

Niches and Coexistence of Ant Communities in Puerto Rico: Repeated Patterns¹

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ABSTRACT

I studied ant coexistence in adjacent areas of upland tropical forest, grassland, and agricultural land in San Lorenzo, Puerto Rico. Data on food utilization, daily activity, nesting sites, microhabitat utilization and interspecific aggression were collected. Ants' tolerance to 45°C was determined in the laboratory.

Agricultural and grassland ants eat grain, liquid food or insects, or grow fungus; only liquid drinking and insectivorous ants occurred in the forest. Some species within food groups in the agricultural and grassland ants differed in size of food consumed or daily activity. Some species from agricultural land were restricted to different crops, but spatial microhabitat utilization contributed little to species separation. Forest species differed in their use of litter depths, daily activity and microhabitat. Results of interspecific aggression were influenced by priority effects and microclimate. I suggest that some species coexist by non-equilibrium processes or by stochastic events.

RESUMEN

Se estudió la coexistencia de hormigas en áreas contiguas de bosque tropical, pradera y zonas agrícolas en San Lorenzo, Puerto Rico. Se coleccionó información sobre hábitos alimenticios, patrones de actividad diaria, lugares de anidación y utilización de microhabitats. Se estudió en el laboratorio la tolerancia de las hormigas a la temperatura de 45°C.

Se encontró que las hormigas de la zona agrícola y de pradera crecen hongos, consumen semillas, toman alimento líquido o consumen insectos. En el bosque se encontraron solamente las hormigas insectívoras y las que consumen alimento líquido. Dentro de estos grupos alimenticios algunas especies diferían en el tamaño de alimento consumido o patrón de actividad diaria. Varias especies de la zona agrícola estaban restringidas a diferentes cosechas, pero la utilización espacial del microhabitat no contribuyó a la separación de especies. Las hormigas del bosque diferían en la utilización de la hojarasca, actividad diaria y microhabitat. Los resultados de la agresión interespecífica estuvieron influenciados por efectos prioritarios y microclima. Sugiero que algunas especies coexisten debido a procesos de desequilibrio y eventos probabilísticos.

ANTS ARE UNIQUE among insects in their dominance as a group (Wheeler 1910). They have very few natural enemies (Wheeler 1910, Skaife 1964, Wilson 1971), and the effect of predators on non-reproductive workers is better described as a parasitic relationship (at the colony level). Losses through foraging mortality are usually compensated by the amount of food taken in exchange (Carroll and Janzen 1973). Ant colonies are remarkably stable due to the longevity of their members, especially the queen (Wheeler 1910, Wilson 1971). Population stability is enhanced by the accessibility of the brood as food when starvation threatens; and larvae, workers and queens can often endure long periods of time without food or water (Brown 1973, Carroll and Janzen 1973). Ants that have storage areas (granivorous ants) or honey pot repletes are furnished with another safety valve against food shortages.

Due to the low predation suffered by ants and their

stability on the temperate zone and some oceanic islands, ants have served as models for the documentation of competition theory in ecology (Brian 1956; Brian *et al.* 1966; Wilson 1971; Levins *et al.* 1973; Culver 1974; Lieberburg *et al.* 1975; Davidson 1977a, b; Taylor and Adedoyin 1978; Whitford *et al.* 1981). Nonetheless, few studies dealing with the factors that structure communities in the complex tropical ant faunas have been conducted (Carroll and Janzen 1973).

In Puerto Rico, ants are the most abundant invertebrates (Levins *et al.* 1973). I attempt to explain how resources are partitioned among the species for three adjacent ant assemblages on the island. Also, I attempt to answer the following questions: does niche dimension compensation (Schoener 1974, Fuentes 1976) exist on these assemblages; does microhabitat affect the outcome of interspecific combats among ants; do species whose niches are included in those of other species tend to be more aggressive; and do priority effects exist in these assemblages that affect the outcome of interspecific ant combats? Torres (1984) explains the factors that determine the number of ant species in these communities.

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MATERIALS AND METHODS

My study site was in San Lorenzo, Puerto Rico, where a dry season (December to April) with an average precipitation of 11.30 cm per month ($SD = 3.35$) alternates with a wet season (May to November) with average precipitation of 21.74 cm per month ($SD = 2.39$). Average monthly temperature was 22.2°C ($SD = 0.65$) in the dry season and 24.5°C ($SD = 0.54$) in the wet season (NOAA 1979).

From July 1978 to September 1980, I studied the ants in three nearby areas: upland tropical forest, grassland, and agricultural land. Two sites were studied in the upland tropical Carite forest: one near route 7740, Km 4.4; the other near Route 184, Km 18.1. Ewel and Whitmore (1973) classified this area as a subtropical wet forest. The tight canopy produced a cooler and wetter microclimate than in grassland and most agricultural land. The ant species were identical in the forested sites.

The grassland and agricultural areas were located near Route 7740 (Km 1.1–2.5). The grassland was dominated by the grass *Chloris radiata*, which was used for cattle grazing. The agricultural areas studied consisted of plantain (*Musa paradisiaca*), coffee (*Coffea arabica*), and yam (*Dioscorea alata*) crops. The coffee groves resembled an early-successional-stage forest with a microclimate similar to that of the forest.

I collected data on feeding by observing four or more ant nests of each species for five minutes per hour. Food that ants were carrying was removed with forceps or a piece of adhesive tape, put on a microscope slide and examined under a dissecting microscope. The size of food taken was measured with calipers. Ants returning to the nest were checked for gastric distention which occurs when they bring liquid food. I classified food in broad categories that I believe are important to the ants. Poor visibility in the forest thwarted most food data collection.

To study spatial utilization in forest litter I took 100 samples, each 25 cm², of each first, second, and third 2.5 cm layers of litter. The litter was sifted and the ants of each species counted. At each study site I investigated several apparently appropriate nesting places and counted the nests of each species. Possible nesting places included dead twigs, grounded logs, beneath rocks, 25 cm² ground quadrats, trees, and stumps.

To study microhabitat preferences I placed tuna fish baits on the ground, rocks, litter and vegetation. I put the baits at a randomly chosen time at a distance of 5–15 m from each other. This was done in sunny, shady, wet, and dry areas, during night and day. Species found in the bait and inside a 25 cm² quadrat around the bait were recorded. I sampled four replicates in each microhabitat every month for a year. This design provided data on daily and seasonal patterns and was used to study aggression among ants (except in the forest where a total

of 20 baits were placed in sunny microhabitats). Microhabitat utilization was calculated by counting the number of times that a given species was found in the baited microhabitats.

An environmental chamber (Enviro-nator Model WL221) with a glass cover was used to determine ants' tolerance to 45°C. Ants were placed in the chamber at 45°C in vials with perforated caps. The time required for 50 percent of the ants to assume a crouched position was used as a measure of tolerance to 45°C. Control ants were kept in vials outside the chamber. I used a minimum of ten ants per vial, and repeated the experiment with individuals from ten colonies for most species.

A species list for these communities was compiled using baits, berlese funnels, pitfall traps, sifting the litter, and searching for nests. The taxonomy of the various monomorphic *Solenopsis* has not been accurately determined (Roy Snelling, pers. comm.) and for this reason I will use letters to differentiate them.

RESULTS

SPECIES AND NESTING SITES.—Table 1 presents the list of ant species found in these communities. In the apparently appropriate nesting places, I found that 64 percent ($N = 621$) were empty in the agricultural land, 43 percent ($N = 400$) in the grassland and 82 percent ($N = 500$) in the forest. This suggests that ants were not limited by lack of nesting places. Competition for food is difficult to separate from competition for nesting sites. The suitability of a nesting site in the face of competition varies with the amount of food the colony can harvest from that particular point (see Carroll and Janzen 1973).

FOOD TYPES.—Tables 2, 3, and 4 summarize the food data which were used in calculating food niche overlaps for 21 species in agricultural land, 17 in grassland and 5 in the forest (Torres 1981). The overlap matrices for each community were treated as matrix of correlation coefficients to perform a principal component analysis (PCA). Results of the PCA were used to classify the ants into functional groups.

The agricultural land ants are divided into four functional groups (Table 1): those that either eat insects and insect parts, bring mostly liquid food in the crop (nectar, honeydew, animal and fruit juices, etc.), eat grain, or grow fungus. The fungus-growing ants use similar vegetable matter and feces to grow their gardens. Although I placed *Solenopsis geminata* in the granivorous group, it also tends insects on the roots of many grasses. Underground feeding was not quantified and for this reason *S. geminata* is excluded from some analyses. *Platythyrea punctata*'s extensive consumption of lepidopteran and coleopterian larvae separates it from the other insectivorous ants. Ants that bring liquid food consume insects and

TABLE 1. *Ants present (X) in the habitats. Diet type: 1 = insectivorous; 2 = liquid food; 3 = granivorous; 4 = fungus growing.*

Species (code)	Grass-land	Agricul-tural land	For-est
PONERINAE			
<i>Amblyopone</i> sp. (Am.s)			X
<i>Anochetus kempfi</i> (An.k)	X	X	
<i>Anochetus mayri</i> (An.m)	X	X	X
<i>Hypoponera opacior</i> (Hy.o)	X	X	X
<i>Hypoponera ergatandria</i> (Hy.e)	X	X	
<i>Odontomachus brunneus</i> (Od.b)	X 1	X 1	
<i>Pachycondyla stigma</i> (Pacs)	X	X	X
<i>Platythyrea punctata</i> (Pl.p)		X 1	
FORMICINAE			
<i>Brachymyrmex beeri</i> (Br.h)	X 2	X	
<i>Brachymyrmex minutus</i> (Br.m)	X	X 2	X
<i>Camponotus ustus</i> (Camu)		X 1	X
<i>Camponotus sexguttatus</i> (Cams)	X		
<i>Myrmelachista ramulorum</i> (Myrr)	X	X	X 2
<i>Myrmelachista</i> sp. (Myrs)			X
<i>Paratrechina microps</i> (Pa.m)	X		X
<i>Paratrechina longicornis</i> (Pa.l)	X 2	X 2	
<i>Paratrechina steinheili</i> (Pa.s)	X 2	X 2	X 1
DOLICHODERINAE			
<i>Iridomyrmex melleus</i> (Ir.m)	X	X 2	X 2
<i>Tapinoma littorale</i> (Ta.l)		X	X
<i>Tapinoma melanocephalum</i> (Ta.m)	X	X	
MYRMICINAE			
<i>Cardiocondyla emeryi</i> (Ca.e)	X 1	X 1	
<i>Cardiocondyla nuda</i> (Ca.n)	X 1	X 1	
<i>Cardiocondyla venustula</i> (Ca.v)	X	X	
<i>Cyphomyrmex rimosus</i> (Cy.r)	X 4	X 4	
<i>Eurhopalothrix</i> sp. (Eu.s)			X
<i>Monomorium ebeninum</i> (Mo.e)	X 2	X 2	
<i>Monomorium floricola</i> (Mo.f)	X 2	X 2	
<i>Mycocarpus smithi</i> (My.s)	X 4	X 4	
<i>Oxyepocus</i> sp. ? (Ox.s)	X	X	
<i>Pheidole exigua</i> (Ph.e)	X 1	X 2	
<i>Pheidole fallax</i> (Ph.f)	X 1	X 1	
<i>Pheidole moerens</i> (Ph.m)		X	X 1
<i>Pheidole sculptior</i> (Ph.s)	X	X	
<i>Pheidole subarmata</i> (Phsu)	X 1	X 1	
<i>Rogeria</i> sp. (Ro.s)	X	X	
<i>Solenopsis</i> A (So.A)	X	X 2	X
<i>Solenopsis</i> B (So.B)	X	X	X 2
<i>Solenopsis</i> C (So.C)	X	X	X
<i>Solenopsis geminata</i> (So.g)	X 3	X 3	
<i>Strumigenys gundlachi</i> (St.g)			X
<i>Strumigenys louisianae</i> (St.l)	X 1	X 1	X
<i>Strumigenys rogeri</i> (St.r)	X	X	X
<i>Tetramorium bicarinatum</i> (Te.b)	X 1	X 2	
<i>Tetramorium caldarium</i> (Te.c)	X	X	
<i>Wasmannia auropunctata</i> (Wa.a)	X 1	X 2	
<i>Wasmannia</i> sp. (Wa.s)	X		

insect parts secondarily, except for *Tetramorium bicarinatum*. *Monomorium ebeninum* and *M. floricola* have very similar diets and are more diversified than those of the other species in the liquid food group.

Grassland ants are grouped in the same manner as in agricultural land (Table 1). The fungus-growing ants use similar substrates for their gardens. *Tetramorium bicarinatum* and *Pheidole exigua* switch to the insectivorous group, but continue to bring great amounts of liquid food in their crops. *Wasmannia auropunctata* appears in the insectivorous group, but I believe belongs to the liquid food group (observation of gastric distention is difficult in this species). Comments on *Monomorium floricola* and *M. ebeninum* in agricultural land observations apply here.

For the few forest species studied only two groups can be defined: the liquid food and insectivorous groups (Table 1). The fungus-growing ants were absent in the forest.

FOOD SIZE AND MICROHABITAT.—Tables 5, 6 and 7 present the microhabitat utilization data, and Figure 1 the food-size distributions which were used in calculating overlap estimates (reported in Torres 1981). Data on microhabitat have spatial and temporal components. Emphasis is given to the microspatial components; the temporal component is discussed later.

NICHE DIMENSION COMPENSATION.—I tested the hypothesis of niche dimension compensation (Schoener 1974, Fuentes 1976) using food-type, food-size and microhabitat overlaps. The median overlap was found on each niche dimension. I assigned a positive sign when the overlap in one dimension for each pair of species was above the median and a negative sign when below. Overlaps in the three dimensions are statistically independent if they follow the expected distribution, $\frac{1}{8}$ (+++), $\frac{3}{8}$ (++-), $\frac{3}{8}$ (+--), $\frac{1}{8}$ (---). Excesses and deficiencies of (+++) imply redundancy and compensation, respectively. Therefore, I reexamined the groups defined in the food-type section to check for compensation or redundancy (compensation or redundancy can be found within subsets even if the whole does not reflect any pattern). This time I assigned a positive sign for all members of a guild as defined by the food-type dimension and checked the sign pattern in the other dimensions. A negative sign indicates compensation in that dimension. Negative signs were checked for included niches (Miller 1968). A symmetrical measure of overlap usually gives low values when we have included niches, when in fact there is 100 percent overlap for one species. Overlap in these cases is inversely proportional to the region of niche space occupied exclusively by one species.

For the agricultural land species, the observed sign distribution follows the expected distribution for no niche compensation ($G = 0.14$, $df = 3$, $P > 0.98$, # species pairs tested = 36). Though compensation or redundancy in overlaps was not found when the whole assemblage was analyzed, I checked for sign patterns within guilds. I found that microspace does not separate ants in the

TABLE 2. Food items carried by ants in agricultural land. See Table 1 for species code.

Species code	5 min observation periods	Seeds	Insects	Insect parts	Ant/ant parts	Insect pupae	Insect larvae	Feces/fungi	Annelids	Insect eggs	Spiders	Aphids	Other invertebrates	Animal matter	Vegetal matter/flowers	Food in crop	Decomposing organic matter	Others
Br.m	20															20		
Camu	228		3	7	13		1	1						1				3
Ca.e	154	1	20	17	3	2	4	3		4				1	7	1		5
Ca.n	112	1	11	9				2						2	4			5
Cy.r	87	3		1			1	73		1				1	3		3	
Ir.m	80		29	60	9	1	1	5				4		1	2	348		16
Mo.e	92	2	66	21	1	2	9	17			1	10		21	4	88		59
Mo.f	10			7				1						6		19		3
My.s	85	15		1	1			97							7		38	5
Od.b	100	2	8	2	6	1	1	4							1		1	1
Pa.l	91		16	10	24	2			1				1	1	1	119		8
Pa.s	33		2	1	1	1										2		
Pl.p	132		6		2		10				1							
Ph.e	34	1	5	7	1					1		3				14		
Ph.f	82	7	213	30	56	3	11	6	1	2	1	8	12	2	18		4	10
Phsu	118	27	43	27	26		10	22			1	2	2	4	6		7	20
So.A	37			6		1		2						6		14		3
So.g	132	102	25	14	16	14	5	3	8			1	9	9	2	7		6
St.l	95		26	3	1												1	4
Te.b	80	1	13	11	2		13	4		1		3		2		34		4
Wa.a	91	7	32	51	34	1	3	7						3	5	25	3	36
Total	1893	169	518	285	196	28	69	247	10	9	4	31	24	60	60	691	57	188

liquid food group nor in the insectivorous food group. Food size separates few insectivorous ants and few members of the liquid food group. In the case of food size, clear patterns of niche inclusion are observed (Fig. 1). However, foraging space separates the species in the liquid food groups from the insectivorous ants. Insectivorous ants preferred to forage on the ground and liquid food ants tended to forage on vegetation, suggesting redundancy in resource utilization. A Kolmogorov-Smirnov test shows no difference in size of food used by the fungus-growing ants ($D = 0.09$, $P > 0.05$). *Platythyrea punctata*, *Camponotus ustus*, *Iridomyrmex melleus* and *Solenopsis* A differ from the other species due to their preference for closed-canopy crops.

The observed sign distribution for grassland ants follows the expected distribution for no niche compensation ($G = 3.42$, $df = 3$, $0.10 < P < 0.50$, # of species pairs tested = 66). In the insectivorous ants, size separates *Odontomachus brunneus* from other species. *Tetramorium bicarinatum* differs from the genus *Cardiocondyla* and *Pheidole exigua* in size of food used, but these species are

included in *T. bicarinatum*'s niche. Space does not separate insect-feeding species.

Food size separates *Paratrechina longicornis* from ants in the genus *Monomorium* in the liquid food group. *Monomorium* are included in the niche of *P. longicornis*. Space separates the species in the liquid food group from those in the insectivorous group, but not within groups. Insect-feeding ants are found within the space-niche dimension of liquid food ants. A Kolmogorov-Smirnov test shows a difference in food size utilized by the fungus-growing ants ($D = 0.28$, $P = 0.05$), but *Cyphomyrmex rimosus* includes *Mycocepurus smithi* in its niche.

Overlap sample sizes were too small for statistical sign analysis to be performed for the forest ants. No separation in food size occurs for the insectivorous ants. *Pheidole moerens* forages on trees, whereas *Paratrechina steinbeili* does not. Food size separates *Iridomyrmex melleus* from *Solenopsis* B in the liquid food group, but *Solenopsis* B is included in *I. melleus*' niche. *Myrmelachista ramulorum* and *I. melleus* are similar in microhabitat (both arboreal) and food-size utilization. *Camponotus ustus*, a nocturnal

TABLE 3. Food items carried by ants in grassland. See Table 1 for species code.

Species code	5 min observation periods	Seeds	Insects	Insect parts	Ant/ant parts	Insect pupae	Insect larvae	Feces/fungi	Annelids	Insect eggs	Spiders	Aphids	Other invertebrates	Animal matter	Vegetal matter/flowers	Food in crop	Others
Br.h	33		4	1	4											18	1
Ca.e	79	1	8	19			4	2		1		1		2	6		13
Ca.n	75	1	4	11	1		4	2		1				4		1	13
Cy.r	82	11		3	1			25		1				1	10		7
Mo.e	80	1	23	37	1	4	3	1				3		15	2	155	19
Mo.f	85	1	31	70		10	2	1		23	1	1		47	6	304	41
My.s	80	3						109							21		1
Od.b	147		1	1	8			1	1				7	1			3
Pa.l	65		6	2	18		1			1	1					53	2
Pa.s	80		9	8	7	1	2				1					19	6
Ph.e	40		5	4	7						1			2		4	11
Ph.f	80	2	235	50	30		14	3	1		6	3	7	5	3	24	39
Phsu	80	5	12	7	10		1	1			1	1		5	1		18
So.g	81	59	1	1	2			1	1					9		1	1
St.l	71		14	10	1		1	1			2						2
Te.b	169	1	75	17	5	4	26	2	2	3	1		1		2	27	6
Wa.a	80	2	12	27	17	5	1	1						3	2	2	11
Total	1407	87	440	268	112	24	59	150	5	30	14	9	15	94	53	608	194

arboreal ant, seems to belong with the insectivorous ants; food size probably separates it from *P. moerens*.

Ant distributions were influenced by depth in the forest litter ($G = 588.60$, $df = 18$, $P < 0.005$). I found three groups of ants: *Paratrechina steinbeili*, *Solenopsis A*, *Pheidole moerens* and *Solenopsis B* were found mostly in the first 2.54 cm layer of litter; *Paratrechina microps* and *Brachymyrmex minutus* in the second layer; *Anochetus mayri* and *Solenopsis C* in the third.

DAILY ACTIVITY.—Using the data on species present on baits put during the day and night, I performed a repli-

cated goodness of fit (G test) to classify ant species as diurnal, nocturnal or both (Table 8). The expected values were calculated by dividing the number of baits put during an interval of time by the total number of baits placed during both intervals. The expected values are the following: agricultural land $P(\text{diurnal}) = 0.75$, $P(\text{nocturnal}) = 0.25$; grassland $P(\text{diurnal}) = P(\text{nocturnal}) = 0.5$; forest $P(\text{diurnal}) = 0.66$, $P(\text{nocturnal}) = 0.33$.

Ants are predominantly diurnal in agricultural land and grassland. *Paratrechina steinbeili*, *Pheidole subarmata* and *Wasmannia auropunctata* can be considered predominantly nocturnal if the number of active workers is taken

TABLE 4. Food items carried by ants in forest.

Species	5 min observation periods	Seeds	In-sects	In-sect parts	Ant/ant parts	In-sect larvae	Feces/fungi	Annelids	In-sect eggs	Animal matter	Vegetal matter/flowers	Food in crop	Others
<i>I. melleus</i>	119		24	38	8		12	1		2	7	73	23
<i>M. ramulorum</i>	80	1	8	39	30	5	22		7	28	5	296	41
<i>P. steinbeili</i>	20		3	3	1		2	1			1		3
<i>P. moerens</i>	29		31	8	2	1	5	3	1	2	2		9
<i>Solenopsis B</i>	30		3	5			9			8		24	6
Total	278	1	69	93	41	6	50	5	8	40	15	393	82

TABLE 5. Ant microhabitat utilization in the agricultural land. S = sun; Sh = shade; N = night

	Ground (S)	Ground (Sh)	Rock (S)	Rock (Sh)	Vegetation (S)	Vegetation (Sh)	Litter (S)	Litter (Sh)	Ground (N)	Rock (N)	Vegetation (N)	Litter (N)
<i>A. kempfi</i>	—	—	—	—	—	—	—	—	—	1	—	—
<i>B. beeri</i>	7	2	6	1	—	—	6	3	—	—	—	—
<i>B. minutus</i>	—	—	—	1	—	1	3	1	—	—	—	1
<i>C. emeryi</i>	3	1	1	—	—	—	5	1	1	—	—	—
<i>C. nuda</i>	19	1	12	5	—	—	6	—	3	3	—	—
<i>C. venustula</i>	1	—	—	1	—	—	1	2	—	—	—	—
<i>C. rimosus</i>	—	—	—	—	—	—	1	—	—	—	—	—
<i>M. ebeninum</i>	3	—	2	—	1	—	2	—	—	—	—	—
<i>M. floricola</i>	—	—	1	—	—	1	3	3	—	—	—	—
<i>O. brunneus</i>	—	1	—	—	—	—	—	—	—	1	—	—
<i>P. longicornis</i>	—	—	1	—	—	—	—	1	—	—	—	—
<i>P. steinheili</i>	—	3	—	1	—	—	2	1	5	—	1	1
<i>P. exigua</i>	—	—	—	—	—	—	—	—	—	—	—	1
<i>P. fallax</i>	27	16	20	23	1	1	18	17	9	3	—	7
<i>P. subarmata</i>	24	29	13	20	—	—	3	10	40	28	—	1
<i>Solenopsis A</i>	—	—	—	—	—	—	—	—	2	—	—	—
<i>S. geminata</i>	38	26	27	23	—	—	14	16	25	15	—	5
<i>T. melanocephalum</i>	4	2	3	6	6	7	11	11	1	2	2	4
<i>T. bicarinatum</i>	—	1	—	2	—	—	—	3	—	3	—	4
<i>W. auropunctata</i>	—	4	1	7	—	2	5	6	3	5	—	6

into account instead of presence or absence at a bait. *Camponotus ustus* is a nocturnal agricultural land species and *Monomorium ebeninum* is diurnal in grassland. Ants tend to be nocturnal in the forest. *Camponotus ustus* is

also a nocturnal forest species. Daily activity does not help much in reducing overlap in the forest.

Ant activity is highly influenced by temperature (Berkelhamer 1980, Whitford *et al.* 1981) and measure-

TABLE 6. Ant microhabitat utilization in the grassland.

	Ground (day)	Rock (day)	Grass (day)	Ground (night)	Rock (night)	Grass (night)
<i>A. kempfi</i>	—	—	—	1	—	—
<i>B. beeri</i>	9	4	5	2	1	1
<i>B. minutus</i>	—	—	—	—	—	1
<i>C. emeryi</i>	8	5	5	2	1	—
<i>C. nuda</i>	17	16	5	4	4	—
<i>C. venustula</i>	1	—	—	—	—	—
<i>C. rimosus</i>	1	1	1	1	2	—
<i>H. opacior</i>	1	1	—	1	—	—
<i>M. ebeninum</i>	1	1	1	—	—	—
<i>M. floricola</i>	4	3	5	—	2	1
<i>O. brunneus</i>	6	—	—	1	2	—
<i>Oxyepoecus</i> sp. ?	—	—	—	2	—	—
<i>P. stigma</i>	1	—	—	—	—	—
<i>P. longicornis</i>	9	5	1	2	4	—
<i>P. steinheili</i>	12	7	4	11	10	13
<i>P. fallax</i>	25	23	11	9	7	9
<i>P. subarmata</i>	27	8	2	23	12	3
<i>Solenopsis A-C</i>	2	—	—	2	—	—
<i>S. geminata</i>	34	23	4	25	15	6
<i>S. louisianae</i>	1	—	—	1	—	—
<i>T. melanocephalum</i>	2	2	4	—	2	4
<i>T. bicarinatum</i>	5	2	4	3	5	3
<i>W. auropunctata</i>	5	6	9	11	9	7

TABLE 7. *Ant microhabitat utilization in the forest. I placed 20 baits in the sunny microhabitats and 48 in the remaining microhabitats. S = sun; Sh = shade; N = night.*

Species	Ground (S)	Ground (Sh)	Rock (S)	Rock (Sh)	Vegetation (S)	Vegetation (Sh)	Litter (S)	Litter (Sh)	Ground (N)	Rock (N)	Vegetation (N)	Litter (N)
<i>B. minutus</i>	1	3	—	—	—	—	—	—	1	—	3	1
<i>C. ustus</i>	—	—	—	—	—	—	—	—	—	—	3	—
<i>I. melleus</i>	2	4	1	7	13	22	5	6	1	4	17	—
<i>P. stigma</i>	—	2	—	—	—	—	—	—	2	—	—	1
<i>P. microps</i>	1	—	—	—	—	—	—	—	1	1	—	1
<i>P. steinbeili</i>	—	11	—	2	—	—	—	4	12	3	—	15
<i>P. moerens</i>	2	11	—	9	2	6	—	15	17	15	4	23
<i>Solenopsis B</i>	—	5	—	4	—	—	—	2	11	8	—	11
<i>Solenopsis A</i>	1	—	—	—	—	—	—	—	3	—	—	—
<i>Solenopsis C</i>	—	—	—	—	—	—	—	—	1	—	—	—
<i>S. rogeri</i>	—	—	—	—	—	—	—	—	1	—	—	—
<i>T. littorale</i>	—	—	—	—	—	—	—	—	—	1	—	—

ments of temperature tolerance can help explain diurnal activity. Tolerance to 45°C is an indication of the amount of time a species can forage at high temperatures (Table 9). I performed a one-way ANOVA using a logarithmic transformation to make the variances homogeneous. Species differ significantly in tolerance in agricultural land ($F = 24.01$, $df = 29$, 228 ; $P = 0.00$). Species that tolerate high temperatures usually do not tolerate low temperatures well (Torres, unpublished). Several species are included in the temperature-niche dimension of other species.

Grassland ants differ in tolerance to high temperature ($F = 19.83$; $df = 30$, 221 ; $P = 0.00$). Temperature influences allocation of resources but there is still overlap. In the agricultural land and grassland, tolerance to high temperatures is similar in the fungus-growing ants and diurnal species stand 45°C better than nocturnal ones (Wilcoxon test, $P = 0.01$).

The ANOVA shows that forest species differ in temperature tolerance ($F = 24.98$; $df = 14$, 115 ; $P = 0.00$). Notably, the forest species withstand high temperatures for much shorter time relative to the species in nonforested

TABLE 8. *Assignment of species to the nocturnal (N), diurnal (D) or shared (S) categories. Diet type: 1 = insectivorous, 2 = liquid food, 3 = granivorous, 4 = fungus growing.*

Species	Agricultural land	Grassland	Forest
	G ^a	G ^a	G ^a
<i>Brachymyrmex heeri</i>	18.98 ^b D	9.60 ^b D2	—
<i>Brachymyrmex minutus</i>	3.48 ^c S2	—	2.05 ^c S
<i>Cardiocondyla emeryi</i>	4.83 ^b D1	11.90 ^b D1	—
<i>Cardiocondyla nuda</i>	7.97 ^b D1	21.30 ^b D1	—
<i>Iridomyrmex melleus</i>	—	—	3.27 ^c S2
<i>Monomorium ebeninum</i>	24.16 ^b D2	—	—
<i>Monomorium floricola</i>	4.89 ^b D2	5.78 ^b D2	—
<i>Paratrechina longicornis</i>	4.60 ^b D2	3.98 ^b D2	—
<i>Paratrechina steinbeili</i>	0.01 ^c S2	2.14 ^c S2	20.54 ^b N1
<i>Pheidole fallax</i>	18.49 ^b D1	14.20 ^b D1	—
<i>Pheidole moerens</i>	—	—	25.93 ^b N1
<i>Pheidole subarmata</i>	3.23 ^c S1	0.01 ^c S1	—
<i>Solenopsis B</i>	—	—	27.97 ^b N2
<i>Solenopsis geminata</i>	6.15 ^b D3	2.11 ^c S3	—
<i>Tapinoma melanocephalum</i>	12.32 ^b D	0.29 ^c S	—
<i>Tetramorium bicarinatum</i>	4.92 ^b N2	0.00 ^c S1	—
<i>Wasmannia auropunctata</i>	0.20 ^c S2	1.05 ^c S2	—
Pooled data for all species	34.15 ^b D	23.70 ^b D	56.83 ^b N

^a $df = 1$ for all tests; ^b $P < 0.05$; ^c not significant.

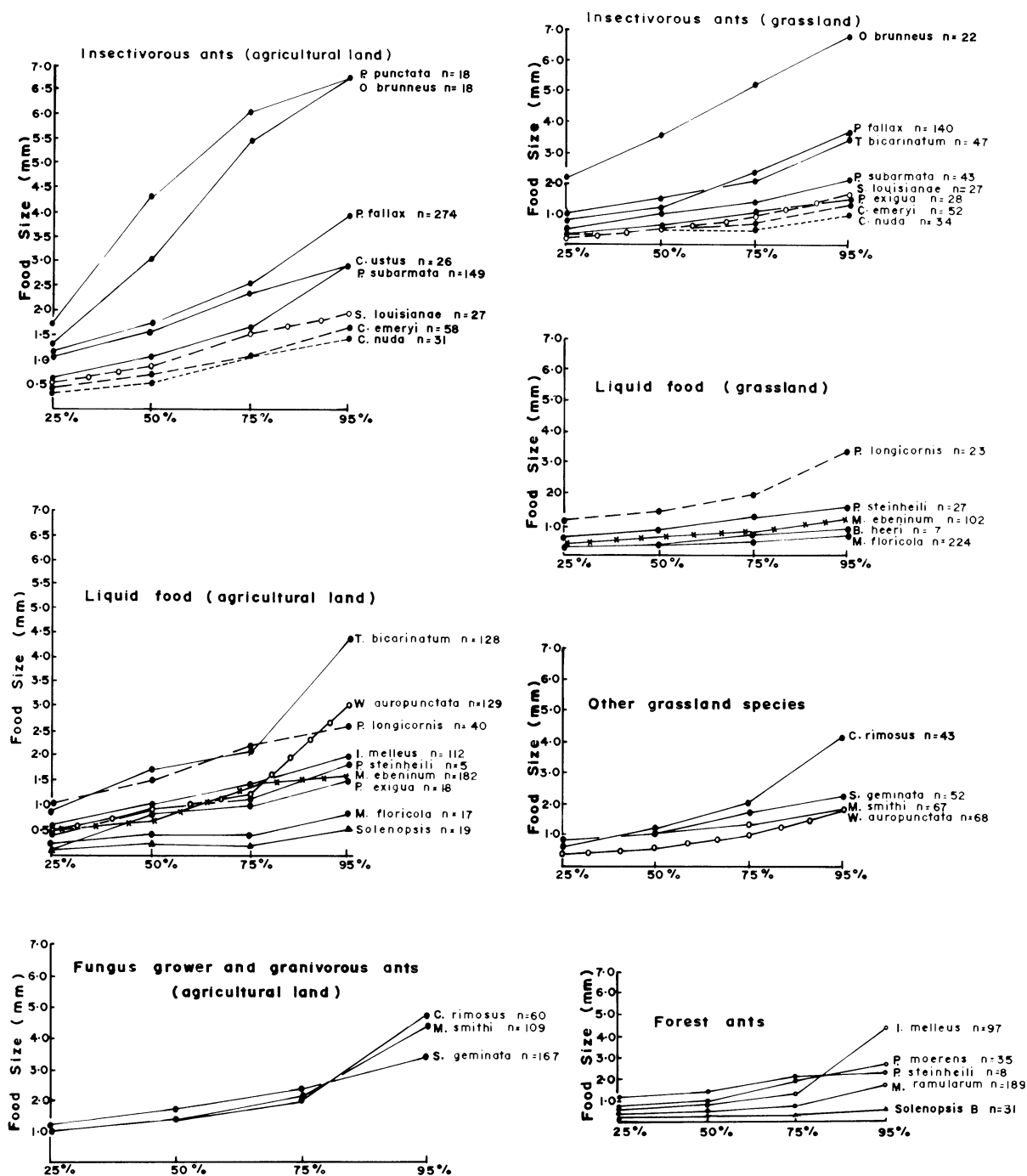


FIGURE 1. Distribution of food sizes consumed by species in the three habitats. Ninety-five percent, 75%, 50%, and 25% of the items fall below the size indicated on the ordinate.

TABLE 9. Mean amount of time tolerated by ants in the agricultural land (A. land); grassland (G. land); and forest at 45°C. Bars represent species with homogeneous means (SNK procedure). See Table 1 for species code.

A. land SNK	(min)	G. land SNK	(min)	Forest SNK	(min)
Pa.m	7.9	An.m	9.1	Pacs	5.0
My.s	8.4	Hy.e	10.2	An.m	5.5
An.m	10.2	Cy.r	10.5	St.g	7.0
Cy.r	11.4	My.s	10.7	Am.s	8.8
Hy.e	11.8	St.l	14.1	Pa.m	9.7
St.l	11.1	Ox.s	14.5	So.C	10.6
Hy.o	12.1	So.C	15.5	St.r	10.9
So.C	12.3	Pacs	16.0	Hy.o	12.1
Pacs	15.7	Hy.o	16.8	So.B	13.4
Br.m	17.6	Phsu	17.0	Pa.s	14.6
Phsu	17.6	Br.m	18.5	Br.m	15.0
Ph.m	18.0	Od.b	18.7	Ph.m	16.2
Od.b	20.9	So.A	22.4	So.A	17.0
Ph.e	21.8	Ph.e	23.2	Ir.m	23.1
Ir.m	22.3	Pa.s	24.6	Camu	31.0
So.B	22.8	Te.b	24.8		
So.A	24.6	Wa.a	26.7		
Wa.a	25.7	Ro.s	26.8		
Pa.s	26.2	So.B	31.8		
Ta.m	33.3	Te.c	33.2		
Te.b	34.2	Ta.m	42.2		
Ph.f	40.8	Ph.f	42.9		
So.g	46.1	Br.h	46.9		
Ca.e	47.5	Co.g	47.6		
Camu	49.2	Ca.n	48.1		
Pa.l	50.8	Pa.l	54.7		
Ca.n	54.2	Ca.e	56.6		
Br.h	57.1	Cams	57.5		
Mo.f	116.2	Mo.f	98.7		
Mo.e	169.2	Ca.v	129.6		
		Mo.e	141.8		

areas. However, the importance of temperature tolerance in the forest should not be overstressed because most forest species are predominantly nocturnal and high temperatures are rarely experienced in the forest, much less at night.

INTERFERENCE COMPETITION.—I monitored 409 interference interactions on tuna fish baits, pooling grassland and agricultural land observations. One species in each pair won in combat, regardless of environmental conditions, except for *Pheidole fallax* vs *P. subarmata* and *P. fallax* vs *Wasmannia auropunctata*. The sample for the latter pair is too small to make any statistical tests. *Pheidole fallax* won diurnal combats and *P. subarmata* nocturnal ones (Fisher's exact test, two-tailed, $P = 0.02$). *Pheidole fallax* won combats in direct sunlight under dry and wet conditions. *Pheidole subarmata* seems to be a better fighter in shade (Fisher's exact test, two-tailed, $P = 0.06$).

There is a priority effect; ants arriving to a bait first have a greater probability of winning a combat. Data for all the species were pooled and tested against the null hypothesis that winning is independent of arrival time.

The null hypothesis was rejected ($G = 22.7$, $df = 1$, $P < 0.005$), indicating an advantage in arriving first. This allows poor competitors to win some encounters, and will sway a competitive situation on behalf of the weaker competitor. This advantage takes place because the first arrivals recruit and outnumber the scouts from other species. Aggressive contacts with the species at the bait seem to discourage scouts from laying odor trails, preventing late-arriving species from recruiting workers.

I constructed an index of wins-per-encounter in which the number of encounters won by a given species over all the other species was divided by the total number of encounters in which the species was involved. This index indicates the species' rank as a fighter (Table 10). Except for *Monomorium ebeninum* and *M. floricola*, those species that have their niches included in that of another are very poor fighters. Many do not display any kind of aggressive behavior. I calculated the index values for different environmental conditions and found that predominantly nocturnal species are better fighters during the night ($\chi^2 = 13.59$, $df = 1$, $P < 0.005$) and in shade ($\chi^2 = 6.70$, $df = 1$, $P < 0.01$). Because poor fighters are found

TABLE 10. *Relative indices of interference.*

Species	Grassland/ crops	Forest
<i>Pheidole moerens</i>	—	.50
<i>Solenopsis geminata</i>	.22	—
<i>Solenopsis</i> B	—	.20
<i>Monomorium floricola</i>	.20	—
<i>Monomorium ebeninum</i>	.10	—
<i>Wasmannia auropunctata</i>	.09	—
<i>Pheidole fallax</i>	.08	—
<i>Odontomachus brunneus</i>	.08	—
<i>Pheidole subarmata</i>	.06	—
<i>Paratrechina longicornis</i>	.06	—
<i>Tetramorium bicarinatum</i>	.06	—
<i>Paratrechina steinheili</i>	.02	.09
<i>Tapinoma melanocephalum</i>	.02	—
<i>Iridomyrmex melleus</i>	.00	.21
<i>Oxyepocus</i> sp. ?	.00	—
<i>Brachymyrmex minutus</i>	.00	.00
<i>Brachymyrmex heeri</i>	.00	—
<i>Hypoponera opacior</i>	.00	—
<i>Cardiocondyla nuda</i>	.00	—
<i>Cardiocondyla venustula</i>	.00	—
<i>Pheidole exigua</i>	.00	—
<i>Paratrechina microps</i>	—	.00

in shaded microhabitats, good fighters in sunlight win more consistently in shade (paired *t*-test, arcsin transformation, $t = 2.43$, $df = 9$, $P < 0.05$).

Aggressive interactions are rare in the forest. I witnessed 27 combats on 464 baits (5.8%) in the forest as compared to 409 combats on 1056 baits (38.7%) in the nonforested areas. There is no advantage to arriving first at a bait in the forest ($G = 0.33$, $df = 1$, $P > 0.50$).

DISCUSSION

Analyses of resource partitioning often have been based on the predictions of simple Lotka-Volterra equations (but see Paine 1966; Caswell 1976; Simberloff 1979; Sousa 1979). The main conclusion obtained from these simple linearized differential equations is that stable coexistence of n species is attained if the species are limited by n factors (Levin 1970). This equilibrium analysis is exemplified in the theory of niche differentiation which predicts that species must differ in order to coexist. This approach has been successful in explaining coexistence in simple communities. Nonetheless, it has failed to explain coexistence in fishes (Sale 1982), tropical plants (Connell 1978) and vegetative clones (Harper 1977).

Nor does classical niche differentiation theory entirely explain species coexistence in these ant communities. Agricultural land ants differ in diet, daily activity, food size and macrohabitat utilization. These differences could facilitate species coexistence in this community. By facilitate I mean that these factors can help but might not be

necessary for species coexistence. However, several species use environmental resources in similar ways (e.g., *Monomorium ebeninum* and *M. floricola*, *Cyphomyrmex rimosus* and *Mycocarpus smithi*, *Cardiocondyla emeryi* and *C. nuda*, *Cardiocondyla* species and *Pheidole fallax*). Differences in diet and daily activity could facilitate coexistence in grassland ants. Species that use the environment similarly occur here as well (e.g., *Cardiocondyla emeryi* and *C. nuda*, *Monomorium ebeninum* and *M. floricola*, *Paratrechina longicornis* and *Brachymyrmex heeri*, *Cyphomyrmex rimosus* and *Mycocarpus smithi*). Diet and litter utilization could facilitate forest species coexistence.

Overlap in different niche dimensions was independent, indicating a lack of overlap compensation. Repeated patterns in the utilization of the environment are seen in these assemblages. Insectivorous ants in the agricultural and grassland communities forage mainly on the ground. Liquid feeding ants in agricultural land and grassland forage mainly on vegetation. In the forest, most ant activity is concentrated within the litter. There is great overlap in size of food carried to the nest by individual workers. Any differences among species are further reduced as food items too large for an individual are overcome by recruiting other individuals. In addition, forest ants tend to be nocturnal and ants in nonforested areas are mostly diurnal.

Although I found differences in temperature tolerance which are correlated with activity patterns, there is also much overlap and many patterns of niche inclusion. The mainly nocturnal habits of the forest species minimize the importance of tolerance to high temperatures for these species.

Food limitation seems to be an important factor in the structuring of these ant assemblages. Interspecific aggression among ants at concentrated food sources supports this contention. Two factors that affect the outcome of these encounters were discovered: microclimate and priority. The influence of microclimate is best observed in interactions between *Pheidole fallax* and *P. subarmata*, but it is also evident when one species' fighting abilities are compared with those of other species. The priority effect observed in combats at tuna fish baits is significant in the allotment of permanent food sources such as nectar-producing plants and honeydew-excreting insects; normally weak competitors can keep their food supply in this manner. For evenly matched species, like *Monomorium ebeninum* and *M. floricola*, priority effects are likely to be more influential. However, the priority effect does not facilitate coexistence in many of the species that have their niche included in those of other species, because most of the former do not exhibit aggressive behavior.

Levins *et al.* (1973), Wilson (1971), and Carroll and Janzen (1973), found priority effects operating at several levels in ant communities. They observed that established colonies have a strong advantage over incipient colonies

and founding queens. Queens of competitively superior species cannot colonize an area already occupied by weak competitors because of predation or aggression by the weak species. I have observed these priority effects in the ant communities studied suggesting that they play an important role in the organization of these communities. In addition, ant aggression is age dependent (Wheeler 1910, Carroll and Janzen 1973) pointing to another effect of age structure in a competitive environment.

Ant aggression was low in the forest compared to the nonforested areas. This is in accordance with the findings of Crowell (1968), Haskins and Haskins (1965) and Culver (1974), who found that aggression is more prevalent in structurally simple habitats. Contrary to the suggestion that species having their niches included in those of other species should behave aggressively in order to coexist (Colwell and Fuentes 1975), I found that these species usually do not behave aggressively or are losers in interspecific combats.

The current finding concerning the greater species coexistence relative to apparent resource numbers is no surprise. Theoretical models dealing with feeding rates not

linearly related to resource abundance, cooperative hunting, multiple nutritional requirements, *etc.*, predict coexistence of n species in $k < n$ resources (Levins 1979, Armstrong and McGehee 1980). The mentioned factors that allow coexistence of n species in $k < n$ resources have been found in several ant communities (Wheeler 1936; Sheppe 1970; Carroll and Janzen 1973; Whitford and Ettershank 1975; Davidson 1977b).

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