

## **Body size and microclimate use in Neotropical granivorous ants**

**Michael Kaspari\***

Dept. of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721 USA

Received: 7 May 1993 / Accepted: 28 September 1993

**Abstract.** The stability of tropical microclimates has left microclimate use by tropical species little unexplored. At La Selva Costa Rica, I related foraging activity at seed baits to humidity in two forests types. I recorded 38 and 35 ant species at seed baits in closed and open canopy forest. The microclimate 5 cm above the forest floor in the younger, Open Forest was warmer, drier, more variable, and more sensitive to current weather than in the older Closed Forest. Ant species within both forests foraged at different Vapor Pressure Deficits (kPa), a measure of the drying power of the air. VPD use was not confounded with diel activity patterns. Body size explained 46% of the variance in mean VPD use among ant species. Small ant species tended to forage in moist microclimates; large species tended to be microclimate generalists. Larger species were also more active in the drier Open Forest. Foraging activity by these assemblages varies 4-fold, and peaks close to the mean VPD for each habitat. The behavior of these assemblages suggest that 1) small ant species at La Selva potentially compete with the entire range of ant body sizes, whereas large ants forage when and where small ants are inactive; and 2) seeds dispersed to the forest floor at dawn will be consumed or further dispersed by a larger suite of ants species than those falling in the heat of the tropical afternoon.

**Key words:** Ants – Neotropics – Microclimate – Community structure – Body size

---

Microclimate has played an important role in theories of tropical diversity (Pianka 1966; MacArthur 1972; Stevens 1989). Adaptation to local microclimates along an altitudinal gradient may erect barriers to gene flow across mountains (Janzen 1967). Within a tropical forest, different habitats (e.g., forest understory, canopy, and treefall gaps) have different microclimates (Karr and

Freemark 1983; Fetcher et al. 1985). Specialization on microclimates particular to these habitats may enhance regional diversity summed across habitats (e.g., Janzen and Schoener 1968).

This emphasis on climate at larger scales has left microclimate use within tropical habitats little explored. Small organisms are prone to desiccation; and thus a focus on microclimate may be especially useful in understanding their distribution and abundance (Edney 1977). Microclimate differences are commonly shown in temperate zone arthropods (Andrewartha and Birch 1954). For example, desert ants may experience summer surface temperatures ranging from 25 to 50° C. In these deserts, different ant species are active at different temperatures (Schumacher and Whitford 1976; Briese and Macauley 1980; Morton and Davidson 1988). In contrast, it is not clear whether tropical habitats provide a large enough range of microclimates to separate species activity.

Two factors, cuticle permeability and body size, are key to understanding moisture tolerances in small arthropods like ants. Arthropod cuticles are efficient at preventing desiccation and can be supplemented with lipids to enhance this effect (Wigglesworth 1945; Edney 1977; Hood and Tschinkel 1990). Since surface area is proportional to mass<sup>2/3</sup> for organisms of a given shape (Calder 1984), small organisms tend to desiccate faster than their larger counterparts when the air is unsaturated. In lab studies, mass-specific water loss in arthropods is an inverse function of weight (Herreid 1969; Edney 1971; Crawford and Wooten 1973). In ants, desiccation LD50's increase with species body size (Talbot 1934; Hood and Tschinkel 1990) and larger workers may be more active at higher temperatures (Rissing and Pollock 1984).

These traits of individual organisms suggest two predictions about the distribution of species across moisture gradients. First, drier habitats should contain larger arthropod species. Second, within habitats, larger arthropod species should have broader microclimate niches since they can be active in drier microclimates unavailable to smaller species. While the question of microclimate niche breadth and body size is still open, moisture

gradients appear to shape the distribution of arthropods over the landscape (Janzen and Schoener 1968; Schoener and Janzen 1968; Janzen 1973; Levings and Windsor 1984).

In this paper, I explore how microclimate shapes the foraging activity in a diverse guild of granivorous ants. To this end, I 1) describe the microclimate of forest floor in 7 and 17 year old regenerating tropical forests; 2) describe the degree to which the granivorous ant species of the two assemblages are active at differing humidities and, 3) evaluate how body size may act as a mechanism for these differences.

## The study site

This study took place during 1990 at the Estacion Biológica La Selva (10.25' N, 84.01' W) on the Caribbean slope of Costa Rica. Holdridge et al. (1971) classify La Selva as tropical wet forest (see Hartshorn 1983 for further site description). I studied these ants during the wet season of 1990 (mean monthly rainfall, 1988–90: May 422 mm, June 411 mm, July: 391 mm). I chose the wet season, since activity of tropical ground ants is greatly reduced in the dry season (Levings and Windsor 1984).

I studied the ant assemblages in two habitats, both recovering from disturbance and on the same alluvial soil. The two habitats were 0.5 km apart and separated by old primary forest. The first (Closed Forest) was abandoned as cattle pasture 17 years before. This site had a closed canopy and a thick blanket of understory palms. The forest floor was in deep shade save for occasional sunflecks. The second habitat (Open Forest) was abandoned as a cacao grove 7 years before, had a broken canopy, and contained patches of grass and ferns. Sunlight was more variable, running from deep shade to intense sun.

In each habitat, I set up transects of 30 sampling stations, 10 m apart and 2 m off-trail. This distance appears adequate to maintain independent discoveries by different ant colonies since colony densities in the litter typically exceeded 4 nests per m<sup>2</sup>, and ants rarely walked more than 1 m to the nest from a station (Kaspari 1993).

## Methods

I used seed baits to study the granivorous ant assemblage (as per Davidson 1977; Morton and Davidson 1988). I sorted milled pearl barley into 4 size categories using Taylor Sieves (0.25, 0.75, 1.2 and 1.7 mm in diameter). I placed these seeds on a platform consisting of 2 glass microscope slides, taped together below and scored with sandpaper above. I arranged the seeds in piles of equal circumference (ca. 1 cm), 2 mm apart, on the platform. Over each station was a foil and hardware cloth shelter to keep out light rain.

I set seed baits out at dawn (ca. 0600 h), and midday (ca. 1200 h). These are the coolest and warmest times of day at La Selva (Fetcher et al. 1985). Starting times were approximate since dawn was often delayed by heavy cloud cover and rains sometimes postponed or interrupted transect runs for up to 45 minutes. I began a day's observations by dispensing seeds at each station. Each station was then visited in sequence (beginning at either end of the transect

equally) for 2 min. I collected any ants harvesting or mandibulating seeds and placed them in a vial unique for that station visit and particle size.

After 2 minutes, I counted the number of ants of each species on the slide. I noted weather (cloudy, clear, partly cloudy or light rain). I recorded temperature (to 0.1 F) and relative humidity (to 1%) from a Cole Palmer Hygrometer within 10 cm of the station. The hygrometer was mounted under a small roof to keep off water, and stood with its element 5 cm off the forest floor. The hygrometer reached 95% of its final value within 2 min. I transformed relative humidities into vapor pressure deficits using the formulae and tables from Cambell (1977).

I ran each transect 8 times: 4 from 600–1100 h, 4 from 1200–1700 h. The first 4 runs included three station visits per day. The remaining runs visited stations twice. I ran transects from May through July.

Ants were sorted to species or morphospecies. I measured maximum head width to 0.01 mm with an ocular micrometer mounted on a dissecting microscope. Head width is a standard and accurate measure of overall body size (Hölldobler and Wilson 1990; Kaspari 1992). I only included species meeting the minimum requirement of 10 microclimate observations in a habitat. I measured head width on 8 individuals each of these 25 species. Some ant species are unnamed or unidentified. Vouchers are deposited at the Harvard Museum of Comparative Zoology, the Los Angeles County Museum, and the Instituto Nacional de Biodiversidad (INBio) in Costa Rica.

## Results

### *Microclimate structure of the forest floor*

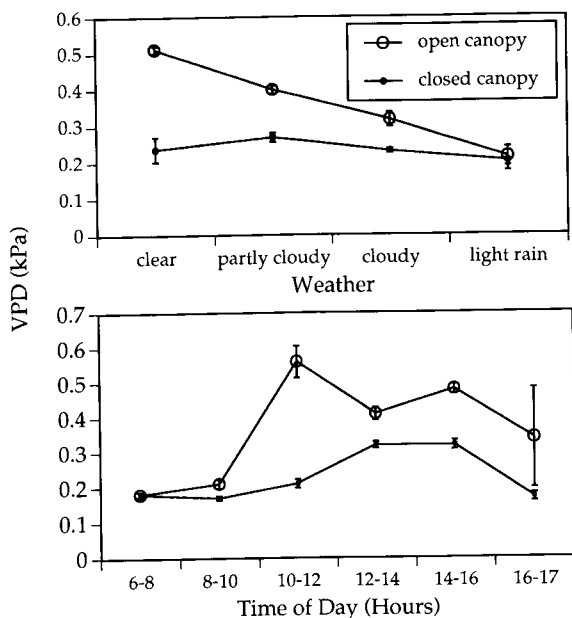
Temperatures 5 cm above the forest floor ranged from 22.1–32.3° C in the Closed Forest and from 22.3–36.9° C in the Open Forest. Vapor pressure deficits (VPD) rarely exceeded 0.5 kiloPascals (kPa) and ranged from 0.032 to 0.681 kPa in the Closed Forest and 0 to 1.12 kPa in the Open Forest. Using a station's mean microclimate as a sample unit, the Closed Forest was both cooler (26.3 versus 27.2 C,  $F_{1,59} = 244.4$ ,  $p < 0.0001$ ) and moister (0.24 vs. 0.34 kPa,  $F_{1,59} = 150.3$ ,  $p < 0.0001$ ) than Open Forest. The Open Forest was more variable in both temperature ( $F_{30,30} = 2.57$ ,  $p < 0.01$ ) and humidity ( $F_{30,30} = 11.26$ ,  $p < 0.01$ ).

Temperature and VPD were strongly positively correlated near the forest floor of La Selva. Principle component analysis using correlation matrices showed that >75% of the variance in the data was explained by this positive relationship in the Closed Forest, 88% in the Open Forest. Here I relate foraging activity to VPD only, acknowledging that any such patterns mirror patterns in temperature, and mechanisms attributed to VPD may be confounded with mechanisms associated with temperature. This will be discussed later.

To better understand why Open Forest VPD's were more variable, I analyzed the contribution of time of day and weather to microclimate variation. I lumped observations into six two-hour time blocks, and four weather categories: "cloudy, clear sky, partly cloudy sky, and light rain". A two-way ANOVA shows that VPD near the ground in the Closed Forest varied significantly with time ( $p < 0.0001$ ) but not weather ( $p < 0.65$ , Table 1). In contrast, both time ( $p < 0.0001$ ) and weather ( $p < 0.0001$ )

**Table 1.** Vapor Pressure Deficits vary with weather and time of day in the Open Forest, and with time of day in Closed Forest (see Fig. 1)

Source	Closed Forest				Open Forest			
	df	SS	F	Pr > F	df	SS	F	Pr > F
Weather	3	0.002	0.55	0.65	3	0.042	8.41	0.0001
Time	5	0.250	40.16	0.0001	5	0.568	67.23	0.0001
Interaction	4	0.008	1.72	0.14	8	0.572	42.31	0.0001
Error	543	0.986			521	0.880		

**Fig. 1.** Vapor pressure deficit, measured at La Selva Costa Rica, varies with weather and the time of day in Closed Forest (dot) and open forest (circle). Error bars are 95% confidence intervals

significantly influenced VPD in the Open Forest (Table 1). Both habitats began with small VPD's at dawn but the Open Forest dried out more quickly toward midday (Fig. 1). Weather seemed to have little effect on VPD in Closed Forest, while VPD decreased steadily with increasing cloud cover in Open Forest (Fig. 1). A significant interaction ( $p < 0.0001$ ) suggests that weather may influence microclimate more at some times of the day, but only in the Open Forest.

I examined VPD patchiness within each of the five most-sampled time blocks with 1-way ANOVA's. The thirty Closed Forest stations were homogenous in VPD ( $F$ 's  $< 0.76$ ,  $p$ 's  $> 0.79$ ) for all time blocks except dawn (0600–0800 h) where there was considerable between station variation ( $F_{30,83} = 2.7$ ,  $p < 0.0002$ ). Likewise, VPD was usually homogenous in the Open Forest ( $F$ 's  $< 0.53$ ,  $p$ 's  $< 0.97$ ) except for midday (1200–1400 h), where stations diverged in VPD ( $F_{30,57} = 2.8$ ,  $p < 0.0005$ ).

In sum, the Open Forest, exposed to greater vagaries of sun and weather, was warmer and more variable than the Closed Forest. Spatial variability within forests was present only at dawn (Closed Forest) and midday (Open Forest).

### Microclimate use by the granivorous ant assemblage at La Selva

Ants were active on the forest floor, occurring at 83% of all bait observations in both habitats during the 2–3 h observation periods. I collected 46 species during this study, 38 in Closed Forest and 35 in Open Forest (Kaspari 1992). The granivorous ants were a subset of the entire litter ant fauna. Many ant genera common on the forest floor (e.g., the tribe Dacetini, and virtually all the Ponerines) were never recorded carrying away seed baits. Moreover, only a few of the species collected at seed baits were likely obligate granivores. This assemblage included the leaf-cutting *Atta* and *Acromyrmex* and many omnivorous species that collect insects and plant exudates (Hölldobler and Wilson 1990; Byrne 1991, Kaspari, unpub. data). I rarely observed aggressive interactions at baits.

Many species in these assemblages were rare (Kaspari 1992). To increase the statistical power of between-species comparisons, I focus on ant species with at least 10 observations in a habitat (Table 2). This results in 19 species in the Closed Forest and 16 in the Open Forest for a total of 25 species. Three tribes, the Attini, Pheidolini and the Solenopsidini, dominated this group (Table 2).

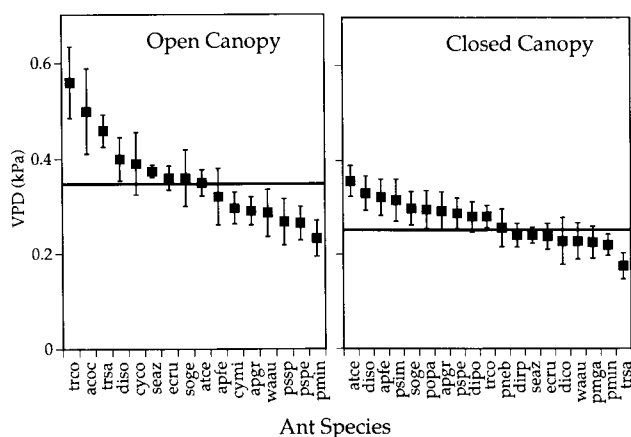
Given the small size and high density of neotropical ant colonies, it is unlikely that workers from a colony forage at more than one station (Kaspari 1993). To calculate species means for VPD, I thus used station means as sample units. This resulted in 4–21 (averaging 11) samples for the 19 species in the Closed Forest, and 3–22 (averaging 13) samples for the 16 species in the Open Forest. There are significant between-species differences (Fig. 2) in VPD use in the Closed Forest ( $F_{18,192} = 1.92$ ,  $p = 0.0163$ ). In the Open Forest, the species were more spread out along the VPD axis (Fig. 2), with corresponding increase in statistical significance ( $F_{15,185} = 3.15$ ,  $p < 0.0001$ ).

### Causes of microclimate use among species

A species' body size may influence its risk of desiccation and hence its activity at different VPD's. I tested the hypothesis that the maximum VPD exploited by an ant species should increase with its body size. I pooled the assemblage data across both habitats, yielding 25 species, and used linear regression to see how a species' maximum, mean, and minimum VPD varied with its head width. Both the maximum and mean VPD for a species

**Table 2.** Granivorous ant species at La Selva, Costa Rica represented by >10 observations and used in this study. "Name" is an abbreviation used in Fig. 2. Number of observations in Closed and Open canopy second growth forest are given

Tribe	Species	Name	Closed	Open
Ectatommini	<i>Ectatomma ruidum</i>	ecru	22	64
Attini	<i>Trachymyrmex saussurei</i>	trsa	27	57
	<i>T. cornetzi</i>	trco	56	12
	<i>Sericomyrmex aztecus</i>	seaz	176	175
	<i>Apterostigma GR</i>	apgr	19	35
	<i>Cyphomyrmex cornutus</i>	cyco		17
	<i>C. minutus</i>	cymi		39
	<i>Acromyrmex octospinosa</i>	acoc		19
	<i>Atta cephalotes</i>	atce	17	42
Pheidolini	<i>Aphaenogaster araneoides</i>	apfe	15	20
	<i>Pheidole mga</i>	pmga	13	
	<i>P. min</i>	pmin	83	10
	<i>P. neb</i>	pneb	26	
	<i>P. sim</i>	psim	16	
	<i>P. spe</i>	pspe	23	34
	<i>P. SS</i>	pspp		15
	<i>P. opa</i>	popa	20	
Ochetomyrmecini	<i>Wasmannia auropunctata</i>	waau	28	32
Solenopsidini	<i>Solenopsis geminata</i>	soge	22	31
	<i>Solenopsis (Diplorhoptum) RP</i>	dirp	28	
	<i>S. PO</i>	dipo	13	
	<i>S. CO</i>	dico	19	
	<i>S. SO</i>	diso	10	14



**Fig. 2.** Mean vapor pressure deficits used by ant species ( $\pm 1$  standard error) vary among common ants in both closed and Open Forests of La Selva, Costa Rica. Species codes are defined in Table 2. The dark horizontal line is the mean VPD for the habitat

increased with head width ( $p$ 's < 0.01, Table 3, Fig. 3). Over 40% of variation in VPD could be attributed to body size. In contrast, the minimum VPD used did not vary with body size ( $p = 0.24$ ,  $r^2 = 0.06$ , Table 3). I used an Analysis of Covariance to tease apart the effects of phylogeny (membership in one of the three dominant tribes) from body size for maximum and mean VPD use (Table 4). Mean VPD use is unconfounded by tribe membership—once body size is removed, the class variable "tribe" does not explain a significant amount of variation in either the intercepts or slopes of the body size/VPD curve. This is not true for maximum VPD (Table 4). There are significant differences in the intercept (tribe effect,  $p < 0.004$ ) and marginal differences in the slope (interaction,  $p < 0.09$ ) of the maximum VPD/body

size relationships. Separate linear regressions for each tribe (Table 4) suggest that the intercepts increase from the small tribe Solenopsidini, through the mid-size Pheidolini through the large Attini (Fig. 3). Concurrently, slopes appear to decrease from tribes with small body size to large, causing the curve for the assemblage to plateau (Fig. 3). In sum, the breadth of microclimates used by ants tends to increase with body size, as larger ants—primarily attines—use drier microclimates without decreasing their use of moist microclimates. The correlation between body size and mean VPD is uncomplicated by phylogeny, while the correlation with maximum VPD varies among tribes.

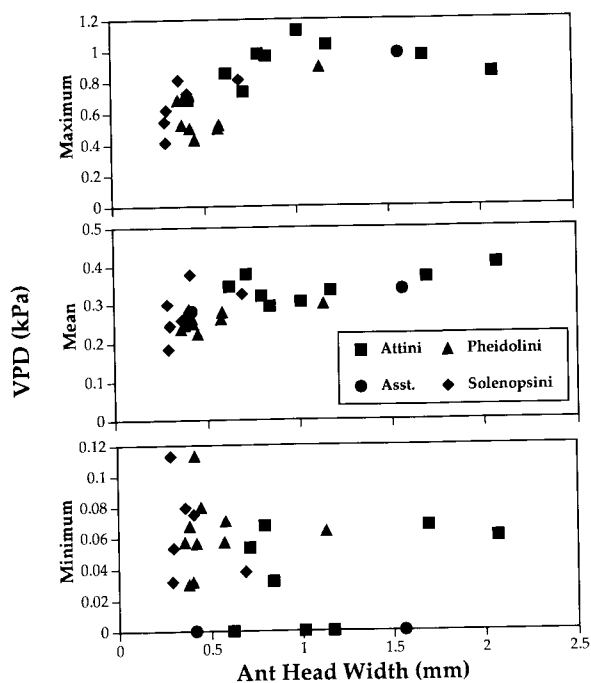
Species may be active at different times of the day for reasons unrelated to VPD, yet resulting in spurious species differences in VPD. To evaluate this, I calculated the time spent foraging at midday versus dawn for each species (i.e., # observations the species was present at baits from 1200–1400 h / bait observations at 600–800 h + 1200–1400 h). I correlated this value with the species' mean VPD. A positive correlation suggests time and microclimate use are confounded in the two assemblages. This was not the case (Closed Forest  $r_{19} = 0.17$ , Open Forest  $r_{16} = 0.6$ ,  $p$ 's > 0.10). Diel preferences do not appear to drive VPD use in these assemblages.

Finally, VPD preferences of ant species may shift between habitats. This could cause the rank order of species means, arrayed on VPD axis, to vary between habitats. VPD use is inconsistent among the 12 species common to Open and Closed Forest (Fig. 2). Some species use the same microclimate in both habitats (e.g., "pmin" and "diso" are confined to moister and drier microclimates, respectively). Other species show dramatic shifts in microclimate use (e.g., "trsa" uses the moistest

**Table 3.** Maximum and mean VPD (vapor pressure deficits), but not minimum VPD, increases with ant head width

Source	df	Maximum VPD			Mean VPD			Minimum VPD		
		SS	F	Pr > F	SS	F	PR > F	SS	F	Pr > F
Head width	1	0.487	17.6	0.0003	0.03279	20.6	0.0001	0.00149	1.45	0.2405
Error	24	0.662			0.03085			0.02462		
Total	25	1.149			0.07085			0.02610		

Max VPD = 0.481 + 0.296 (head width).  $r^2 = 0.42$   
 Mean VPD = 0.241 + 0.077 (head width).  $r^2 = 0.46$   
 Minimum VPD = 0.061 - 0.016 (head width).  $r^2 = 0.06$

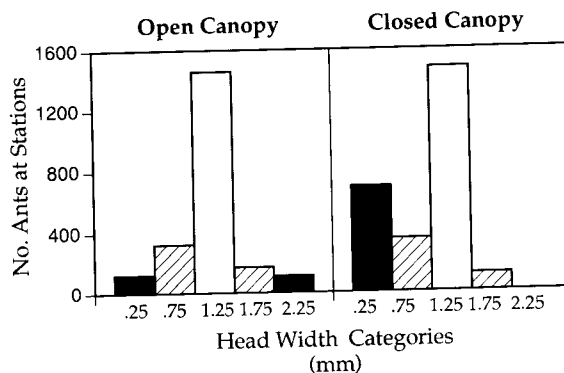


**Fig. 3.** The maximum and mean vapor pressure deficit increases with body size in granivorous ants of La Selva, Costa Rica. Minimum VPD does not vary with ant size. Symbols represent different tribes; "Asst." are Ectatommini (the right-most dot) and Ochetomyrmecini (the left-most dot)

microclimate in the Closed Forest and among the driest in the Open Forest). Species' VPD use is not correlated between habitats (Spearman  $r_{12} = 0.04$ ,  $p = 0.91$ ). So VPD use for an ant species at La Selva is not fixed, but is to some extent habitat dependent.

**Table 4.** Regression intercepts decrease from the Attini to the Solenopsidini for Maximum VPD. Membership in the three dominant tribes does not affect body size regression for Mean VPD. Attini: Max VPD = 0.92 - 0.012 (head width)  $r^2 = 0.00$   
 Pheidolini: Max VPD = 0.38 + 0.324 (head width)  $r^2 = 0.29$   
 Solenopsidini: Max VPD = 0.28 + 0.340 (head width)  $r^2 = 0.56$

Source	DF	Maximum VPD			Mean VPD		
		SS	F	PR > F	SS	F	PR > F
Head width	1	0.1074	6.18	0.0229	0.0316	6.84	0.0176
Tribe	2	0.2605	7.50	0.0043	0.0072	1.74	0.2043
Interaction	2	0.1012	2.91	0.0802	0.0037	1.25	0.3093
Error	23	13.32			0.0689		

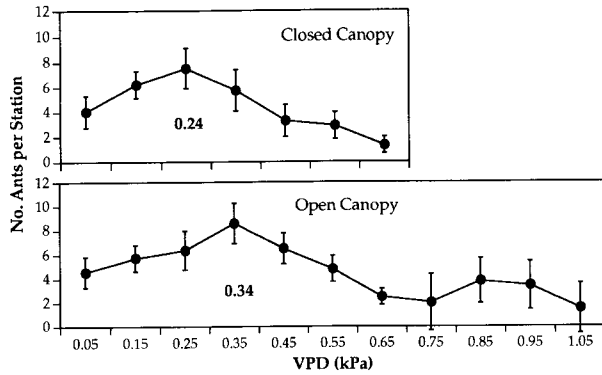


**Fig. 4.** Smaller ants are more active in Closed Forest in La Selva, Costa Rica. Frequency distribution of species, lumped into size classes and weighted by the number of individuals that show up at baits

*Microclimate and rates of granivory*

One consequence of body size constraints on VPD is that larger granivorous ants may be more active in drier, Open Forest. I lumped species into size classes of 0.5 mm increments and plotted foraging activity—the total number of ants recorded at the end of a station's 2 minute observation—for each size class (Fig. 4). In both habitats, intermediate sized ants were the most active. However, smaller ants were more active in the Closed Forest ( $X^2_{2,5} = 488$ ,  $p < 0.001$ ). This is likely a liberal test, since one of ten cells (2.0–2.5 mm ants in Closed Forest) lacked the largest species entirely. Granivore activity appears skewed toward smaller ants in the cooler, moister habitat.

Total granivore activity varied four-fold across the range of possible microclimates. I broke VPD into



**Fig. 5.** Ant activity, measured as the mean number of ants per bait station ( $\pm 95\%$  confidence intervals), peaks at intermediate vapor pressure deficits in open and Closed Forests of La Selva, Costa Rica. Numbers in **bold** are mean VPD's available in each habitat

0.10 kPa blocks, comparing the total number of ants as before. Ant activity varied strikingly with VPD in the Closed Forest (Kruskal Wallis  $X^2_{7,580} = 32.2$   $p = 0.0001$ ) and less so in the Open Forest (KW  $X^2_{11,580} = 19.5$ ,  $p = 0.0338$ ). In both cases, activity started at about 4 ants/station near vapor saturation (VPD=0, Fig 5). Activity then doubled to 8 ants/station and gradually declined to about 2 ants/station. Peak activity in both forests occurred near the mean VPD for that habitat (Closed Forest: 0.20–0.30, habitat mean = 0.24, Open Forest: 0.30–0.40, habitat mean = 0.34).

## Discussion

Between-habitat microclimate specialization is key to some models of tropical diversity (Janzen 1967; Stevens 1989). This paper takes the next step and asks if tropical species use different microclimates *within* a tropical habitat. Two Costa Rican lowland forests, in different stages of regeneration, had different microclimates 5 cm above the litter. Temperature and vapor pressure deficit (VPD), a measure of the drying potential of the air, were highly correlated. An Open-canopy Forest abandoned as a cacao plantation 7 years before had a warmer, drier and more variable microclimate than a Closed-canopy forest abandoned as cattle pasture 17 years before. Microclimate was similar at dawn (and presumably overnight) but diverged three-fold by midday (Fig. 1, see also Geiger 1965). This divergence seems linked to the buffering effect of the Closed Forest's canopy: increasing cloud cover dramatically lowered VPD in the Open Forest but had no detectable effect in the older, Closed Forest (Fig. 1). In contrast, sample stations within habitats were relatively homogenous.

Microclimate patterns 5 cm off the ground are similar to those measured 70 cm off the ground at La Selva, Costa Rica (Fetcher et al. 1985). At that height, VPD and temperature were more variable in open second growth forest compared to primary forest understory. One key difference was the magnitude of the rise of VPD toward mid-day. At 70 cm the mean peak in VPD was about twice that found at 5 cm (ca. 1.2 kPa, interpolated from

Fig. 2 in Fletcher et al. 1985, versus 0.55, this study). This highlights a measurement bias of this study since ants experience the microclimate at the forest floor, while I measured microclimate 5 cm higher (since the element of the hygromicrograph couldn't get wet!). Vapor diffuses from the ground in daylight hours, creating a gradient of decreasing vapor pressure with increasing height (Geiger 1965; Rosenberg 1974). Differences in VPD use reported here likely reflect even smaller differences in VPD used at the litter layer.

Species in both habitats differed in the VPD they exploited for foraging (Fig 2). About half the variance in mean VPD could be attributed to body size. As predicted by the surface area/volume hypothesis, larger ant species exploited drier microclimates than smaller ants (Fig. 3). In lab studies, larger ant species withstand desiccation better than small species (Talbot 1934; Hood and Tschinkel 1990). This is the first study to my knowledge that links body size to microclimate niche breadth in the field.

Body size does not perfectly predict VPD use in ants (e.g., see *diso*, *trsa* in Fig 2). The tribe Solenopsidini possess many small species that use a variety of microclimates (Fig. 3, Adams and Traniello 1981; Morton and Davidson 1988; Cotter, pers. comm.) and are abundant from the moist rain forest understory soil to the drier canopy (Longino and Nadkarni 1990, Kaspari unpub. data). Other traits, like lighter integument color (Morton and Davidson 1988) thicker epicuticular waxes (Hood and Tschinkel 1990) or underground foraging tunnels (Tennant and Porter 1991) may allow small ants to forage in drier microclimates. The factors determining microclimate use in arthropods are complex, but body size appears to play a major role.

One intriguing result from this study was the shifting of mean VPD's among species shared between the Closed and Open Forest. VPD use is not fixed, but fairly malleable at least for some species. The causes of these niche shifts, be they random or due to population interactions, lies in further study of these hyper-diverse assemblages.

What factors might confound this study's correlation between body size and VPD use? Recorded responses to VPD may be responses to temperature. However, temperature and VPD should have complementary effects since cuticle permeability in arthropods increases with cuticle temperature (Edney 1977). A second possibility is that larger species may have colonies with larger energy budgets, forcing them to forage a larger percentage of the day to meet daily requirements. At the present, I have no data to evaluate this hypothesis. Finally, apparent microclimate differences may simply reflect differences in the time of day that species prefer to forage. However, there is little relationship between a species' diel activity and its mean VPD. This is consistent with other studies, where microclimate preferences in a changing environment generate shifting daily activity schedules (Whitford and Ettershank 1976; Briese and Macauley 1980; Porter and Tschinkel 1987; Andersen 1992).

One characteristic of any assemblage of species is the distribution of species body sizes (Hutchinson and MacArthur 1959; Schoener and Janzen 1968; Brown and

Maurer 1986). Small species of arthropods were most abundant and diverse at the wet end of a moisture gradient in a Costa Rican dry forest (Janzen and Schoener 1968). Small ant species were more active in the moister Closed Forest at La Selva (Fig. 4) compared to a nearby Open Forest. If desiccation is a major risk to small invertebrates (Edney 1977), and if smaller species can maintain larger populations and subdivide the environment better than larger species (Hutchinson and MacArthur 1959; May 1978; Kaspari 1992), then wet sites—even in the wet tropics—may be local centers of arthropod species diversity and critical refugia during dry episodes. However, other factors associated with moisture gradients, notably productivity (Whittaker 1970) and plant species diversity (Gentry 1988), may confound this interpretation. More quantification of moisture–diversity trends and their mechanisms is needed.

In conclusion, microclimate can be an important determinant of ant activity even in the “stable tropics” where temperature and humidity vary little compared to temperate zone habitats. Ant activity is highest at the most common microclimate in both habitats. Smaller ants tend to be more active in cooler, moister microclimates; larger ants tend to be microclimate generalists. Tropical ants are speciose (>150 species in <1 ha, Hölldobler and Wilson 1990), destroy 12–17% of the annual leaf production (Cherret 1986), rearrange seed shadows (Beattie 1985; Levey and Byrne 1993; Kaspari 1993) and shape arthropod populations (Franks and Bossert 1983). The rules determining the distribution, and activity patterns of ants should help us understand population interactions. For example, if seeds are limiting, small ants may compete with the entire ant assemblage, while large ants spend some of their time foraging only amongst themselves. Second, as ants are the rapid and primary removers of small seeds in this forest (Levey and Byrne 1993; Kaspari 1993), seeds deposited at dawn will be dispersed and depredated by a larger suite of ants than those seeds falling in the heat of a tropical afternoon.

**Acknowledgements.** This project could begin due to the fine efforts of Dr. Thomas Miller and the staff of the Arizona Cancer center. M. Byrne, D. & D. Clark, D. Levey, B. Loiselle, and J. Longino provided help and logistical support in the field. J. Bronstein, D. Davidson, M. Donoghue, B. Loiselle, M. Rosenzweig, S. Russel, P. Smallwood and C. Vleck read various versions of the manuscript. David Vleck and Judy Brostein were particularly generous with their time and greatly improved the manuscript. Funding was graciously supplied by the Organization for Tropical Studies, the Pew Charitable Trust, Sigma Xi, and the Roosevelt Fund. And thanks to the ants.

## References

- Andersen AN (1992) Regulation of “momentary” diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. *Am Nat* 140:401–420
- Andrewartha HG, Birch LC (1954) *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago
- Beattie AJ (1985) *The evolutionary ecology of ant-plant mutualisms*. Cambridge University Press, Cambridge
- Briese DT, Macauley BJ (1980) Temporal structure of an ant community in semi arid Australia. *Austral J Ecol* 5:121–134
- Brown JH, Maurer BA (1986) Body size, ecological dominance and Cope’s rule. *Nature* 324:699–700
- Byrne MM (1991) *Ecology and coexistence mechanisms of tropical twig-dwelling ants*. M.S. University of Florida, Gainesville, USA
- Calder WA III (1984) *Size, function, and life history*. Harvard University Press, Cambridge, USA
- Cambell GS (1977) *An introduction to environmental biophysics*. Springer, Berlin Heidelberg New York
- Cherrett JM (1986) History of the leaf cutting ant problem. In: C.S. Lofgren and R.K. Vander Meer (ed) *Fire ants and leaf cutting ants: biology and management*. Westview Press, Boulder
- Crawford CS, Wooten RC (1973) Water relations in *Diplocentrus spitzeri*, a semimontane scorpion from the Southwestern United States. *Phys Zool* 6:218–229
- Davidson DW (1977) Species diversity and community organization in desert seed-eating ants. *Ecology* 58:711–724
- Edney EB (1971) Some aspects of water balance in tenebrionid beetles and a thysanuran from the Namib Desert of South Africa. *Phys Zool* 44:61–76
- Edney EB (1977) *Water balance in land arthropods*. Springer, Berlin Heidelberg New York
- Fetcher N, Oberbauer SF, Strain BR (1985) Vegetation effects on microclimate in lowland tropical forest in Costa Rica. *Int J Biometeorol* 29:145–155
- Franks NR, Bossert WH (1983) The influence of swarm raiding army ants on the patchiness and diversity of a tropical leaf litter ant community Sutton EL, Whitmore TC, Chadwick AC (eds) pp 151–163
- Geiger R (1965) *The climate near the ground*. Harvard University Press, Cambridge
- Gentry AH (1988) Changes in plant community diversity and floristic composition on environmental and geographic gradients. *Ann Mo Bot Gard* 75:1–34
- Hartshorn GS (1983) Introduction to Plants. In: Janzen DH (ed) *Costa Rican Natural History*. University of Chicago Press, Chicago, USA
- Herreid CF (1969) Integumental permeability of crabs and adaptation to land. *Comp Biochem Physiol* 29:423–429
- Holdridge LR, Grenke WC, Hatheway WH, Liang T, Tosi JAJ (1971) *Forest environments in tropical life zones: a pilot study*. Pergamon Press, New York, USA
- Hölldobler B, Wilson EO (1990) *The Ants*. Belknap Press, Cambridge
- Hood WG, Tschinkel WR (1990) Desiccation resistance in arboreal and terrestrial ants. *Physiological Entomology* 15:23–35
- Hutchinson GE, MacArthur RH (1959) A theoretical ecological model of size distributions among species of animals. *Am Nat* 93:117–125
- Janzen DH, (1967) Why mountain passes are so high in the tropics. *Am Nat* 101:233–249
- Janzen DH (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54:687–708
- Janzen DH, Schoener TW (1968) Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49:96–110
- Jeanne RL (1979) A latitudinal gradient in rates of ant predation. *Ecology* 60:1211–1224
- Karr JR, Freemark KE (1983) Habitat selection and environmental gradients. *Ecology* 64:1481–1494
- Kaspari M (1992) *Niche relationships in an assemblage of neotropical granivorous ants*. Ph. D. Dissertation, University of Arizona, Tucson, USA
- Kaspari M (1993) Removal of seeds from Neotropical frugivore droppings: ant responses to seed number. *Oecologia* 95:81–88
- Levey DJ, Byrne MM (1993) Complex ant-plant interactions: *Pheidole* as secondary dispersers and postdispersal seed predators of rain forest plants. *Ecology* 74:1802–1812



- Levings SC, Windsor DM (1984) Litter moisture content as a determinant of litter arthropod distribution and abundance during the dry season on Barro Colorado Island, Panama. *Biotropica* 16:125–131
- Longino JT, Nadkarni NM (1990) A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a neotropical montane forest. *Psyche* 97:81–92
- MacArthur RH (1972) *Geographical Ecology*. Princeton University Press, Princeton
- May RM (1978) The dynamics and diversity of insect faunas. Pages 188–204. in L.A. Mound, N. Waloff. *Diversity of Insect Faunas*. Blackwell Scientific, New York
- Morton SR, Davidson DW (1988) Comparative structure of harvester ant communities in arid Australia and North America. *Ecol Mono* 58:19–38
- Pianka ER (1966) Latitude gradients in tropical diversity: a review of concepts. *Am Nat* 100:33–46
- Porter SD, Tschinkel WR (1987) Foraging in *Solenopsis invicta* (Hymenoptera: Formicidae): effects of weather and season. *Environmental Entomology* 16:802–808
- Rissing SW, Pollock GB (1984) Worker size variability and foraging efficiency in *Veromessor pergandei* (Hymenoptera: Formicidae). *Behav Ecol Sociobiol* 15:121–126
- Rosenberg NJ (1974) *Microclimate: the biological environment*. Wiley Interscience, New York
- Schoener TW, Janzen DH (1968) Notes on environmental determinants of tropical versus temperate insect size patterns. *Am Nat* 102:206–224
- Schumacher A, Whitford WG (1976) Spatial and temporal variation in Chihuahuan ant faunas. *Southw Nat* 21:1–8
- Stevens GC (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am Nat* 133:246–256
- Talbot M (1934) Distribution of ant species in the Chicago region with reference to ecological factors and physiological toleration. *Ecology* 15:416–439
- Tennant LE, Porter SD (1991) Comparison of diets of two fire ant species (Hymenoptera:Formicidae): solid and liquid components. *J Entomol Sci* 26:450–465
- Whitford WG, Ettershank G (1975) Factors affecting foraging activity in Chihuahuan desert harvester ants. *Env Entomol* 4:689–696
- Whittaker RH (1970) *Communities and Ecosystems*. Macmillan, New York
- Wigglesworth VB (1945) Transpiration through the cuticle of insects. *J Exp Biol* 21:97–114
- Wilson DS (1975) The adequacy of body size as a niche difference. *Am Nat* 109:769–784