in the type of webs placed on shrubs and trees. This could be the result of a structural constraint that limits the ability of spiders to build three dimensional webs on shrubs. However, we observed both types of webs on each substrate, but proportionally more orb webs on shrubs. Additionally, webs tended to be oriented more vertically on shrubs than trees. That web type and angle of placement differ between placement sites suggests that different prey capture strategies may be more effective in different locations. Substrate clearly affects the form and orientation of spider webs, and further studies of building patterns could lead to a better understanding of the effects of site selection and orientation on damage and prey capture efficiency of spider webs.

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# Circadian foraging patterns in *Paraponera clavata*

Jonathon C. Raffensperger

*Abstract: Paraponera clavata* is a large ponerine ant that feeds on nectar and insects in the understory of tropical forests. Although foraging activity of this ant has been shown to be higher at night than during the day, the mechanism behind this increased rate is unclear. I predicted that individual workers would forage both day and night, becoming more active after dark, and that insect abundance and activity would he higher at night, resulting in a larger percentage of insects in the food brought back to the nest. While I found no difference in the percent composition of food by day versus night, it appears from observations of individually marked ants that daytime workers do remain active and increase their foraging rate at night, but are also joined by a group of exclusively nocturnal foragers.

*Key Words: ant foraging, food availability, giant tropical ant, nectar, social organization*

## Introduction

The giant tropical ant, *Paraponera clavata*, is a common understory forager in the Atlantic coastal lowlands of Costa Rica whose nests are constructed at the bases of large trees and house colonies of 700 to 1,400 workers. This species has been observed to be most active at night, although some workers can be found on foliage and tree trunks during daylight hours (Janzen and Carroll 1983). It is not known, however, whether this nocturnal increase in activity is the result of a general increase in foraging rate, or whether there is some division of labor among workers between day and night, with a larger "night shift" taking over once the sun goes down. Be-

cause these eusocial yet relatively primitive ants are solitary foragers that do not recruit colony members to food sources or exhibit organized colony defense (Wilson 1971, Janzen and Caroll 1983), I hypothesized that *P. clavata* would not exhibit the colony-level organization required to finely divide foraging effort. I thus predicted that the same workers observed during the day would forage at night as well, but at a higher rate.

Novello (1999) observed that *P. clavata* most commonly returned to the nest with drops of nectar or nothing at all, although the ants feed on insects as well. He also found, however, that they did not show a preference for one type of food over the other, and suggested that they are opportunistic foragers, simply taking the first item they find. I predicted, due to my preliminary observations of increased nighttime insect abundance, that the percentage of insect food brought back by ants would be greater at night than during the day assuming that insect activity would be greater at night.

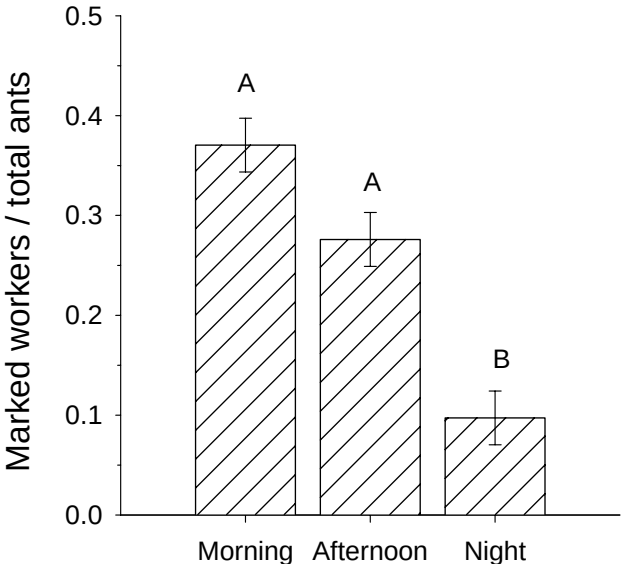


Figure 1. Ratio of marked individuals to total workers in the morning, afternoon, and at night. ($F = 25.63$, $df = 1, 18$, $P < 0.0001$). Letters distinguish means within columns that are significantly different (Tukey comparison $\alpha = 0.05$).

## METHODS

On 13 February 2005, I marked 70 *P. clavata* worker ants in a colony beside the Arboretum Trail, approximately 30 m from the laboratory at La Selva Biological Research Station, Costa Rica. These haphazardly selected individuals were captured using forceps and marked with a white paint pen. I then performed six sets of four 0.5-h observations: two in the morning (0700 - 0900, 0900 - 1100), two in the afternoon (1300 - 1500, 1500 - 1700), and two in the evening (2200 - 2400, 2400 - 0200). For each observation period, I recorded the number of marked individuals, workers carrying nectar, workers carrying insects, and total ants entering and leaving the nest. For night observations, I used the low-intensity beam of a headlamp to illuminate the tree in order to view the ants with minimal disturbance.

I compared total ants observed, number and percentage of marked individuals, and percent nectar and insects between day and night using 2-way ANOVAs, fitting a full model testing for effects of time of day, and sampling date. Analyses were performed using JMP 5.0.1, and data conformed to the assumptions of parametric tests.

Table 1. Mean numbers of total ants, marked ants, and ants returning with nectar or insect food in the morning, afternoon, and at night. Letters distinguish means within columns that are significantly different (Tukey comparison $\alpha = 0.05$).

| | Total Ants | Marked Ants | Percent Ants with Insects |
|---|---|---|---|
| Morning | a 12.6 ± 6.2 | a 5.9 ± 1.4 | a 38.5 ± 8.3 |
| Afternoon | a 29.9 ± 6.2 | a 7.6 ± 1.4 | a 42.8 ± 8.3 |
| Night | b 185.6 ± 6.2 | b 17.4 ± 1.4 | a 28.5 ± 8.3 |

## RESULTS

The total number of ants observed differed as a function of both time of day ($F = 236.02$, $df = 2, 18$, $P < 0.0001$) and sampling date ($F = 28.03$, $df = 1, 18$, $P < 0.0001$). More ants were observed at night than during the morning or afternoon (Table 1), and more were observed on the second sampling date (95.0 ± 5.1 SE) than the first (57.1 ± 5.1 SE; $F = 7.58$, $df = 5, 18$, $P < 0.004$). There was no interaction between time of day and sampling date ($F = 1.10$, $df = 2, 18$, $P = 0.38$).

The abundance of marked individuals varied only with time of day ($F = 680.25$, $df = 2, 18$, $P < 0.001$) There were more marked individuals entering or leaving the nest during the night than during the morning or afternoon (Table 1). There was no difference between sampling dates ($F = 60.17$, $df = 1, 18$, $P = 0.07$), nor was there an interaction between time of day and sampling date ($F = 31.58$, $df = 2, 18$, $P = 0.38$).

The ratio of marked individuals to total workers observed was significantly lower at night, but there was no difference between numbers observed in morning and the afternoon (Fig. 1). There was no difference between sampling dates ($F = 2.19$, $df = 1, 18$, $P = 0.16$), and no significant interaction between date and time of day ($F = 2.19$, $df = 2, 18$, $P = 0.15$).

The percent of insects (ants carrying insects/total ants returning with all food types) in the ants' diet did not vary as a function of time of day ($F = 0.78$, $df = 2, 18$, $P = 0.47$). There was no difference between sampling dates ($F = 0.16$, $df = 1, 18$, $P = 0.70$), and no significant interaction between date and time of day ($F = 0.07$, $df = 2, 18$, $P = 0.93$).

## DISCUSSION

As I predicted, the number of marked individuals entering and leaving the nest increased from day to night, suggesting that workers active during the day increase their foraging rate once night falls. The percentage of total ants made up by marked individuals decreased, however, indicating that unmarked workers not active during the day came out to forage at night. It is possible that these "night shift" ants, having spent the day resting, could forage at a higher rate, entering and leaving the nest more often than workers that are active at all hours. This would amplify the observed difference in percentages of marked individuals. No difference was found in percentage of marked individuals between morning and afternoon observations, suggesting that this influx of new

foragers takes place entirely after sundown instead of gradually over the course of the day.

Contrary to my predictions, there was no change in relative composition of the food brought back by foraging workers as the day progressed. It is possible that, while insects are generally more active at night, there is no change in the abundance of the slow or dead insects that are most easily encountered and subdued by foraging ants (Janzen and Connell 1983). Droplets of transparent nectar were difficult to see in the daylight but reflected the light of my headlamp at night, and at least part of the observed increase in nectar retrieval may have been due to better nighttime visibility. This would artificially increase the daytime insect percentage and might conceal a real difference between day and night.

While patterns in one *P. clavata* colony may not hold true for the species as a whole, it is interesting nonetheless that these ants, whose social organization seems at first glance to be relatively primitive compared to more eusocial species, exhibit a division of labor in foraging that is so seemingly complex. These results suggest that further investigation into the specific roles of workers within the colony and how those roles are determined could reveal an unexpected degree of sophistication in these giants of the ant world.

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# CHANGES IN LEAF LITTER ACROSS AGES OF *HYERONIMA ALCHORNEOIDES* TREES

CHAD M. VALDERRAMA

Abstract: A leaf can be an asset or a cost to its parent plant, depending on how much energy it produces and consumes. When leaves are no longer beneficial, a tree can drop them in the form of leaf litter. At La Selva, Costa Rica, I examined the leaf litter of young *Hyeronima alchorneoides* trees located in three adjacent monoculture plots planted in 1991, 2001, and 2004. I found evidence for changes in leaf lifespan with tree age. This may support the idea that inter-leaf competition and the permanence of fixed carbon change as *H. alchorneoides* trees age.

*Key Words: canopy cover, canopy volume, photosynthesis, respiration*

## INTRODUCTION

A leaf can be an asset or a cost to a plant, depending on how much energy it produces or consumes. As trees increase in height and grow new leaves high in their canopies, old leaves that are lower in their canopies may become shaded and respire in excess of their photosynthetic contribution. Such leaves that become a net cost to their parent tree are often dropped in the form of leaf litter. Thus, the rate of leaf litter fall may serve as an indicator of inter-leaf competition within trees.

The rate of leaf litter fall from a tree may also serve as an indicator of leaf lifespan. Assuming that the lifespan of leaves is equal across trees with different numbers of leaves, then the number of leaves falling from the tree per unit time should be in proportion to the number of leaves on the tree. If the ratio of the number of leaves falling per unit time to the number of leaves on a tree is not equal across ages, then the lifespan of leaves on a tree may be changing as a tree ages.

I collected data on how leaf litter changes with tree age in monocultures of *Hyeronima alchorneoides*, a tropical, non-deciduous tree. Such changes in leaf litter may be insightful in understanding how inter-leaf competition and leaf lifespan change with tree age.

These relationships may also illuminate how the dynamics of carbon storage change with tree age. The carbon that is fixed by trees with short leaf lifespans may be cycled back into the atmosphere more rapidly, through leaf decomposition, than carbon that is fixed by trees with long leaf lifespans. This suggests that trees which allocate fixed carbon to long-lifespan leaves may serve as longer-term carbon sink than trees that allocate fixed carbon to short-lifespan leaves. Understanding these potential changes in the dynamics of carbon storage across tree ages is an important goal for *H. alchorneoides*, since it is a candidate for reforestation and silviculture in Central America (Jimenez 2002).

## METHODS

I studied *H. alchorneoides* in an experimental monoculture plantation located at the confluence of the Puerto Viejo and

Sarapiqui Rivers at La Selva Biological Station, Costa Rica. The monoculture was composed of three adjacent similarly sized plots of *H. alchorneoides*. One plot was planted in 1991, a second in 2001, and a third in 2004 (Haggar 1997). The density of the monoculture was constant across tree ages, with one tree planted approximately every 3 m. In each plot, I randomly placed three, 9 $m^2$ quadrats. Each quadrat was bounded by four trees, with one tree in each corner of the quadrat.

*H. alchorneoides* leaves turn a reddish-orange color before they fall and become brown as they decompose on the ground, allowing for easy identification of recently fallen leaf litter. Within each quadrat I quantified the abundance of recently fallen (red-orange) *H. alchorneoides* leaf litter and measured the area [leaf length*leaf width] of each leaf. I summed the areas of all individual leaves per quadrat to calculate total area of leaf litter per quadrat.

All of the relationships I examined appear to be non-linear. However, because I had multiple replicates for each tree age, I was able to use one-way ANOVAs to examine how leaf litter abundances (total number of leaves) per quadrat, average leaf area per quadrat, and total leaf area per quadrat change with age (JMP 5.0.1). Because of unequal variances in my samples, I was unable to meet assumptions of normality. However, I had a balanced experimental design and therefore was able to use parametric tests.

## RESULTS

The quadrats of one year-old trees contained the fewest leaves (mean ± SE, 2.37 ± 1.93), quadrats of four year-old trees contained the most leaves (11.11 ± 0.68), and quadrats of 14 year-old trees contained an intermediate number of leaves (6.95 ± 0.89; $F = 13.32$, df = 2, 6, $P < 0.01$, all means significantly different from each other, Tukey $\alpha = 0.05$).

The quadrats of one year-old trees had the largest average leaf size (475.1 ± 57.6 $cm^2$), four year-old tree quadrats contained intermediate-sized leaves (282.90 ± 20.20 $cm^2$), and 14 year-old tree quadrats contained the smallest leaves (171.9 ± 26.4 $cm^2$; $F = 13.17$, df = 2, 6, $P < 0.01$, all means significantly different from each other, Tukey $\alpha = 0.05$ ).

One year-old trees produced the least amount of total leaf litter per quadrat (1267 ± 32 $cm^2$) and four year-old trees produced the most total leaf litter per quadrat (2177 ± 224 $cm^2$). The 14 year old trees produced an intermediate amount of total leaf litter per quadrat (6130 ± 441 $cm^2$; ANOVA, $F = 87.73$, df = 2, 6, $P < 0.01$, all means significantly different from each other, Tukey $\alpha = 0.05$).

## DISCUSSION

Although the data I collected show that total area of leaf litter per quadrat peaks at an intermediate age, my informal observations suggest that total canopy cover increases with age. This implies that the lifespan of leaves on 14 year-old trees might be longer than the lifespan of leaves

on four year-old trees. If the lifespan of leaves were equal across trees of different ages, then the number of leaves in the leaf litter should be in proportion to the number of leaves on the tree. However, the four year-old *H. alchorneoides*, which I informally observed to have fewer canopy leaves when compared to 14 year-old *H. alchorneoides*, produced more leaves in its leaf litter than the older 14 year-old *H. alchorneoides*. Therefore, the lifespan of leaves is probably not equal for these trees of different ages; four year-old trees may rapidly drop the leaves they produce.

What might cause these differences in leaf lifespan? Perhaps the short leaf lifespan on four year-old *H. alchorneoides* is a result of high inter-leaf competition for light. Future studies should examine how mutual shading by canopy leaves changes with tree age and determine whether abcission rates and leaf longevity change accordingly.

It is likely that mutual shading by leaves is only one of many factors that may influence the lifespan of leaves. Other factors that influence leaf longevity might differentially affect leaves on trees of different ages. Herbivory, for example, might cause a leaf to be dropped from the canopy, if it causes the leaf to be a net cost to a plant. Leaves on younger trees and older trees could be differentially affected by leaf herbivory.

Regardless of the mechanism, the suspected short lifespan of leaves on four year-old *H. alchorneoides* implies that, all else being equal, carbon fixed by *H. alchorneoides* remains fixed for different periods of time at different stages in the tree's life. Since canopy cover is increasing as a tree grows, every unit leaf area that is dropped from the canopy is subsequently replaced by at least one equal unit leaf area. Therefore, a short leaf lifespan necessitates a high leaf turnover rate and a high allocation of fixed carbon towards leaf replacement. Because trees fix carbon by taking $CO_2$ out of the atmosphere, differential carbon fixation across tree ages is important in assessing permanence of carbon stores and potential atmospheric $CO_2$ reduction resulting from planting trees.

This study was limited to the early life stages of *H. alchorneoides.* Obtaining data over the entire lifespan of *H. alchorneoides* would be insightful in understanding the potential influence of leaf longevity on carbon fixation over the entire life of a tree. Because larger trees have more leaves, any possible implications of differences in leaf litter amounts across ages found in my data, such as potential differences in carbon storage permanence, could be exaggerated in the oldest *H. alchorneoides* individuals.

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# INFLUENCE OF LIGHT AVAILABILITY ON DELAYED GREENING STRATEGY IN *WELFIA GEORGII*

ANNA R. NOWOGRODZKI, MELISSA A. BARGER, CAYELAN C. CAREY AND CHELSEA L. WOOD

*Abstract:* In tropical forests, to deter herbivores and reduce losses to herbivory in young leaves, some plants delay the greening of leaves with chlorophyll until chemical and structural defenses have developed. We hypothesized that *Welfia georgii* would adjust delayed greening strategy depending on light availability. We predicted that the proportion of *W. georgii* individuals exhibiting delayed greening would decrease with canopy openness, because the cost of decreased photosynthesis resulting from delayed greening (i.e., in an environment in which light is highly available) would be greater than the benefit of decreased herbivory. Contrary to this hypothesis, we found that the proportion of individuals with delayed greening increased with canopy openness. We propose that this may be due either to light saturation of *W. georgii* under open canopy or to higher herbivory pressure in tree-fall gaps. We also found that young leaves without delayed greening had more damage from herbivory than young leaves with delayed greening, suggesting that this defense is effective against herbivores.

*Key Words: canopy openness, herbivory, light saturation, photosynthesis, tree-fall gap, tropical rain forest, understory*

## INTRODUCTION

Herbivory in tropical forests occurs mostly on young, expanding leaves (Coley and Aide 1991, Coley and Kursar 1996). Delayed greening is a strategy that reduces the resources lost to herbivory by postponing production of valuable chlorophyll in young leaves until after chemical and structural defenses have developed (Coley and Kursar 1996). Consequently, leaves with delayed greening are less nutritious and less preferred by herbivores (Coley and Kursar 1996). While delayed greening helps protect young leaves against herbivory, there is a high cost associated with allocating resources to a leaf that does not fix carbon through photosynthesis.

*Welfia georgii*, an abundant palm at La Selva Biological Station, in the Atlantic lowlands of Costa Rica, exhibits delayed greening. It can germinate and develop slowly in low light, but grows rapidly when a light gap is created after a tree or branch fall (Vandermeer 1983). We hypothesized that *W. georgii* would adjust its delayed greening strategy based on light availability. We expected that, for *W. georgii* in high light conditions, the cost of decreased photosynthesis resulting from delayed greening would be greater than the benefit of decreased herbivory, because *W. georgii* can take advantage of ample light resources (Fig. 1). We predicted that *W. georgii* under high canopy cover would exhibit more delayed greening than those under low canopy cover. We also predicted that there would be less herbivory on

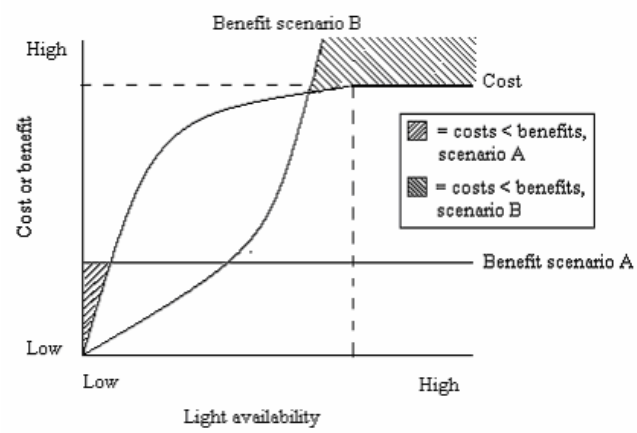


Figure 1. A theoretical model of costs and benefits of delayed greening with changes in light availability. All axes are in fitness units. Dashed lines represent the light saturation point of leaves. "Cost" represents the cost of delayed greening in terms of lost photosynthesis opportunity. "Benefit scenario A" represents the benefit of delayed greening in terms of herbivory prevention, when this benefit is constant over different light environments. In this case, delayed greening should occur only at low light availability, which was consistent with our prediction, but inconsistent with our findings. "Benefit scenario B" represents the benefit of delayed greening in terms of herbivory prevention, when this benefit increases exponentially with light availability. In this case, delayed greening should occur at high light availability, which is consistent with our findings. Examining how these costs and benefits change with light availability is crucial to a full understanding of delayed greening response in *Welfia georgii*.

young leaves with delayed greening than on those without delayed greening.

## METHODS

On 13 and 14 February 2005, we sampled 137 *Welfia georgii* along the Camino Experimental Sur from 10 to 772 m from the trail head at La Selva Biological Station, Costa Rica (excluding the restricted access plot from 450 to 550 m). We measured *W. georgii* height, canopy openness, leaf maturity, and percent herbivory for all individuals within 5 m of the trail. We also assessed whether each plant exhibited delayed greening, defined as possessing a young leaf with any red coloration.

We identified the youngest leaf of each plant, which had a central position relative to other leaves. Because all leaves eventually turn green, we wanted to ensure that the color of leaves reflected their delayed greening strategy, not their age (i.e., that we were not sampling leaves that once had delayed greening, but had since matured). To do so, we rated the maturity of the youngest leaf on a scale from 0 (unopened leaf) to 5 (nearly mature) by comparing degree of folding, color, and texture to mature leaves on the same plant. According to this scale, younger leaves had more folding, lighter coloration (red or green), and less toughness than more mature leaves.

We chose only plants shorter than 4 m possessing one young leaf (defined as less than or equal to five on this scale). We excluded plants with ambiguous red coloration at the base of the leaflets. We measured each plant's height with a meter stick and assessed openness of the canopy above each plant with a spherical densiometer. We estimated the percent of young leaf area removed by herbivores by averaging the visual estimates of three observers.

All statistical analyses were performed using JMP 4.0.0. Data met or were transformed to meet all assumptions of parametric tests. Percent herbivory was normalized by an arcsine transformation.

## RESULTS

Of the 137 *W. georgii* sampled, 66 exhibited delayed greening in their youngest leaf and 71 did not. Maturity of the youngest leaves on each plant did not differ between delayed greening and non-delayed greening plants (Wald test for ordinal logistic fit, $\chi^2 = 1.36$, df = 1, P = 0.24), and was not related to canopy openness (Wald test for ordinal logistic fit, $\chi^2 = 0.004$, df = 1, P = 0.95). The proportion of *W. georgii* exhibiting delayed greening increased with canopy openness, although this result was not significant (logistic regression, $\chi^2 = 2.35$, df = 1, P = 0.13; Fig. 2).

Percent herbivory on young leaves was greater for non-delayed greening plants (2.87 ± 0.52%) than for delayed greening plants (0.58 ± 0.54%; F = 9.84, df = 106, P = 0.002; Fig. 3). However, we found no relationship between percent herbivory and canopy openness ($r^2 = 0.003$, df = 135, P = 0.51).

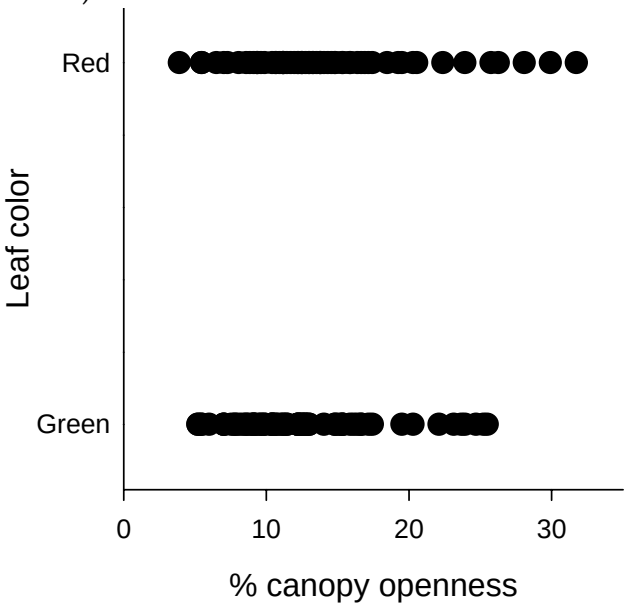


Figure 2. The proportion of *Welfia georgii* exhibiting delayed greening (i.e., red coloration) increased with canopy openness (n = 137).

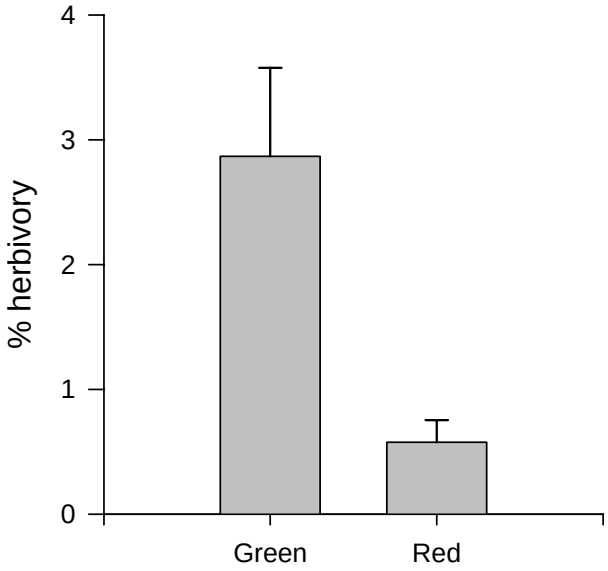


Figure 3. More herbivory was observed on young leaves of *Welfia georgii* without delayed greening (youngest leaf was green) than on young leaves of plants with delayed greening (youngest leaf was red).

## DISCUSSION

We found no difference in maturity between young leaves exhibiting delayed greening and those lacking this defense. This suggests that delayed greening in *W. georgii* is a plastic response, rather than a fixed stage in leaf development. We observed nearly as many newly unfolding completely green leaves as red leaves, which supports this conclusion. Our finding that leaves with delayed greening had less herbivory than green leaves suggests that delayed greening is effective in preventing herbivory. The result that percent herbivory increases with leaf maturity is to be expected, since older leaves have accumulated herbivory damage over a longer period of time than younger leaves.

Contrary to our hypothesis that delayed greening would be more costly for plants in gaps than in the understory, we

found that the proportion of *W. georgii* with delayed greening increased with canopy openness. This could be due to differences in light availability. Plants in gaps may be light saturated, so that maximum photosynthesis occurs even if plants only capture a fraction of available light. Possession of non-photosynthetic tissue (i.e., leaves with delayed greening) is, therefore, not as costly to the overall rate of photosynthesis for a plant. Plants in the shaded understory receive less light, often in the form of transitory sunflecks, and may need to capture as much of this light as possible to maximize photosynthesis.

In minor light gaps *W. georgii* grows quickly and competes well, but in the shaded understory it grows slowly (Vandermeer 1983). This indicates that *W. georgii* leaves probably have an intermediate light saturation point. In gaps, *W. georgii* may reach its saturation point. In this case, photosynthesis would be occurring at the maximum rate, and non-photosynthetic tissue would be less costly.

An alternative explanation for the positive relationship between canopy openness and delayed greening is that pressure from herbivores may be higher in gaps. Gaps contain faster-growing, poorly defended, and more palatable plants than the understory, and may attract more insect herbivores (Coley and Kursar 1996). Higher abundance of herbivores would increase the advantage of delayed greening (i.e., Benefit scenario B in Fig. 1), which is consistent with our finding that leaves with delayed greening have less herbivory. Although we found no relationship between herbivory levels on young leaves of *W. georgii* and canopy openness, it is possible that our measurements of herbivory do not reflect relative herbivore abundances in the two habitats.

We suggest that, based on the natural history of *W. georgii*, light availability and its effect on herbivory may drive the trend towards increased delayed greening in gaps. Further studies could compare the abundance of herbivores on *W. georgii* in gaps and in the understory to determine if the benefits of delayed greening in terms of herbivory prevention change with light availability (see Fig. 1). A study to determine the light saturation point of *W. georgii* would provide information about the potential for *W. georgii* saturation in gaps.

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# EFFECT OF FOOD RESOURCES ON THE ABUNDANCE OF *DENDROBATES PUMILIO* TERRITORIES

ELVINA C. CHOW, S. ALLIE HUNTER, JENNY E. JUN AND EMILY L. SHARP

*Abstract:* The poison dart frog *Dendrobates pumilio* defends reproductive resources in territories year-round (Donnelly 1989). We hypothesized that *D. pumilio* territory abundance was also related to the abundance of food resources. We predicted that there would be fewer territories in areas with lower insect abundance than in areas with higher insect abundance. We measured insect and frog territory abundances in two forest types. Secondary forests were found to have higher insect and frog abundances than primary forests, and *D. pumilio* territory abundance increased with increasing small insect abundance. We suggest that the density and location of *D. pumilio* territories may be determined by food abundance in addition to reproductive resources.

*Key Words: food availability, frog density, strawberry poison dart frog*

## INTRODUCTION

The strawberry poison dart frog, *Dendrobates pumilio*, is commonly found in tropical lowland forests. They maintain territories year-round by calling, and the number of calling frogs is indicative of the number of territories in an area (Savage 2002). It has been proposed that the main purpose of these territories is to secure reproductive resources such as bromeliad tanks and leaf litter (Donnelly 1989). Because *D. pumilio* require high abundance of small insects (< 3 mm) to meet their metabolic needs (Savage 2002), we hypothesized that *D. pumilio* territories might be

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# EFFECT OF FOOD RESOURCES ON THE ABUNDANCE OF *DENDROBATES PUMILIO* TERRITORIES

ELVINA C. CHOW, S. ALLIE HUNTER, JENNY E. JUN AND EMILY L. SHARP

*Abstract:* The poison dart frog *Dendrobates pumilio* defends reproductive resources in territories year-round (Donnelly 1989). We hypothesized that *D. pumilio* territory abundance was also related to the abundance of food resources. We predicted that there would be fewer territories in areas with lower insect abundance than in areas with higher insect abundance. We measured insect and frog territory abundances in two forest types. Secondary forests were found to have higher insect and frog abundances than primary forests, and *D. pumilio* territory abundance increased with increasing small insect abundance. We suggest that the density and location of *D. pumilio* territories may be determined by food abundance in addition to reproductive resources.

*Key Words: food availability, frog density, strawberry poison dart frog*

## INTRODUCTION

The strawberry poison dart frog, *Dendrobates pumilio*, is commonly found in tropical lowland forests. They maintain territories year-round by calling, and the number of calling frogs is indicative of the number of territories in an area (Savage 2002). It has been proposed that the main purpose of these territories is to secure reproductive resources such as bromeliad tanks and leaf litter (Donnelly 1989). Because *D. pumilio* require high abundance of small insects (< 3 mm) to meet their metabolic needs (Savage 2002), we hypothesized that *D. pumilio* territories might be

affected by food resources in addition to the availability of reproductive sites. If so, we would expect fewer territories in areas with lower insect abundance than areas with higher insect abundance. We predicted that *D. pumilio* territories would be more abundant in secondary forests than in primary forests, and that they would be correlated with higher insect abundance in secondary forests than in primary forests.

## METHODS

We sampled four 50 m trail sections (transects) in primary and secondary forests on alluvial soil along the STR, CCL and CES trails at La Selva Biological Station, Costa Rica on 13 - 15 February 2005. To sample insects, we haphazardly placed four pitfall traps and two sticky traps along each transect within 5 m of either side of the trail. We collected traps after 24 h and quantified insect abundance, grouping insects into two size classes: small (< 3 mm) and large (> 3 mm) body lengths, representing edible and non-edible insect resources. We sampled *D. pumilio* territory abundance by walking along each transect and counting the number of distinct calling individuals within hearing distance, (~ 5 m on each side of the trail). We compared both insect and territory abundance between forest types with one-way ANOVAs. We used a linear regression to examine the effect of insect abundance on frog territory abundance and then compared the means of the residuals for each forest type with a one-way ANOVA to remove the effect of insect abundance. All data met the assumptions of parametric tests and were analyzed using JMP 5.0.1.

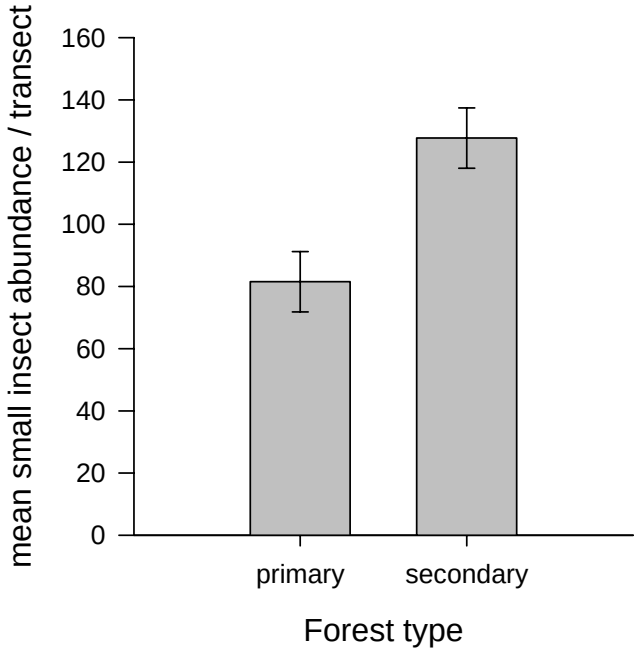


Figure 1. Mean abundance of small insects (body length < 3 mm) in primary and secondary forests transects at La Selva, n = 4, 50 m transects in each forest. There were more small insects in secondary forest than in primary forest.

## RESULTS

We sampled four 50 m transects in each forest type. The abundance of small insects (< 3 mm) per transect in each forest type was greater in secondary forest transects (mean = 127.7 ± 9.7 SE) than in primary forest transects (mean = 81.5 ± 9.7 SE; F = 11.37, df = 1, 7, P = 0.015; Fig. 1). Mean abundance of large insects (> 3 mm) per transect did not differ between forest types (primary: 11.8 ± 3.0 SE individuals, secondary: 5.0 ± 3.0 SE individuals; F = 2.55, df = 1, 7, P = 0.16).

*Dendrobates pumilio* territory abundance per transect ranged from 0 to 3 terri-

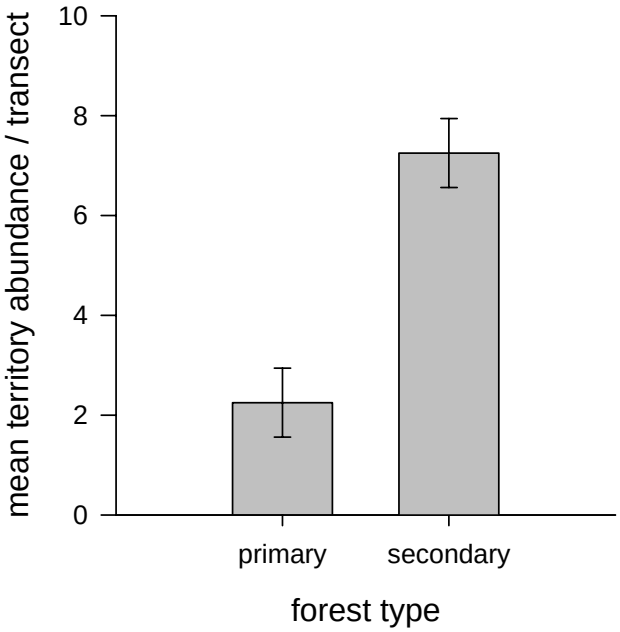


Figure 2. *Dendrobates pumilio* territory abundance in primary and secondary forest transects at La Selva. n = 4, 50 m transects in each forest type. There were more territories in secondary forest than in primary forest.

tories in primary forest and 2 to 9 in secondary forest, with a lower mean number of territories per transect in primary forest (2.3 ± 0.69 SE) than in secondary forest (7.3 ± 0.69 SE; F = 26.09, df = 1, 7, P = 0.002; Fig. 2).

There was a positive relationship between *D. pumilio* territory abundance and small insect abundance across forest types ($r^2$ = 0.44, df = 7, P = 0.07; Fig. 3). There was no difference in the means of the residuals from this regression (F = 1.86, df = 1, 7, P = 0.22). There was no relationship between large insect abundance and *D. pumilio* territory abundance ($r^2$ = 0.29, df = 7, P = 0.17).

## DISCUSSION

As we predicted, secondary forest had higher small insect abundance compared to primary forest. The physical characteristics of secondary forests, such as a denser understory and increased leaf litter (French 1999), may create the increased abundances of insects.

In addition to higher small insect abundance, secondary forests had increased *D. pumilio* territory abundance; therefore, it was difficult to determine if the increased *D. pumilio* territory abundance was caused by small insect abundance or forest type. When the effect of small insect abundance was removed, there was no difference in residual *D. pumilio* territory abundance between forest types. This suggests that forest type did not drive the observed trend in *D. pumilio* territory abundance; instead, it was driven by small insect abundance.

The location of *D. pumilio* territo-

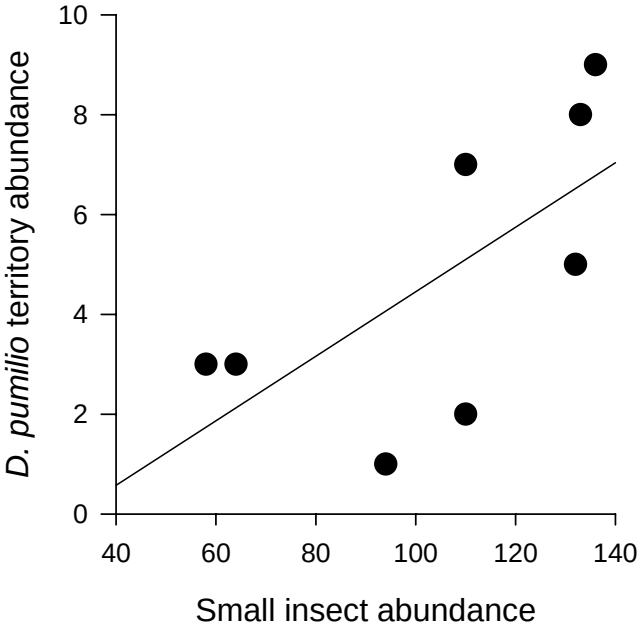


Figure 3. Relationship between *Dendrobates pumilio* territory abundance and small insect abundance across primary and secondary forest transects. The number of territories increases with small insect abundance.

ries appears to be determined by food resources, because *D. pumilio* territory abundance increased in areas with increased small insects, but was not affected by large insect abundance. This indicates that food abundance in addition to reproductive resources might determine territory location and local abundance of *D. pumilio*.

Our study was limited in several ways. We had a low number of transects in each forest due to limitations in time and equipment. Larger sample sizes and more replication would no doubt have improved our ability to make inferences from our results. Also, we were not able to control for variations in reproductive resources between forest types, which we believe is necessary to more fully assess the relative importance of reproductive and food resources in determining *D. pumilio* territory abundance.

## ADDENDUM:
## Notes on distinguishing between sexes in *Dendrobates pumilio*

*Dendrobates pumilio* exhibit year-round territoriality in lowland tropical forests in Costa Rica. Males aggressively defend territories against other males by physical combat and aggressive vocalizations throughout the year (Donnelly 1989); however, it is unknown whether males would equally defend their territory against female intruders during the non-breeding season. We had initially planned to determine whether males show differential territorial response to different sex intruders. Male intruders may increase competition for food and reproductive resources, (i.e., mates or bromeliads), and provide no benefit to the resident male. Female intruders may increase competition for food; however, they are a potential mate for the resident male. If this cost-benefit analysis could be shown to be valid, we could predict that males would defend their territories against females during the non-breeding season, but that their response would be less aggressive than towards male intruders.

We found conflicting information in literature and field observations that made the project unfeasible. Donnelly (1989) states that males and females can be identified by differences in coloration and texture on the throat; males have a dark central throat spot due to the presence of a vocal sac. Our preliminary observations revealed that these traits were not always visible on the frogs. Savage (2002) reports that only *D. pumilio* males call; however, we found several calling individuals with typical female coloration. Furthermore, there is disagreement in the literature about the ecology of *D. pumilio*. Savage (2002) describes a year-round mating season and female territoriality, while Donnelly (1989) describes a seasonal mating period with non-territorial females.

These conflicting results cast doubt on whether the sexes or breeding season have been accurately identified. Future researchers should take caution when designing studies that require identification of the sexes or specifics regarding the mating season in *D. pumilio*.

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# DUNG PREFERENCE AND DIURNAL FORAGING IN DUNG BEETLES

RICHARD W. TRIERWEILER AND DANIEL J. MADIGAN

*Abstract:* Scarabaeinae dung beetles are a major consumer of feces in tropical rain forests. Past studies have indicated that dung beetles prefer human over horse feces, but it is unclear how much they discriminate or whether it is due to nutritional value. We tested whether they prefer omnivore (protein-rich) over vegetarian feces, and whether different species are more active in the day or night. Contrary to our predictions, there were more beetles at the vegetarian feces, although the difference was not significant. Beetles were more active at night, especially larger species, suggesting a possible trade-off between increased competition and decreased predation at night.

*Key Words: Coleoptera, decomposition, Scarabaeinae, temporal variability*

## INTRODUCTION

Dung has been known to disappear from tropical forest within hours of being deposited, largely due to the activity of dung beetles and fly larvae (Forsyth and Miyata 1984). Dung beetles (Coleoptera: Scarabaeidae) that roll balls of dung away from the dung source and bury them, have been shown to prefer human feces to horse feces, suggesting that the beetles perceive human feces to be more nutritious and are able to sense and act on this difference (Cook et al. 1993). The extent of beetles' ability to discriminate between the nutritional values of dung sources has not been thoroughly tested. To test the ability of dung beetles to assess the value of dung, we used feces from human omnivores and vegetarians, assuming that the omnivore dung would be more nutritious and protein-rich than vegetarian dung (Forsyth and Miyata 1984). We predicted that more beetles would be attracted to traps baited with omnivore feces.

Dung beetles are active during the night and day, although more active at night (Alexander et al. 2002). We hypothesized that different types of dung beetles would utilize feces at night compared to day. Specifically, we predicted that certain beetles would forage during the day, risking greater predation for less competition, while other beetles would forage only at

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night, minimizing predation but increasing competition for the dung resource.

## METHODS

We set 20 pit fall traps in primary forest along the CES trail (between 150 - 750 m) at La Selva Biological Station, Costa Rica. Traps consisted of a tablespoon of human dung placed in a spoon, inserted in the ground at an angle of approximately 30°. Below the dung, a 20 oz Dixie cup was inserted into the ground, flush with the ground surface, to collect beetles.

We set traps in 10 pairs approximately 50 m apart along the trail. We baited one trap in each pair with herbivorous (vegetarian) dung, and the other with omnivorous (meat and vegetable consuming) dung obtained from several different individuals. We set traps within pairs approximately 1 m apart. We baited traps with fresh dung and collected beetles in the morning (0800) and evening (1800) on 2 days, 13-14 February 2005.

Beetles captured were placed in ethanol and categorized by morphotype and by size class: small (< 9 mm), medium (9 - 15 mm), and large (> 15 mm). Morphotypes were then identified to genus using the ALAS arthropod collection. We used a two-way ANOVA to analyze differences in the total number of beetles collected and morphotype abundances with respect to time of day (day or night) and dung type (herbivorous or omnivorous). We used a contingency analysis to compare frequencies of beetle size classes to time period. Data were statistically analyzed using JMP v. 5.0.1. Abundance data were log transformed to meet assumptions of statistical analyses.

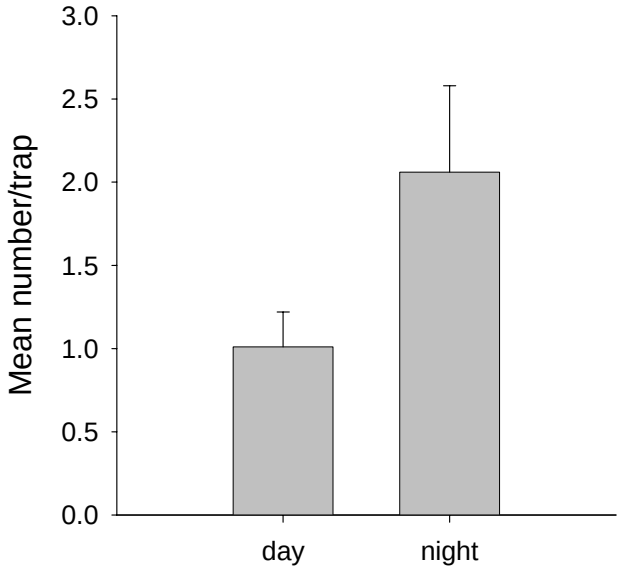


Figure 1. Mean beetles per trap (+ 1 SE) for day and night treatments (n = 80 traps). There were more beetles caught per trap at night than during the day (P = 0.07).

## RESULTS

We caught a total of 127 beetles, representing 14 different morphotypes within 8 genera (Table 1), all in the subfamily Scarabaeinae. The difference in abundance of beetles caught per trap during the day (1.01 ± 0.21) and during the night (2.06 ± 0.52) was marginally significant (2-way ANOVA, F = 3.30, df = 1, 78, P = 0.07; Fig. 1). There was no difference in the number of beetles caught per trap between herbivorous (1.80 ± 0.38) and omnivorous (1.27 ± 0.42) dung (2-way ANOVA, F = 1.82, df = 1, 78, P = 0.18; Fig. 2). There was no interaction between time period and dung type (2-way ANOVA, F = 0.06, df = 1, 78, P = 0.81). Different dung beetle morphotypes foraged at different times of the day ($X^2$= 39.45, df = 125, P < 0.0001). Large (genus *Dichotomius*) and medium (genus *Copris*) morphotypes were caught only at night,

Table 1. Genera and numbers of beetles collected (n = 127) along the CES trail, La Selva Biological Station, Costa Rica. All genera identified were within subfamily Scarabaeinae. Relative size, total found, and number and percentage caught at night are shown for each genus.

| Genus | Size class* | Total found | number (%) caught at night |
|---|---|---|---|
| *Canthidium* | small | 10 | 2 (20%) |
| *Canthon* | small | 3 | 2 (67%) |
| *Onthophagus* | small | 47 | 28 (60%) |
| *Scatinus* | small | 11 | 9 (82%) |
| *Unidentified* | small | 4 | 3 (75%) |
| *Copris* | medium | 37 | 37 (100%) |
| *Dichotomius* | large | 15 | 15 (100%) |

* small (< 9 mm), medium (9-15 mm), and large (> 15 mm).

while small morphotypes were caught both during the day and at night (Table 1).

## DISCUSSION

Although we found more beetles in traps baited with vegetarian feces, there was no statistical difference in the abundance of dung beetles visiting herbivorous and omnivorous dung. Either these beetles may not sense a difference in the nutritional value of feces, or the diets of the herbivores and omnivores were not different enough to elicit an overall response. Our predictions may also have been incorrect since the ball-rolling behavior of Scarabaeinae is facilitated by high fiber content (Kroenlein 1997), which was observed to be more common in the herbivore dung. Thus, there may be a trade-off between nutrient-rich omnivore and fibrous vegetarian dung. Since we used feces from FSP students, and each FSPer's diet is similar except for relatively small quantities of meat, beetles may not have been able to detect any difference. Future studies should use subjects with greater differences in diet to test beetle preferences.

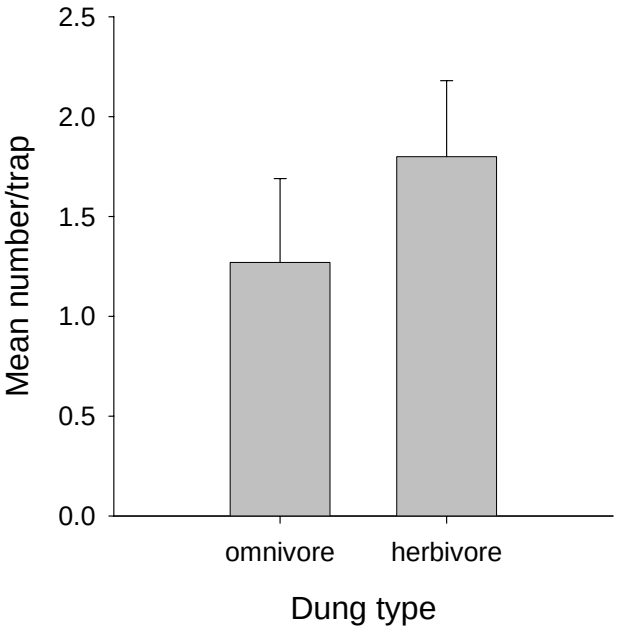


Figure 2. Mean number of beetles per trap (+ 1 SE) for omnivore and herbivore dung (n = 80 traps). There was no statistical difference between the two means (P = 0.18)

Dung can be deposited during day or night. Because small beetles are active during both time periods, they could exploit day- as well as night-deposited dung resources, thus limiting resources for those beetles that are active only at night. Medium and large dung beetles that forage only at night may only be able to utilize night-deposited dung resources. The use

of daytime foraging by small beetles may decrease their competition with the larger species, but increase their risk of predation by diurnally active predators. If large beetles foraged during the day, they would be more visible than smaller beetles, making them easier targets for visual predators. Therefore night foraging in the larger species may be a strategy to minimize predation risk, but their larger size may allow them to out-compete smaller beetles at night-deposited dung resources.

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