Distribution of dung beetles across three forest types and effects of intraspecific and interspecific competition on foraging

Melissa R. Kang, Patrick S. Leslie, and Gabrielle A. Miller-Messner

Abstract: Between 40 to 60 dung beetle species (Scarabaeinae) are known to inhabit Costa Rican forests. Assuming different vegetation cover is found in different forest types and that beetles may prefer more vegetation cover, we hypothesized that the dung beetle distribution would differ among three forest types. We found that the mean abundances of beetles were significantly greater in the early successional forest than the primary forest, and that diversity was greatest in the secondary forest. We hypothesized that intraspecific and interspecific competition, because of the patchy and ephemeral nature of the food resource, would have different effects on foraging and potentially on distribution patterns. In a laboratory experiment we found that changes in the beetle mass, reflecting foraging abilities of different morphotypes, were negligible and similar between the treatments, thus we could draw no conclusions on effects of intraspecific and interspecific competition. *In situ* studies could reveal how differing dung distribution across forest types may drive competition.

Key Words: early successional forest, primary forest, Scarabaeinae, *secondary forest.*

Introduction

Mammal dung is a patchy, ephemeral, and limiting resource for dung beetles in the subfamily Scarabaeinae in lowland tropical forests. Between 40 to 60 species of dung beetles are known to inhabit Costa Rican forests (Janzen 1983). Dung left in a pasture, even in close proximity to a forest, will remain untouched by dung beetles longer than an equivalent sample left in the forest (A. Solis pers. comm.). This finding suggests that although resources are available in different habitats, the beetles may be reluctant to forage in habitats that offer little cover. Thus the distribution of these beetles may depend on both the distribution of mammals among forest types and the amount of vegetation cover. In La Selva Biological Station, a variety of different habitats exists, such as primary, secondary, and early successional forests. Assuming that different vegetation cover is found in different forest types we hypothesized that dung beetle distribution would be influenced by forest type.

Additionally, differences in competitive abilities may be driving the distribution of these organisms across different forest types. When resources are patchy and ephemeral, interspecific competition has been shown to decrease (Begon et al. 1990). In such conditions, different species have independent, aggregated distributions, and thus the dominant species may be absent from many resource patches, allowing inferior species to persist (Begon et al. 1990). If so, it follows that interspecific competition among dung beetles should be low while intraspecific competition may still be high. We hypothesized that differences in intraspecific and interspecific competitive ability should exist among different dung beetle morphotypes. We tested this hypothesis with laboratory foraging experiments. We predicted that we would observe a greater differential in the consumption of dung (measured by the gain in body mass) between beetles of the same morphotype than those in the treatment with different morphotypes.

Methods

We sampled three forest types for beetle diversity and abundance on 14-16 February 2001 at La Selva Biological Station, Costa Rica. We set up 20 pitfall traps in the primary forest on Camino Circular Lejano, 20 traps in the 13 to 25-year old (this information provided from GIS) secondary forests on Sendero Sarapiqui and Sendero El Atajo, and 10 traps in the 3-5 year-old early successional forest plots located at the end of Sendero Oriental. We set up only 10 traps in the early successional forest due to the small size of the plots. Each pitfall trap consisted of a 12 oz. plastic cup with a teaspoonful of human feces positioned above the cup using a spoon stuck in the ground at an angle of approximately 30 degrees. We filled each cup half way with water and covered it with a leaf to prevent rain from filling the cup. The traps were left out for approximately 20 h, after which the beetles were collected and classified by morphotypes. We calculated the Shannon-Weiner diversity index and evenness index for dung beetle morphotypes for each forest type.

To assess the potential effects of intraspecific and interspecific competition on foraging, we tested the two most abundant and visually distinct beetle morphotypes, classified in this study as A and B, in three treatments. We placed two type A beetles in 10 replicates of Treatment 1, two B beetles in nine replicates of Treatment 2, and one A and one B beetle in 10 replicates of Treatment 3. Each pair of beetles was matched as best as possible by similar mass and placed in a 20 oz. plastic cup with less than a quarter-teaspoon of human feces for 12 h (from 17 February at 03:00 until 18 February at 15:00). We weighed the beetles using analytical balances (± 0.001) before and after the treatments for proportional body mass changes reflecting the competitive abilities of different morphotypes. The proportional body mass change was normalized using a log transformation.

Results

We found a total of 222 dung beetles in our sampling: 66 from the primary forest, 83 from the secondary forest and 73 from the early successional forest. The mean abundances of beetles were significantly different across forest types (ANOVA, $F = 4.24$, $df = 2, 47$, $P = 0.02$; Fig. 1). Tukey HSD pairwise comparisons revealed that beetle abundance was significantly greater in the early successional forest than in the primary forest but mean beetle abundance in the secondary forest was not significantly different than in other forest types. We found six morphotypes from primary and early successional forests and eight from the secondary forest. Shannon-Weiner indices showed greatest species diversity and evenness in the secondary forest and least in the primary forest (Table 1).

There were no significant changes in the proportional body mass of the individuals after the 12 h feeding time between treatments (ANOVA, $F = 0.56$, $df = 2, 47$, $P = 0.58$). Changes in the proportional body mass for morphotypes A and B in Treatment 3 were also not significantly different (t-test, $t = 0.02$, $df = 18$, $P = 0.83$).

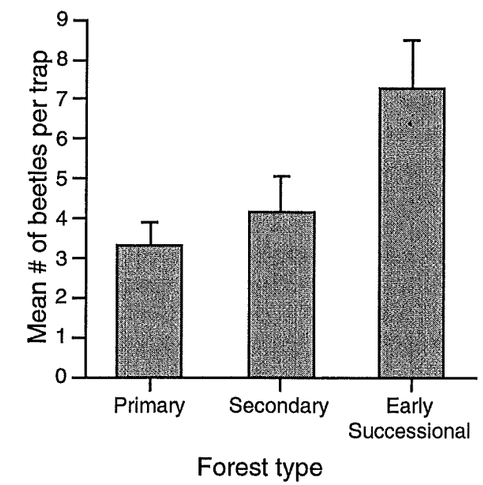

Fig. 1. Mean number of beetles per trap ± 1 SE in three forest types in La Selva Biological Station, Costa Rica. (n = 20 for primary and secondary forests, n = 10 for early successional forest)

Table 1. Shannon-Weiner diversity and evenness for dung beetles sampled in three forest types at La Selva Biological Station, Costa Rica.

Forest Type	Diversity	Evenness
Primary	0.98	0.55
Secondary	1.95	0.94
Early Successional	1.10	0.61

Discussion

Dung beetle abundance was greater in the early successional forest than in the primary forest, perhaps because of greater cover and food availability provided by the dense shrubs in this habitat. We observed that the 3 – 5 year successional forest had more dense herbaceous growth than primary forest. Dense shrubs may provide dung beetles with protection from predators and desiccation. In addition, dense shrubs may also provide cover for small mammals such as agoutis and other small rodents that produce food for beetles. Thus, dung beetle abundance may be greater in the early successional forest because dung may be more abundant there than in the primary forest.

The intermediate disturbance hypothesis (Connell 1978) suggests that an intermediate frequency of disturbance leads to increased species richness by allowing for the colonization of many species while preventing the exclusion of others by the dominant species. In accordance with this concept, we found the greatest dung beetle diversity in the secondary growth forest, where the frequency of disturbance falls between the two other forest types, and thus allows for the coexistence of many species of varying degrees of dominance.

In our experiment to test the effects of competition that may influence dung beetle distribution, proportional beetle mass changes were negligible and similar between the treatments. Thus, we could draw no conclusions comparing the relative levels of interspecific and intraspecific competitions. The competition experiment was initiated approximately 30 h after the first batch of individuals was collected. The confinement of beetles in plastic cups for this duration of time may have placed stress on the beetles that led to low levels of consumption. Some beetles, such as *Dichotomius* sp. that occurs commonly in the low elevations (Howden 1983) and was observed in our sampling, are nocturnal foragers. Thus, beginning our experiment at 03:00, after the majority of their foraging time had passed, may also explain why we observed negligible changes in body mass. Further study of competition could consider developing *in situ* methods for testing competition in order to minimize potential effects of experimentation on beetles. *In situ* studies would allow one to test how differing resource distribution across forest types may drive competition, and thus have important implications for beetle distribution.

Acknowledgements

We would like to thank Matt Clark from the GIS lab and Angel Solis from the ALAS lab for the knowledge and time they provided.

Literature Cited

Begon, M., J.L. Harper, and C.R. Townsend. 1990. Ecology. Second Ed. Blackwell Scientific Publications, Boston, MA, USA.

Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. Science 199: 1302-1310.

Howden, H.F. 1983. *Dichotomius carolinus colonicus*. Pp. 713 – 714 *in* D.H. Janzen, editor. Costa Rican Natural History. The University of Chicago Press, Chicago, IL, USA.

Janzen, D.H. 1983. Insects. Pp. 641 *in* D.H. Janzen, editor. Costa Rican Natural History. The University of Chicago Press, Chicago, IL, USA.