with two young nestlings in the Talamanca Mountains of Costa Rica. I hypothesized that her activity schedule would be most constrained by (1) her energy requirements, (2) the energy requirements of the nestlings, or (3) the thermoregulation requirements of the nestlings. For 3.5 hours on the afternoon of 29 January, and for 4 hours on the morning of 30 January, I observed the nest area and recorded the female's activities (630 events total) , ambient temperature, and nestling temperature. It appears that both the female's energy requirements and the nestlings' energy requirements were important determinants of the female's activity schedule, but that the nestlings' thermoregulation requirements did not play an important role. It is likely that the tiny nectar- and insect-feeding bird cannot afford to significantly reduce her own energy intake to feed her nestlings, and instead must increase overall foraging effort.

Key words: foraging, nutritional requirements, thermoregulation

INTRODUCTION

On the morning of 29 January 2004, I discovered a volcano hummingbird nest near the Cuerici Biological Station, in the Talamanca mountain range of Costa Rica. The cup-shaped nest was situated in the fork of a blackberry vine 1.5 m off the ground in an area of relatively open second-growth dominated by fuchsia, blackberry, and alder. The nest contained two nestlings (as is typical in the tropics) which I estimated to be only 2 - 3 days old. I looked at a day in the life of the mother, hypothesizing that her activity schedule would be most constrained by (1) her energy requirements, (2) the energy requirements of the nestlings, or (3) the thermoregulation requirements of the nestlings. Under H1, I predicted that she would forage most heavily in the early mornings (when her energy supplies are low), and in the late afternoons (to build up energy reserves for the night), to the neglect of nestling feedings; under H2, I predicted that nestling feedings would be relatively high in the early morning (when the nestlings' energy supplies are low), and in the late afternoons, but that foraging would not show corresponding peaks; and under H2, I predicted that she would brood more often in the early morning, when temperatures are lowest, to the neglect of both foraging and nestling feeding activity.

METHODS

For 3.5 h between 1330 and 1800 on 29 January and for 4 h between 0600 and 1030 on 30 January, I observed the nest area while sitting quietly in a green chair 5 m away. I continuously recorded the location and activity of the female, and took periodic measurements of the ambient temperature, and, when possible, the skin temperature of the nestlings. At the end of the observation period, I mapped all the locations where the female was observed (Appendix 1), and measured the dimensions of the nest.

RESULTS

I calculated rates of various activities during six time periods (early morning, mid-morning, late morning, early afternoon, mid-afternoon, and late afternoon), each of which corresponded to a continuous observation period of 1.05 to 1.77 h.

Both nectar and sally foraging rates were relatively high early and late in the day, and low in the middle of day. Nectar foraging was relatively high mid-morning, however, whereas mid-morning sally foraging rate dropped off steeply from the early morning rate (Fig. 1). Nestling feeding rate was relatively high early in the day and low in the middle of the day. No nestling feedings were observed in mid or late afternoon (Fig. 2). Buzz rate was very high in mid-afternoon and late afternoon and relatively low at all other times (Fig. 3). Brooding rate was relatively high in the early morning, intermediate mid-morning, and low late morning and late afternoon; no broodings were observed in the early afternoon or mid-afternoon (Fig. 4). Mean temperature was relatively low in the early morning (6.5° C), high in the mid-morning (17.5° C) and late morning (20.4° C), and intermediate in the early afternoon (14.0° C), mid-afternoon (13.8° C), and late afternoon (11.23° C).

Table 1. Number of times 11 different activities were observed in 7.5 h of observation of a female volcano hummingbird.

Activity	Number of times observed
Perch	249
Sally	97
Nectar foraging	94
Buzz	83
Out of sight	68
Feeding nestlings	13
Brooding	7
Chased	2
Chases	2
Chased/chases	2
Nest pass	1

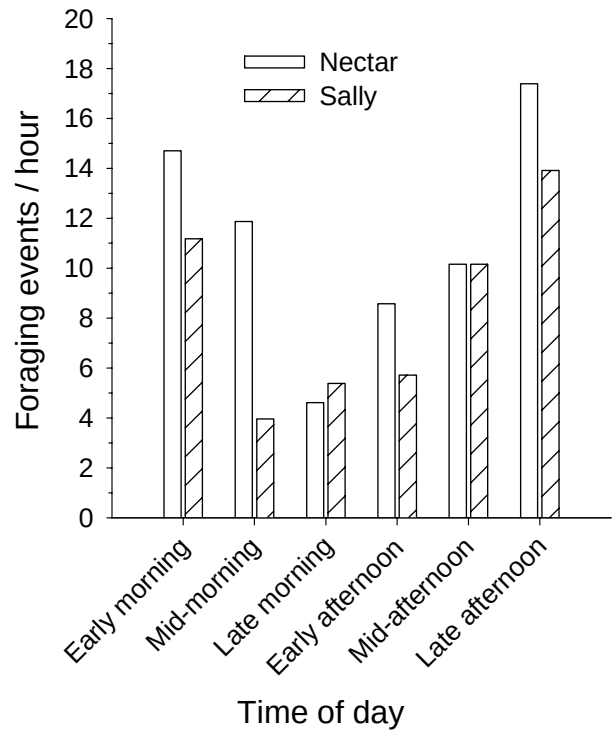

Figure 1. Number of nectar foraging events and sallies vs. time for a female volcano hummingbird with two young nestlings.

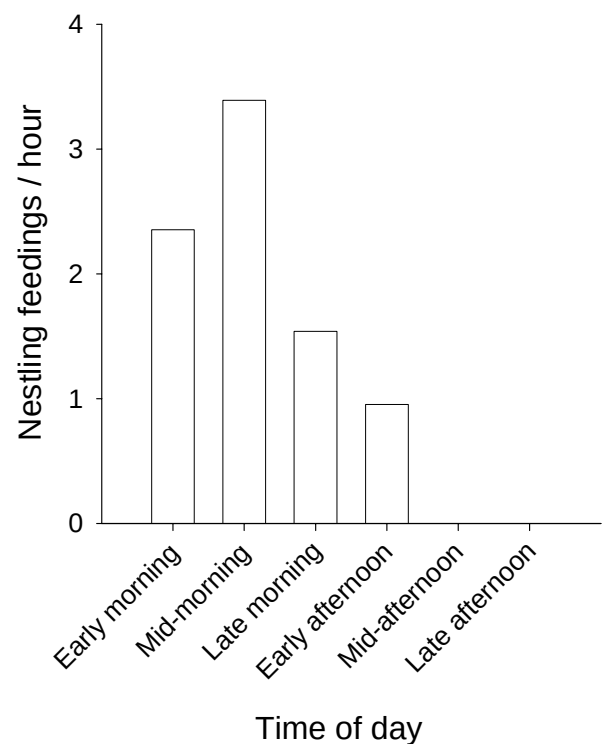

Figure 2. Number of nestling feeding events vs. time for a female volcano hummingbird with two young nestlings.

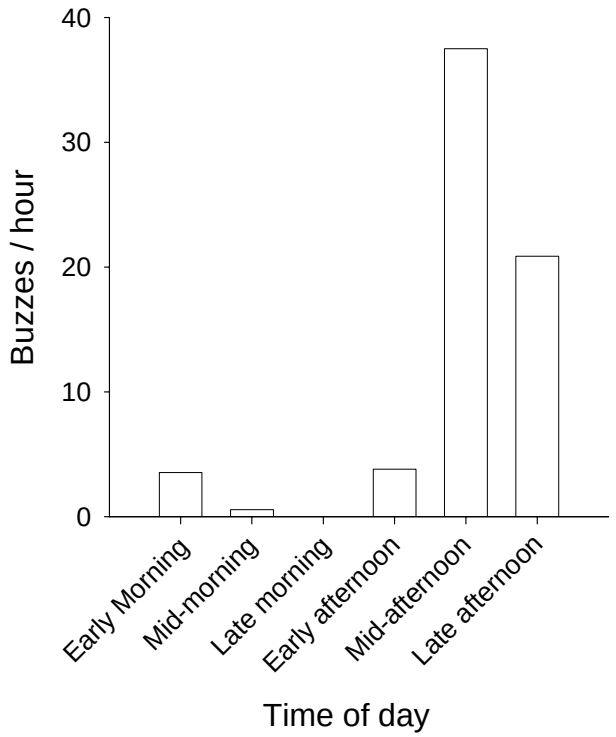

Figure 3. Number of buzzes (hovering flights < 1m from me with no apparent foraging behavior) vs. time for a female volcano hummingbird with two young nestlings.

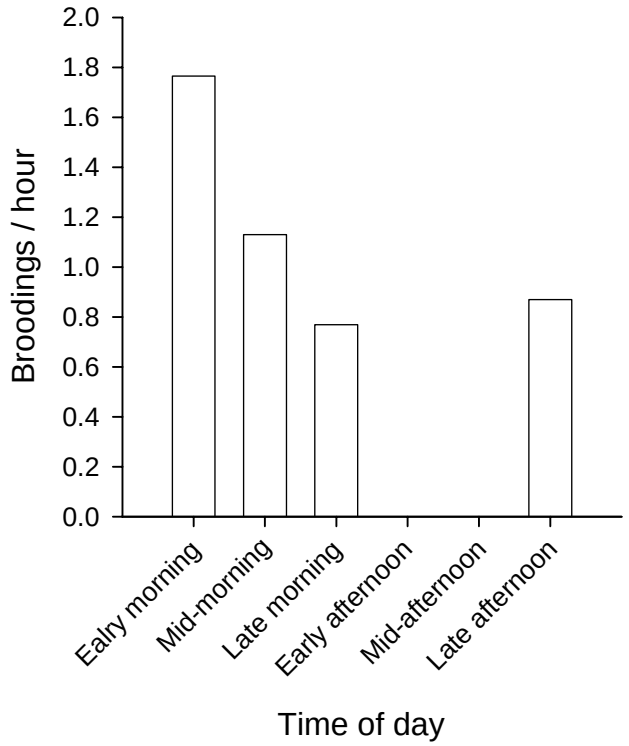

Figure 4. Number of brooding events vs. time for a female volcano hummingbird with two young nestlings.

I did not use nestling skin temperature measurements for any analyses because they appeared to vary greatly with location of the sensor on the nestlings.

The nest was 6.5 cm tall, with an external diameter of 6 cm, and an internal diameter of 4 cm.

Discussion

It appears that both the female's energy requirements and the nestlings' energy requirements were important determinants of the female's activity schedule, but that the nestlings' thermoregulation requirements did not play an important role. Foraging rate and nestling feeding rate were high early in the day, as predicted, when energy supplies would be expected to be low. Foraging rate was also high late in the day, possibly to build up energy supplies for the coming night, or, alternatively, as a response to high resource availability (assuming that nectar levels refilled after morning foraging, and that aerial insect abundance was higher late in the day). Nestling feeding rate would be expected to show a corresponding increase late in the day, especially since the smaller nestlings (with higher surface area : volume ratios) should need proportionately larger energy reserves than the female to make it through the night. However, this was not seen. The total absence of nestling feedings late in the day corresponded to very high buzz rates and low visitation of the nest in general, suggesting that the female may have been avoiding the nest because of my presence, so as not to reveal its location. Another afternoon of observation, after the female had apparently become habituated to my presence, would be needed to test this hypothesis. One difficulty of distinguishing between the relative importance of female nutritional requirements and nestling nutritional requirements is that the activity measures I used cannot so easily be sepa-

rated into those two categories; nestlings are fed both nectar and insects gathered during foraging activity (Stiles and Skutch 1989).

The locations and activities of the female during her 68 absences from my view are unclear. During some of them, she must have simply been perched nearby, but obscured by vegetation (it is easy to hide if you are 7 cm tall). Considering her aggressive defense of the area around the nest from conspecific individuals, it seems logical that she would only leave the area to seek better foraging opportunities. This was supported by her relatively high absence rate during early morning and late afternoon–the times of highest observed foraging activity (Fig. 5).

It is not surprising that both the female's energy requirements and the nestlings' energy requirements were important. All organisms must compromise between allocating resources to survival and reproduction. Many factors, including metabolic rate, can influence the nature of this compromise; it is likely that volcano hummingbirds have such high metabolic rates, due to their small size and active lifestyle, that a female cannot afford to significantly reduce her own energy intake to feed her nestlings. If so, total foraging effort, and possibly mortality, would be expected to increase during the brooding period. Future studies could look more closely at the nature of the compromise between survival and reproduction in volcano hummingbird females by comparing the activity schedules of females with and without nestlings, and looking for a decrease in overall foraging in females without nestlings.

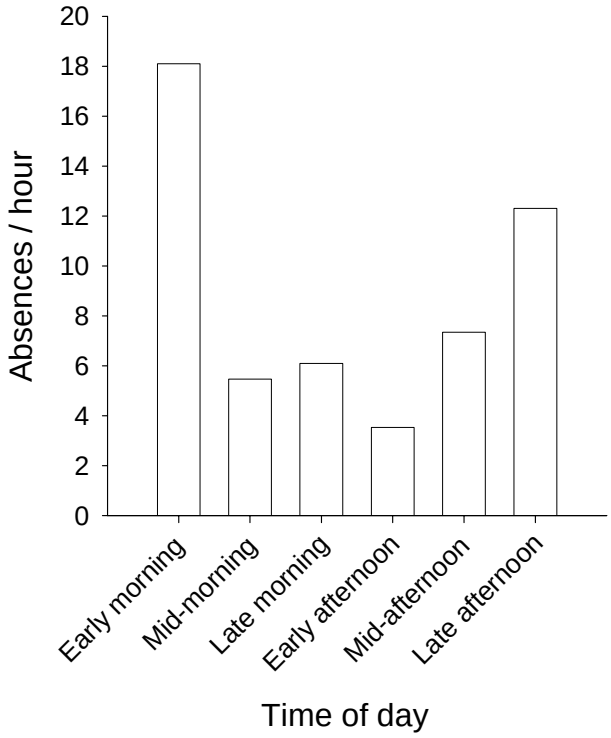

Figure 5. Number of absences from view vs. time for a female volcano hummingbird with two young nestlings.

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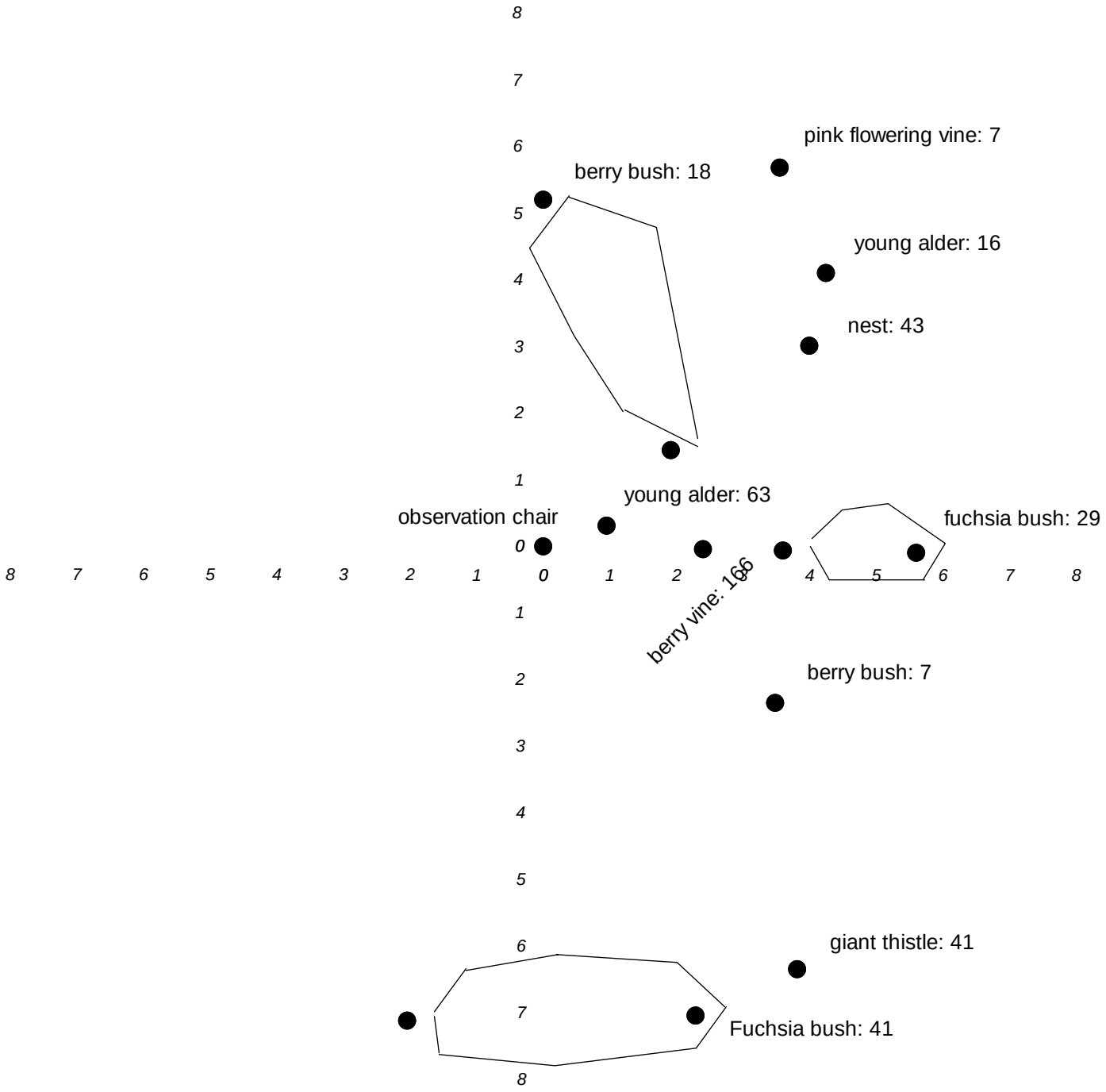
Appendix 1. Common perches and nectar sources (with number of times female was observed at each in 7.5 h of observation) of a female volcano hummingbird with two young nestlings. Distance axes are in meters.