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Ant Activity along Moisture Gradients in a Neotropical Forest[1]

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ABSTRACT

Insect activity often tracks moisture gradients. We studied ant activity, size, and diversity along three moisture gradients in a Panamanian rain forest. Ant activity at baits increased by 25 percent from the dry to the wet season, and > 200 percent on a topographical gradient from a ravine to an exposed plateau. Activity varied little from day to night. Three microhabitats—tree trunk, shrub, and litter—showed different responses to these three gradients. The size distribution of the species pool ($N = 63$) was right skewed, but the average size of ants at a bait was strongly bimodal. Ants active in moister times and places were not significantly smaller. We suggest that gradients of desiccation risk and food availability were the two most likely causes of these patterns. Two temporal niche axes (daily and seasonal) showed little species specialization, but half of the common species could be categorized as litter or plant microhabitat specialists.

RESUMEN

Nosotros estudiamos actividad de hormiga, tamaño, y diversidad en 4 microhabitats a lo largo de tres gradientes de humedad en un bosque Panameño. La actividad de hormiga aumentada por 25 percent desde la seca a la temporada mojada, y > 200 percent sobre un gradiente topográfico desde un barranco a una meseta expuesta. La actividad varió poco desde el día a la noche. Tres microhabitats—tronco de árbol, arbusto, y la hojarasca—mostró respuestas diferentes a estos tres de gradientes. El tamaño la distribución de las especies combina ($N = 63$) tuvo razón skewed, pero el tamaño promedio de hormigas a una carnada era fuertemente bimodal. Las hormigas activas en los lugares y veces más húmedas no eran significativamente menores. Nosotros sugerimos que los gradientes de desecamiento arriesgan y la disponibilidad alimentaria son los dos muy probables ocasiona de estos modelos. Dos temporal los nichos (diarios y estacionales) mostraron poca especialización de especies. La mitad de las especies comunes podría categorizarse como hojarasca o plantada microhabitat especialistas.

Key words: *activity; ants; Formicidae; humidity; Hymenoptera; microhabitat; Panama.*

ABIOTIC FACTORS HAVE LONG BEEN LINKED to the behavior and population dynamics of terrestrial arthropods (Andrewartha & Birch 1954, Price 1997). Ants are common, ecologically important insects in tropical ecosystems (Fittkau & Klinge 1973, Höllbdobler & Wilson 1990). Ants collect and disperse seeds (Horvitz & Schemske 1986, Kaspari 1993b, Levey & Byrne 1993), recycle nutrients (Haines 1978), and harvest vegetation (Cherrett 1986). Understanding the factors that shape ant foraging activity thus should increase our understanding of many population- and ecosystem-level processes. For example, high temperatures and low humidity create gradients of desiccation risk that can shape activity in desert ants greatly (*e.g.*, Whitford *et al.* 1975, Briese & Macauley 1980, Lighton & Feener 1989).

These effects may not be restricted to areas of low absolute humidity. In tropical ecosystems, where temperature is relatively constant, increases in humidity often are associated with increased insect abundance and activity (Janzen & Schoener 1968, Janzen 1973, Levings & Windsor 1984, Wolda 1988, Levings & Windsor 1996). In a seasonal rain forest, Levings (1983) combined comparisons of litter-ant activity along moisture gradients with watering experiments to suggest that ant activity tracks moisture. In a relatively aseasonal Costa Rican rain forest, small species of seed-harvesting ants were more likely to forage in the humid portions of the day and and in moister habitats (Kaspari 1993a). Combined, these patterns suggest the desiccation hypothesis: humidity regulates ant activity by regulating desiccation risk.

Moist litter, however, is not just a humid microhabitat for litter ants. Moist litter may be more likely to release nutrients, and bolster populations of microbes and microfauna that form the base of the litter food web (Levings & Windsor 1984, Byrne 1994, Coleman & Crossley 1996, Levings

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& Windsor 1996). Increased ant activity in wet seasons and habitats may thus reflect colonies tracking food availability, reducing desiccation risk, or some combination of both. One way to distinguish between these causes is to extract more predictions from the desiccation hypothesis.

Ant workers span almost four orders of magnitude in body size (Kaspari & Weiser 1999). Surface area increases as a function of mass$^{2/3}$; therefore, larger ants expose proportionately less tissue to the environment and are less prone to desiccation. Small ants desiccate more quickly (Hood & Tschinkel 1990) and were less active during the drier afternoon in one tropical forest (Kaspari 1993a). If desiccation risk drives activity along a moisture gradient, then we would expect smaller ants to be more active in moister conditions. It is not clear why this should be so if food limitation drives such changes.

In this study, to further evaluate the desiccation hypothesis, we identified three moisture gradients for ants in a seasonal tropical forest on Barro Colorado Island (BCI), Panama. We then explored how the ant activity, size, and diversity in four microhabitats varied along these gradients.

MATERIALS AND METHODS

BCI is a 1500-ha island surrounded by the waters of Lake Gatun in the Panama Canal Zone, and is covered with second growth and old-growth lowland seasonal tropical forest (Leigh *et al.* 1996).

The basic sampling units of this study were baits, which were placed in four microhabitats at a station. Thirty stations were arrayed, 5 m apart, along 150-m transects. The transects were 1 m off established trails. Each bait consisted of *ca* 1 ml of peanut butter. In three microhabitats (under the litter, on top of the litter, and in low woody shrubs that failed to reach the canopy) the peanut butter was squirted into a 20-ml (1.6 × 5.8 cm) glass scintillation vial. In the woody plant, the vial was wired into the plant *ca* 1 m off the ground. In the fourth microhabitat, canopy trees ≥1 m diameter at breast height (DBH), *ca* 1 ml of peanut butter was spread in a thin line *ca* 5 cm long on the trunk. After one hour, vials were collected and capped, and ants at tree baits were aspirated.

Three moisture gradients.—The first moisture gradient we considered was topographical, the habitat exposure gradient. BCI is an island hilltop cut by numerous streams and capped by a flat, basalt plateau (Leigh *et al.* 1996). Forest floor habitats range from those deep in ravines to those on a plateau 100 m higher and exposed to drying breezes (Croat 1978). The ravines radiate from the plateau to the lakeshore, and are crowned by ridges. Soil moisture in these ravines is consistently higher than the exposed plateau, with ridgetops intermediate (Levings 1983). To evaluate this gradient, one transect was located on the plateau (near AVA Trail), one in a ravine along a stream (along the Allee Trail), and one on a ridge above this ravine (the Fausto Trail).

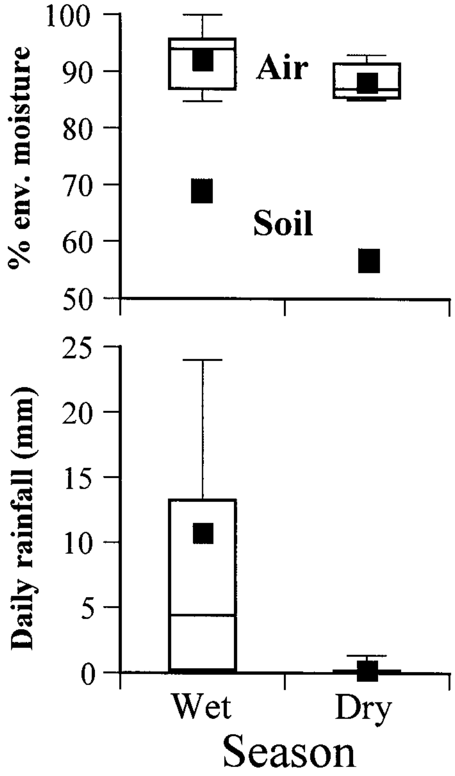

FIGURE 1. Average daily rainfall, daily relative humidity (box plots), and monthly percent soil moisture (by weight) recorded at the main weather station on Barro Colorado Island from June to July 1994 (wet season), and in late December 1997 (dry season).

The second moisture gradient we considered was the seasonal gradient. On BCI, 90 percent of the annual 2.6 m of rainfall occurs from May through December (Dietrich *et al.* 1996). This variation in rainfall creates seasonal cycles of air and soil moisture (Fig. 1) with profound impacts on the forest biota (Leigh *et al.* 1996). Transects were run in June and July 1994 (wet season) and late December 1997 (early dry season, brought on by an El Niño).

TABLE 1. *Abundance of ants attracted to peanut butter baits on BCI. Abundance is measured by the number of collection records (max. = 1415) and the number of stations (max. = 90). Species are listed in order of decreasing worker mass.*

Species	Records	Stations	Mass (mg)
Paraponera clavata	3	3	18.647
Camponotus cf. *simillimus*	3	3	8.690
C. atriceps	1	1	7.521
Pachycondyla impressa	2	2	6.586
Atta columbica	1	1	6.231
Pachycondyla villosa	1	1	5.999
Odontomachus bauri	24	17	5.862
Ectatomma tuberculatum	13	11	4.054
Pachycondyla harpax	30	20	2.304
Ectatomma ruidum	218	78	2.103
Pachycondyla sp. 1	1	1	1.987
Aphaenogaster araneoides	1	1	1.693
Pheidole hirsuta	16	10	1.675
Pachycondyla sp. 2	1	1	1.326
Pseudomyrmex boopis	1	1	0.936
Labidus coecus	2	1	0.837
Pheidole skd	1	1	0.832
Crematogaster stolli	1	1	0.688
Azteca sp. 1	23	17	0.527
Pheidole ske	3	3	0.522
P. susannae	10	7	0.500
Pheidole sp. B	1	1	0.461
Apterostigma sp. 1	2	2	0.408
Pheidole radoszkowskii	204	63	0.371
P. cocciphaga	2	2	0.299
Trachymyrmex sp. 1	1	1	0.254
Rogeria sp. 1	1	1	0.249
Pheidole tiny	9	7	0.191
Azteca sob	1	1	0.189
Technomyrmex sp. 1	2	2	0.173
Pheidole sensitiva	3	2	0.155
Pheidole hair	1	1	0.151
Azteca sp. 3	1	1	0.143
Technomyrmex sp. 2	1	1	0.141
Pheidole sp. E	16	8	0.121
Crematogaster carinata	1	1	0.121
Azteca sp. 2	1	1	0.119
Pheidole bigb	9	7	0.100
Brachymyrmex sp. 1	2	2	0.094
Pheidole dasyllis	4	3	0.093
Paratrechina ha	39	22	0.087
Oligomyrmex sp. 1	1	1	0.087
Crematogaster sp. 2	30	22	0.087
Pheidole spi	2	2	0.069
Pheidole skb	1	1	0.062
Crematogaster crucis	1	1	0.062
Pheidole ruida	15	14	0.056
Solenopsis sp. 1	36	23	0.054
Crematogaster JTL-014	2	2	0.053
Wasmannia auropunctata	112	50	0.041
Solenopsis brdipl	12	10	0.040
Pheidole rugiceps	36	24	0.040
Tetramorium sp. 1	2	1	0.031
Pheidole sph	1	1	0.029
Pheidole spg	4	4	0.029
Pheidole sp. F	4	4	0.027
P. multispina	26	25	0.023
Solenopsis D. dior	26	21	0.020
Pheidole sp. D	1	1	0.020
Pheidole sp. A	1	1	0.020
Solenopsis D. ditt	58	41	0.016
Pheidoleteki	2	2	0.015
Solenopsis D. diss	19	14	0.013

The third moisture gradient occurred over 24 hours—the time of day gradient. At the litter layer vapor pressure deficits (a measure of the drying power of the air) ranged from 0.18 to 0.55 kPa and were typically highest at midday, dropping quickly at sunset (Kaspari 1993a). Desiccation risk at the litter layer was thus greater at midday than during the evening (Kaspari 1993a). To evaluate daily moisture gradients, transects were run within two hours of 1200 h where no rain had fallen in the previous six hours (day), and at *ca* 2200 h where no rain had fallen in the previous six hours (night).

The 4 microhabitats, 30 stations, 3 habitats, 2 daily samples, and 2 seasons yielded 1440 collections. Ant activity was measured as the number of ants collected at a station during a transect run. The small size (Kaspari & Vargo 1995) and foraging range (Byrne 1994) of most tropical litter-ant colonies likely resulted in little overlap of colony use among stations. When $\log_{10}$ transformed, activity was normal, and was analyzed with a three-way ANOVA.

To examine specialization along moisture gradients, we used Feener and Schupp's (1998) definition of "specialist" as a species collected at one end of the moisture gradient at $\geq$ 90 percent of the stations. We used only common species (*i.e.,* those found at $\geq$ 6 stations).

To measure ant size, head lengths (mm) of at least five workers of each species were measured on pinned specimens using an ocular micrometer. These were converted to dry body mass (mg) using allometric equations (Kaspari & Weiser 1999) and the average size of a species per bait was calculated.

To study microhabitat effects, we averaged ant activity in each microhabitat at each station. Ant activity across microhabitats was non-normal despite transformations, largely due to a number of sites where shrub and trees never yielded ants. Likewise, the average size of ant species at baits was

TABLE 2. *Common ant species that specialize on different seasons, time of day, habitat exposure, and microhabitats (plant and litter habitats pooled). Specialists were defined as common species (represented by six or more station records) in which ≥90 percent of the records came from one end of the gradient. Spatial specialization was more common than temporal specialization.*

Time		Space	
Season (9% of spp.)	Time of day (5% of spp.)	Habitat exposure (17% of spp.)	Microhabitat (46% of spp.)
Wet	**Night**	**Ravine**	**Litter (under+top)**
			Pachycondyla harpax
Pheidole tiny	*Solenopsis* brdipl		*Pheidole hirsuta*
P. hirsuta			*Pheidole* sp. E
			P. multispina
			P. rugiceps
			Solenopsis diss
Dry	**Day**	**Plateau**	**Tree+Shrub**
		Solenopsis brdipl	*Azteca* sp. 1
		Pheidole sp. E	*Crematogaster* sp. 2
		P. hirsuta	*Ectatomma tuberculatum*
			Solenopsis brdipl

always non-normal, due to bimodality (see below). For these cases, we used Kruskal-Wallis tests and one-tailed P values corresponding to the predicted response to humidity gradients.

RESULTS

We collected 22,730 ant workers, including 63 species from 22 genera (Table 1). Less than 1 percent of insects in vials were non-ants (mostly Blattidae). Of the 1440 baits used in this study, 25 (<2%) were lost and discarded from the data set. The species found in the greatest numbers at the 90 stations were *Ectatomma ruidum* (87%), *Pheidole radoszkowskii* (70%), *Wasmannia auropunctata* (56%), and *Solenopsis* ditt (46%). Together, these four species spanned three orders of magnitude in size and accounted for 56 percent of all species records at baits (Table 1). Our sampling missed many trophically specialized species (*e.g.,* the tribe Dacetini, the army ants, and the fungus-growing Attini).

There was little specialization by season or time of day (Table 2). Along the seasonal gradient, two *Pheidole* species were wet season specialists. Likewise, there was one nocturnal specialist, a *Solenopsis,* on the daily gradient. To measure specialization in space, we compared the ravine and plateau fauna. This yielded three specialists, all on the plateau (Table 2). Likewise, we compared the shrub+tree species and those from the two litter strata. Nearly half the common species specialized on microhabitat: six in the litter microhabitats and four in the plant microhabitats (Table 2).

TABLE 3. *Three-way ANOVA predictions of the effects of three humidity gradients—season (wet vs. dry), habitat exposure (low, medium, high), and time (day vs. night). Only season and habitat samples differed in ant activity, and did so consistently across all treatment combinations.*

Source	df	Type III SS	*F*	*P*
Season	1	1.487	3.57	0.0299
Habitat exposure	2	12.262	14.71	0.0001
Season*Exp.	2	0.831	1	0.3701
Time of day	1	0.898	2.15	0.0716
Season*Time	1	0.154	0.37	0.5442
Exp.*Time	2	0.068	0.08	0.9214
Season*Exp.*Time	2	0.650	0.78	0.4592
Error	348	145.09		

PATTERNS OF ANT ACTIVITY.—Season and habitat exposure, but not time of day, significantly shaped ant activity (Table 4; Fig. 2). As transects became more sheltered (from the plateau, to the ridge, to the ravine) the number of ants collected at baits nearly tripled ($P < 0.0001$). Ant activity also increased by 25 percent from the dry to the wet season ($P < 0.03$); however, ant activity increased only marginally ($P < 0.07$) from day to night. As none of these main effects yielded significant interaction terms ($P > 0.3$) there was no evidence of synergy among season, time of day, and habitat exposure.

Total ant activity varied among microhabitats,

TABLE 4. *Changes in species composition for the tree assemblage along two temporal gradients (only species found at three or more stations are listed). Species in* ***bold*** *are plant specialists. At bottom are the summed contribution of plant specialists and microhabitat generalists.*

Dry season	Trees	Wet season	Trees
***Crematogaster* sp. 2**	**13**	*Pheidole radoszkowskii*	19
Ectatomma ruidum	9	***Azteca* sp. 1**	**13**
Wasmannia auropunctata	9	*Wasmannia auropunctata*	12
***Azteca* sp. 1**	**4**	*Ectatomma ruidum*	10
***Solenopsis* brdpl**	**4**	*Paratrechina* ha	8
Solenopsis sp. 1	4	*Solenopsis* dior	6
Ectatomma tuberculatum	**3**	***Crematogaster* sp. 2**	**3**
Pheidole ske	3	*Ectatomma tuberculatum*	**3**
		***Solenopsis* brdipl**	**3**
Plant/Generalist	**24/25**	Plant/Generalist	**22/55**
Day	Trees	Night	Trees
***Azteca* sp. 1**	**13**	*Pheidole radoszkowskii*	18
Wasmannia auropunctata	12	*Wasmannia auropunctata*	11
Ectatomma ruidum	11	***Crematogaster* sp. 2**	**8**
***Crematogaster* sp. 2**	**9**	*Ectatomma ruidum*	8
Pheidole radoszkowskii	5	*Paratrechina* ha	8
Solenopsis sp. 1	5	***Azteca* sp. 1**	**7**
		***Solenopsis* brdipl**	**6**
		Solenopsis dior	6
		Ectatomma tuberculatum	**4**
		Pheidole susannae	4
		P. ruida	4
Plant/Generalist	**22/33**	Plant/Generalist	**25/59**

and activity trends differed along moisture gradients. More ants were found at litter baits than tree or shrub baits (Fig. 2); however, the baits sampled the ant community in different ways (see Materials and Methods). Ant response to microhabitats differed along humidity gradients (Fig. 2). From the dry to the wet season, ant activity increased by 30 percent in shrubs ($KW_{90,90} = 5.8$, $P < 0.008$) and 20 percent in trees ($KW_{89,90} = 5.91$, $P < 0.008$), but failed to change in litter microhabitats ($P > 0.25$). From the plateau to the ravine, ant activity increased in all but the tree microhabitat. In the shrub layer, activity nearly tripled ($KW_{30,30,30} = 8.09$, $P < 0.009$); in both litter habitats, activity nearly doubled from plateau to ravine/ridge (KW30,30,30 > 7, all $P < 0.02$). From day to night, ant activity was relatively constant in all but the tree microhabitat, where it nearly doubled after sunset ($KW_{90,90} = 10.5$, $P < 0.0006$; Fig. 2).

PATTERNS OF ANT SIZE.—The mean worker mass (dry weight) of ant species collected at baits varied over three orders of magnitude, with a median of 0.15 mg and a significant right skew even after log10 transformation (Fig. 3; Shapiro-Wilk $W = 0.93$, $P < 0.0040$; $N = 63$). In contrast, the average mass of ants at baits was strongly bimodal, with one mode at 0.04 mg and a second at 2.1 mg (Fig. 3).

This bimodality decreased our ability to detect changes in size distributions along the three moisture gradients (Fig. 4). In all three cases, ant sizes in moist environments were 20–50 percent smaller on average, but none of these individual trends was significant ($KW < 1.4$, all $P < 0.25$). The odds that these trends would fall in the same, predicted direction were $1/2*0.5^3 = 0.0625$.

There were significant differences in the average size of ant species using the four microhabitats ($KW_{34,42,82,74} = 16.7$, $P < 0.0008$). Shrub ants tended to be the largest, averaging 0.99 mg, followed by those at the top of the litter (0.92 mg) and under the litter (0.81 mg). The tree ants, on average, were half the size of the shrub fauna (0.46 mg).

DISCUSSION

Ants of tropical forests are patchy in species composition (*e.g.*, Wilson 1958), nest density (*e.g.*, Kaspari 1996a, b), and activity (*e.g.*, Levings 1983, Horvitz & Schemske 1990, Feener & Schupp 1998). Ecologists are challenged to link this patchiness to underlying biotic and abiotic gradients

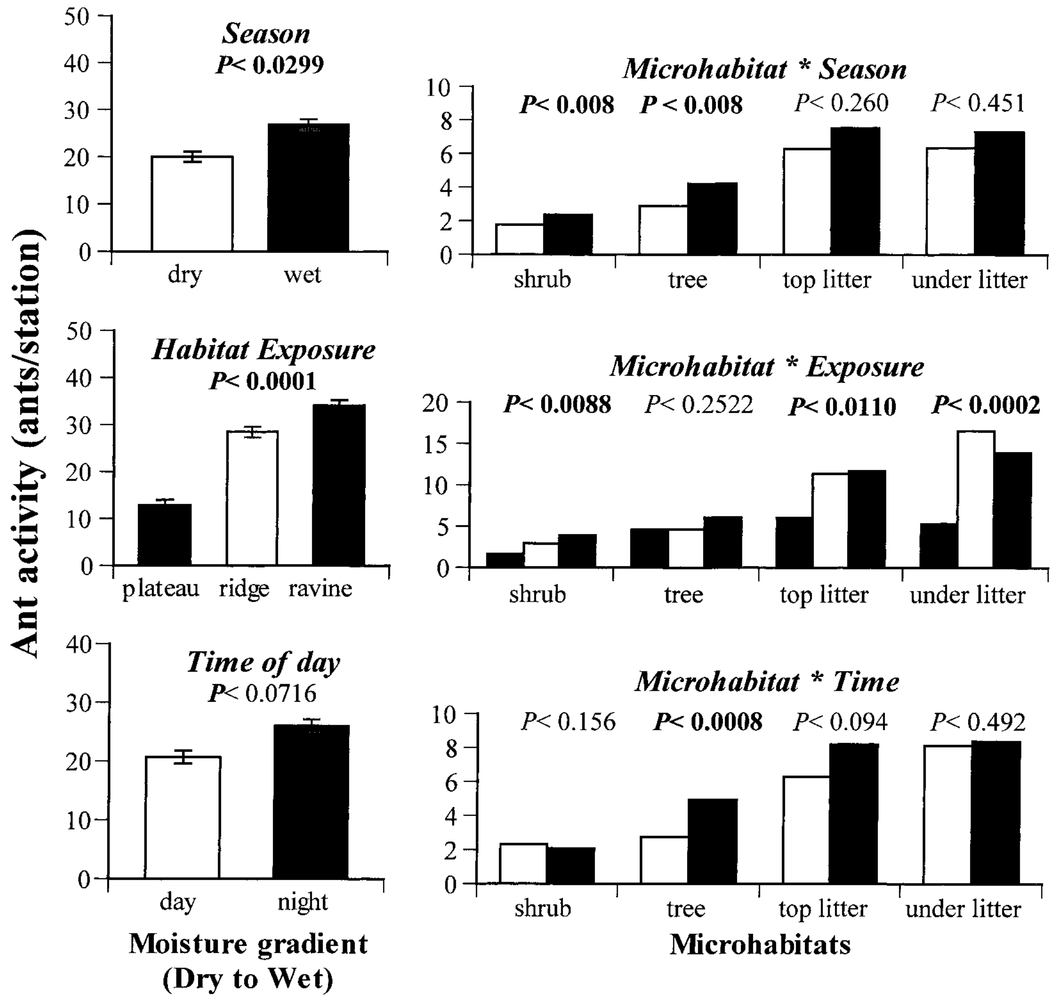

FIGURE 2. Ant activity partitioned along three humidity gradients (left) and the microhabitats within each gradient (right). Humidity gradients are the least square means (±1 SE) of ant activity at each station, plus the significance value of a three-way ANOVA. Microhabitat*humidity gradients plot the mean number of ants per microhabitat, with significance value from separate Kruskal-Wallis tests.

(Whittaker 1970). Here we show that ant activity increased 200 percent across a habitat moisture gradient, 25 percent from the dry to wet season, and, marginally, 15 percent from day to night. Many of these patterns are consistent with the hypothesis that foraging ants avoid desiccation. Two phenomena, however, caution against desiccation as a single overriding mechanism. First, if desiccation risk alone drove ant activity on BCI, we would expect synergy among the gradients; ravines in the wet season would be more than active ravines in the dry season and the plateau on a dry season day would have proportionately less activity than one at night. However, there were no significant interactions among the three gradients (Table 2). Second, in no case was there a significant increase in the body size of ants using the drier part of the moisture gradients. We conclude that ant activity on BCI arises from a number of factors, desiccation risk among them. This is clear from the variety of activity patterns found among the microhabitats.

Litter ants (both surface and subsurface) significantly increased activity along the habitat gradient alone (Fig. 2). Levings (1983) also found a two-fold increase in activity from ravine to plateau. The failure to find similar increases seasonally, and from day to night, may be in part a function of the patchiness of the litter (Kaspari 1996a) that

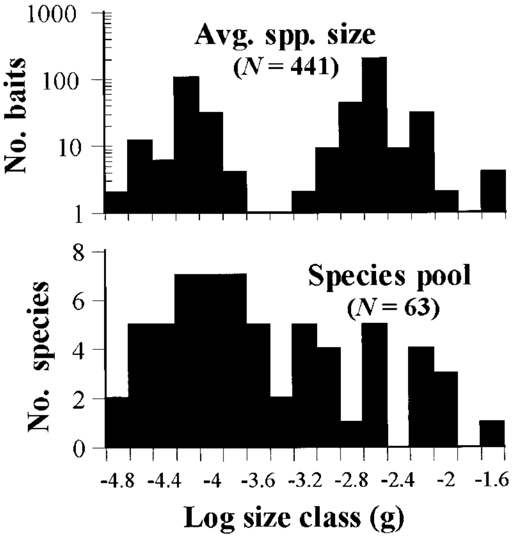

FIGURE 3. Size distribution of the available species in this study (bottom), and the distribution of sizes of species at baits, $\log_{10}$ transformed (top).

prevents statistical resolution despite trends in the predicted direction; however, it also may reflect the buffered nature of the litter environment, where the ground effect insulates litter ants from the temporal changes in humidity (Oke 1978, Fetcher *et al.* 1985). It is possible that the moister ravine habitats yield a wider array of arthropod prey. Levings (1983), however, was able to increase ant foraging activity in the dry season 24 hours after watering plots—too short a time for considerable recruitment of prey. A second possibility, that nest densities are higher in the ravine, was not supported with litter ants (Kaspari 1996b).

Ants foraging in shrubs increased activity from the dry to wet season, and from ravine to plateau, but not from day to night. As vapor pressure deficits increase vertically, the shrub microhabitat likely exacerbates seasonal differences in desiccation rates; however, plant exudates also increase in the wet season (Schemske 1982, Rico-Gray & García-Franco 1998). Some plant ants (*e.g.,* the exudate feeding *Ectatomma tuberculatum*) thus may be tracking these resources, not humidity—an explanation consistent with the lack of change in foraging activity from day to night.

Ants foraging in trees showed still a third pattern—significant increases from dry to wet season and day to night, but not along the habitat gradient. Tree trunks are the meeting place for two separate faunas—the canopy and litter (Longino & Colwell 1997). Table 4 lists the species found on at least three tree trunks along the two temporal gradients. In both cases, the increased tree activity in the wet season and at night did not result from great increases in the incidence of tree specialists. Instead, the incidence of microhabitat generalists doubled in the wet season and at night. The three most common generalist species behaved differently. *Pheidole radoszkowskii* occupied the moist end of the gradients. This is consistent with the hypothesis that the wet season and nightfall both release litter ants like *Pheidole* from desiccation risk (nocturnal foraging also may lower vulnerability to visually oriented phorid parasites; Orr 1992). Two other common species, *W. auropunctata* and *E. ruidum,* are common Neotropical generalists that showed remarkably constant foraging activity.

There is also evidence for segregation among the canopy fauna. *Crematogaster* sp. 2 and *Azteca* sp. 1, the two most common canopy species in this study, showed complementary distributions. *Crematogaster* sp. 2 was most active in the dry season and equally active from day to night. *Azteca* sp. 1, in contrast, was more active in the wet season, and during the day.

One pattern that would have buttressed the desiccation hypothesis did so weakly—ants were not consistently smaller on the moist end of the gradient (Fig. 4). Factors beyond body size and activity can reduce desiccation risk (*e.g.,* Hood & Tschinkel 1990); and body size in ants is influ-

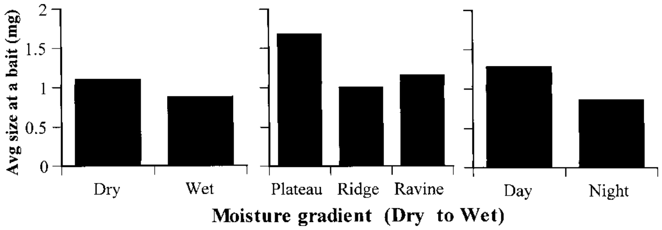

FIGURE 4. Mean species sizes at baits along three moisture gradients.

enced by a variety of factors (Hölldobler & Wilson 1990, Kaspari & Weiser 1999). Ant size distributions at baits tended to be bimodal (Fig. 3), a pattern also found in a closed canopy forest of Costa Rica (Kaspari 1993a). The causes of this bimodal distribution in activity (relative to the unimodal distribution of the canopy fauna; Yanoviak & Kaspari 2000) are poorly understood.

One implication of the bimodal distribution is that items on the forest floor have a roughly equal chance of encountering two very different-sized ants. This may have consequences for the many plants having seeds that are dispersed and preyed upon by ants. Small ants (*e.g., Solenopsis [Diplorhoptrum*] and *W. auropunctata*) may prove to be poor dispersers (Horvitz & Schemske 1986)., guarding and shredding the elaiosome without moving the seed (Horvitz & Schemske 1986, Kaspari 1993b, Levey & Byrne 1993). In contrast, large ants (*e.g., E. ruidum* and *Pachycondyla harpax*) often move seeds out from under parent plants. On BCI, seeds likely stand an equal chance of encountering either fate.

What are the implications for seed-dispersal syndromes? If ants attracted to baits are a major subset of those attracted to seeds, our studies, combined with those of Feener and Schupp (FS; 1998) and Levings (L; 1983) suggest this emerging picture for BCI. Plants that depend on ants for seed dispersal will encounter more ants in moist ravines than on exposed ridgetops (this study, L) and more ants in the wet season than the dry season (this study, FS, L). Seeds likely are not dispersed more at night versus the day (this study; *cf.* FS), or more in gaps versus old growth forest (FS). The degree to which this portrait of the BCI ant fauna matches other tropical forests remains to be seen.

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