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Predatory Behavior and Prey Selection by Army Ants in a Desert-Grassland Habitat

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Summary. Colonies of *Neivamyrmex nigrescens* conduct extensive nocturnal raids on other ants and termites in the desert-grassland of Arizona–New Mexico. We collected quantitative data on several aspects of raiding to pinpoint differences due to colony size and behavioral phase. In the nomadic phase, colonies began raiding at sunset and continued until dawn. Larger colonies covered more area, discovered more prey sites, and collected more booty than smaller colonies, but there were no systematic changes in raid intensity over the course of the nomadic phase. In the statary phase, raiding occurred less frequently and was less intense when it occurred; however, at the end of this phase, raiding was similar to nomadic phase raids in extent, duration, and booty captured.

N. nigrescens preyed exclusively on termites and ants, and appeared to select certain species of *Pheidole* in preference to other ants. *Pheidole* was the most abundant genus, but was preyed upon twice as often as expected based on relative colony density. *Pheidole* attempted to avoid predation by fleeing or defending their nest, but rarely succeeded. Because they are about the same size as army ants and lack defensive chemicals, *Pheidole* made comparatively easy prey.

N. nigrescens ignored or was repelled by other ants (*Pogonomyrmex, Novomessor, Iridomyrmex, Myrmecocystus*) during the early summer, when *Pheidole* was abundant; however, in late summer when *Pheidole* was less available, the army ants preyed upon *Novomessor cockerelli.*

N. harrisi raided in close proximity to *N. nigrescens*, but preyed exclusively on *Solenopsis xyloni*. Selection of prey and partitioning of resources are now indicated in several army ant species; these processes have probably been important factors in the evolution of the ants' predatory behavior.

Introduction

Predation by New World army ants (Ecitoninae) has been studied principally by Schneirla (1934, 1940, 1958, 1971) and Rettenmeyer (1963), both of whom described army ant raids, the organization of mass foraging, and the principal types of prey taken by several species. Considerable research has since been devoted to the behavioral mechanisms by which these ants find and recruit to food (Chadab and Rettenmeyer 1975; Topoff and Mirenda 1975; Topoff and Lawson 1979; Topoff et al., to be published, a), but little is yet known about the ecological aspects of raiding. A complete list of the types of prey taken by any Ecitonine has yet to be compiled, while quantitative data on prey intake and the utilization of space during raids are largely lacking. Such information would be useful in evaluating theories of the evolutionary origin and proximate causation of army ant behavior (Schneirla 1957, 1971; Wilson 1958, 1971) and also contribute to our understanding of insect community dynamics.

The lack of information results in large part from the difficulty of monitoring the activity of *Eciton burchelli* and *E. hamatum*, the most commonly studied species. Colonies of these ants contain between 150,000 and 2,000,000 adults, are active at most times during the day and night, and occur in tropical habitats where it is often difficult to observe behavior. To avoid these difficulties, we studied the predatory behavior of *Neivamyrmex nigrescens* (Cresson), an army ant whose colonies are considerably smaller than those of *E. burchelli* or *E. hamatum* (Schneirla 1958, 1971; Mirenda 1978). The study was conducted in the southwestern United States in the summers of 1976 and 1977, when *N. nigrescens* was active on the surface at night, in a habitat where surface activities were easily observed.

In this paper, we present a quantitative description

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of several features of raids (times of occurrence, numbers of columns and raid sites, area covered, prey captured) and relate these characteristics to colony size and the colony's position in its nomadic-statary cycle (Schneirla 1971). In addition, a list of all the types of prey taken by *N. nigrescens* in this habitat is presented, along with evidence of a surprisingly narrow range of prey selection in *N. nigrescens* and *N. harrisi* (Haldeman).

Materials and Methods

The study site was located 8 km NW of Rodeo (Hidalgo County), New Mexico. At an elevation of 1,250 m, this desert-grassland community (Lowe 1964) receives about 28.7 cm of rain annually and has mixed vegetational cover. A variety of shrubs dominate the landscape for most of the year but, following the rains in July, grasses and a wide variety of annual flowering plants come to predominate in this ungrazed portion of valley bottomland. Parts of the study site are flooded for several hours to a day following the cloudbursts.

Surface soil temperatures averaged 50° C at 1,500 hours (MST) and 17° C at 0200 hours throughout the summer. Most days were hot and dry, and the stability and aridity of the climate provided us with an important advantage: the ants did not begin their surface activities until approximately 1900 hours on most days and ceased surface activity around 0500 hours; thus it was possible for a small research group to monitor all surface activities as they developed.

A second advantage provided by this site was the excellent view of the ants' surface activity. Approximately 70% of the pavementlike substrate is exposed and unsheltered by vegetation in July. This percentage gradually shrinks to about 30% by mid-September as grasses and annuals proliferate. However, even in late summer, the ground cover did not obscure more than a meter or two of any column observed. In addition, most of our observations were made in the early summer.

Colonies of *Neivamyrmex* were located while walking through the study area in the evening with a Coleman lantern. Three species were encountered: *N. nigrescens, N. harrisi,* and *N. fallax* (Borgmeier). Each colony was designated by year, species, and number. For example, the designation 76N-3 refers to the third colony of *N. nigrescens* encountered in 1976. Colonies were observed at close range with rechargeable miner's cap lamps.

During the nomadic phase (NP), bivouac location was the key to colony identity from one nomadic day (ND) to the next. On most NDs, the colonies were observed through the cessation of activity at sunrise, when the bivouac had already been formed. On the remaining NDs, the colonies were checked at least once between 0200 and 0500 hours to determine bivouac location. Movements during the statary phase (SP) were unlikely, but colonies were nevertheless checked every 2–3 h on statary days (SDs) for any activity.

In 1976, we observed events at the basal portion of columns. A column was defined as a trail of ants that had a separate connection with the nest opening, extended at least 5 m from that opening, and was used for at least 15 min. Army ants use columns for raiding (the capture of prey) and emigrating (the change of nest location). An observer was stationed alongside a clearly exposed section of each column (within 5 m of the nest opening). With four hand counters the observer recorded the number of larval, pupal, adult forms of ants, and termite prey being carried by the raiders back to their nest. Counts were made for 5-min periods at intervals beginning every 15 min. Observations usually began at the onset of raiding and continued on most nights until surface activity ceased.

To determine a colony's gram intake, booty counts from each night's raiding were multiplied by the wet weight of the average piece of booty captured. During periods when no counts were made, the intake was estimated. The hours of raiding for which there were no counts were multiplied by either (a) the rate of gram intake at the time the counts ceased that evening or, if there were no counts that evening, (b) the average rate of gram intake for the remainder of that colony's behavioral phase.

In 1977, columns were observed at the periphery of the raid nexus. We determined the number and distribution of raid sites, cache sites, potential nest sites explored by the ants, and other major features of the raiding pattern. We also recorded the types of prey attacked and the defensive behavior of the prey at their nests. These observations were made primarily with nomadic colonies from the onset of raiding until the emigration started.

A raid site was defined as any hole in the ground where the ants entered empty-mouthed and left carrying a piece of booty. A cache site was any location along a column that ants entered with booty and left without the booty. We also noted other holes that the ants explored; these might have become the next nest for the colony. The compass direction (North = 0°) and straight-line distance from the nest opening to each site was measured.

Raid and emigration routes were sketched roughly as they developed, then recorded permanently the next morning in maps incorporating the important sites on each column. An estimate of the area covered by each raid column was obtained by treating the sites on the raid nexus as points on a plane surface and forming a convex polygon whose vertices were the nest and the outermost sites on the column. The area measure was taken from maps like those in Fig. 1. These maps do not show the full area covered by a colony during raiding. For every branch of the columns shown in the maps, there were many more that formed but did not persist long enough to be mapped. The convex polygon around the raid sites may overestimate the area covered by a column, but it is at least certain to include the area covered by the more ephemeral branches of the fast-changing raid column.

Colony size was determined during emigrations. *N. nigrescens* usually sent out only one raiding column before an emigration, a phenomenon that facilitated the size estimates. We started counting as the colony became active. One observer counted the ants leaving the bivouac; a second observer counted the ants returning. When the emigration began (i.e., when the first larva was carried out of the nest), the first observer began to count the ants moving outward carrying larvae; the second observer counted ants moving outward not carrying larvae; a third observer counted ants returning to the nest (always unladen). All counts were made simultaneously during 2-min periods at intervals beginning every 6 min. Combining the counts of each observer in appropriate ways tells the number of adults and number of larvae in the colony (Mirenda 1978).

Results

Temporal and Spatial Aspects of Raiding

All colonies were inactive on the surface during the day. Unless it was an unusually cool or cloudy day, the colonies did not become active on the surface until sometime after sunset (1800–1900 hours MST). In the NP (nomadic phase), virtually all raids began between 1900 and 2000 hours. The raid of colony

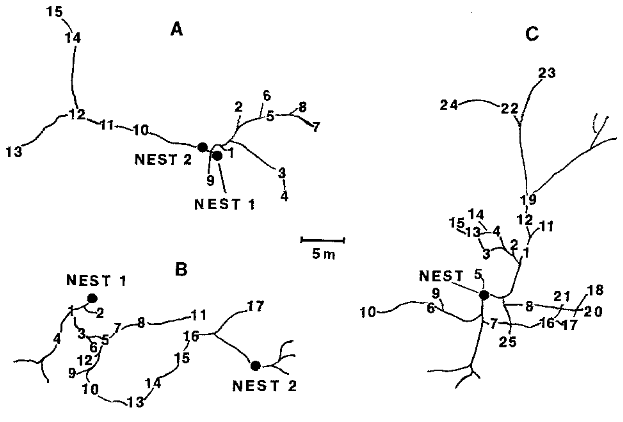

Fig. 1 A–C. Raiding and emigration activity of three nomadic colonies during 1977. *Numbers* indicate the location of sites where prey was taken and the order in which the sites were discovered. **A** Activity of 77N-1A on ND 11 (8/2–8/3) from 1800 to 0500 hours. All the raid sites were discovered before the emigration began at 0430 hours (nest 1 to nest 2). **B** Activity of 77N-5 on ND 14 (7/18–7/19) from 1800 to 0100 hours. All the raid sites were discovered before the emigration started at 0000 hours. **C** Activity of 77N-7 on 7/21–7/22 (late in nomadic phase) between 1830 and 0030 hours. The colony raided extensively in many directions but did not emigrate

76N-8 on ND (nomadic day) 8 began at 2300 hours following an early emigration. Nomadic raids generally lasted until 0500 hours, except when long emigrations began late in the evening, or when bad wheather disrupted all activity. There was no systematic change in starting or ending times of raids as a function of ND.

Raiding was more variable in the SP (statary phase). On the first two SDs (statary days), raiding began between 2000 and 2200 hours and ended after 1–5 h. Between SD 3 and SD 10, very little raiding occurred, and raids that did occur began late in the evening and lasted briefly. From SD 11 onward, raiding was more frequent, began earlier in the evening and lasted longer, resembling NP raids in most respects.

Figure 1 shows typical raid patterns for three nomadic colonies studied in 1977. Once colonies became active on the surface, it was impossible to predict the direction a raid column would take. Raids generally covered new ground, but occasionally moved back in the direction of the previous night's emigration. Prey sites were abundant and continuously distributed in the area around the bivouac, and colonies invariably found prey close to their bivouacs in whatever direction they raided. The time and distance to successive raid sites averaged over all columns studied are shown in Fig. 2. The ants discovered a new site every 22 min at 2-m increments from the nest. Despite the almost continuous discovery of new raid sites, the ants passed near but missed many nests of potential prey.

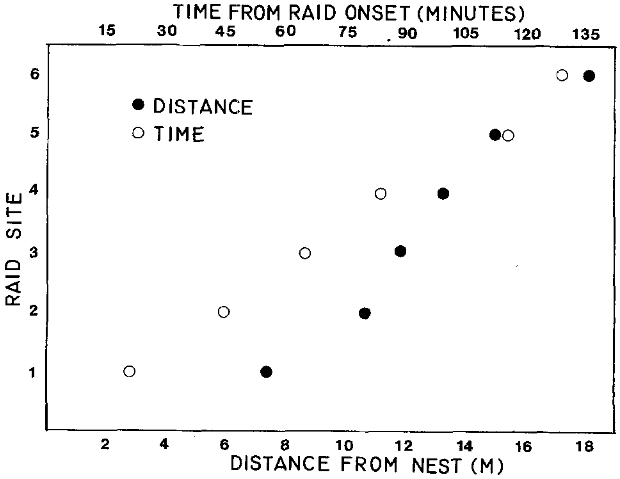

Fig. 2. The discovery of raid sites as a function of time active and distance traveled from the nest. The *data points* are average values for all columns of two colonies listed in Table 1

Table 1 shows several characteristics of the raids of three nomadic colonies. There was no systematic change in the magnitude of these characteristics as the NP progressed, but there were striking differences between the colonies. For example, two colonies in Table 1 were observed for about the same number of NDs and total hours, but 77N-5's raiding statistics were about twice those of 77N-1A in every category. These differences are related to colony size. Colony 77N-1A had only 9,500 workers while 77N-5 had about 25,000 workers. As a further comparison, the raiding activity of colony 77N-7, whose worker force exceeded 80,000 during this NP, for part of one ND is shown in Table 1. This colony's activity exceeded the average of the other two colonies. No further data were taken from this colony because it was too difficult to monitor accurately; however, the level of activity reported in the table was typical for this colony throughout its NP.

Booty Intake

In 1976, counts of the booty brought back to the nest were made throughout a complete behavioral cycle (one nomadic and one statary phase) of two colonies. A total of 147 h of raiding was observed on 18 NDs, which represents 90% of the hours these colonies were active on those days, and 60% of the total estimated time the colonies were raiding on a total of 26 NDs. In the SP, 61.3 h of raiding were observed on 28 SDs, which represents 92% of the hours these colonies raided on those days and 70% of the total estimated time the colonies were active on 34 SDs.

Table 1. Indices of raiding activity in three colonies during nomadic phase

Colony	Nomadic day	Raid columns	Raid area (m^2)	Raid sites	Hours observed	$\frac{m^2}{Hour}$	$\frac{\text{Raid sites}}{\text{Hour}}$
77N-1A	2	2	64	7	4.5	14	1.6
	6	2	118	9	4.0	30	2.3
	7	2	173	6	4.0	43	1.5
	8	1	77	6	4.0	19	1.5
	9	2	25	6	8.5	3	0.7
	10	2	71	6	8.5	8	0.7
	11	2	338	15	11.0	31	1.4
	12	1	149	2	2.0	75	1.0
Totals	8	14	1,015	56	46.5	22	1.2
77N-5	5	2	113	4	4.5	25	0.9
	6	4	241	15	8.5	28	1.8
	7	1	314	8	4.5	70	1.8
	8	1	102	4	0.5	203	8.0
	9	9	498	23	6.0	83	3.8
	10	2	238	9	5.0	48	1.8
	11	4	587	23	8.5	69	2.7
	12	2	191	15	2.8	68	5.4
	14	1	228	17	6.0	38	2.8
Totals	9	26	2,542	118	46.3	54	2.5
77N-7	?	2	554	25	8.0	69	3.1

Table 2. Comparison of raiding activity in two colonies through one nomadic-statary cycle. Mean ± SD of grams (g) collected and hours (h) raided per day are shown for the first and second half of each phase. The total grams collected, hours raided, and days for each colony in each phase are also shown

Colony		76N-3		76N-8	
Phase		Nomadic	Statary	Nomadic	Statary
1st half	g/day	16.7 ± 7.1	0.4 ± 0.9	6.3 ± 3.4	2.5 ± 2.7
	h/day	9.6 ± 0.6	1.3 ± 1.7	9.7 ± 0.4	2.2 ± 2.0
2nd half	g/day	12.8 ± 7.2	4.5 ± 4.4	11.8 ± 6.4	4.7 ± 6.0
	h/day	8.5 ± 3.8	3.9 ± 3.1	9.8 ± 0.2	2.9 ± 2.6
Total	grams	189.7	43.3	120.5	57.1
	hours	116.8	46.8	126.5	41.0
Phase	days	13	18	13	16

Table 2 shows the total gram intake and hours raided for these two colonies. In the NP, colony 76N-3 collected an average of 14.6 ± 7.2 g/ND; colony 76N-8 averaged 9.3 ± 5.8 g/ND. Both colonies averaged between 9 and 10 h of raiding during each ND. The table also shows the amount of booty and number of hours for each half of the NP. Colony 76N-8 collected almost twice as much booty in the second half of its NP as in the first, half. This difference was largely due to three days (NDs 10–12) of heavy raiding at the very end of the NP. The booty intake and hours raided for 76N-3 decreased slightly from the first to the second half of its NP, but this difference is entirely accounted for by the failure to raid on ND 12, when inclement weather disrupted all activity. Though there was substantial variation in the booty intake per ND for both colonies, it was not systematically related to ND.

During the SP, the colonies were not active on the surface every night. Colony 76N-3 averaged only 2.6 ± 2.7 h of raiding per SD while 76N-8 averaged 2.5 ± 2.6 h per SD. Colonies also gathered much less booty in the SP (Table 2). However, in both colonies, the amount of booty captured began to increase steadily at the end of the SP, and the hours of raiding and the rate of booty intake were similar to those of NP raids.

Clearly there is a phase difference in raiding intensity. In addition, colony 76N-3 gathered more booty in its NP than did 76N-8, and gathered it at a higher rate. These differences are also related to colony size. During its NP, 76N-3 had more than 23,000 workers while 76N-8 had about 12,000; however, 76N-3 also had more larvae to feed (33,160 vs 22,300). When this factor is taken into account, the booty intake is more comparable. Colony 76N-3 gathered 0.44 mg/larva/ND while 76N-8 gathered 0.41 mg/larva/ND. The foragers of 76N-8 actually worked harder to keep that pace than those of 76N-3, gathering 0.77 mg/worker/ND against 0.62 mg/worker/ND.

Prey Selection

Table 3 shows the prey taken by colonies 77N-1A and 77N-5, and the frequency of predation on each species. Of the 17 species preyed upon, 16 were ants; *Gnathamitermes* sp. was the sole exception. On a few occasions carabid and scarab beetles were found in raiding columns, but they appeared to have wandered in the columns by accident, and were not sought out by the ants. Such booty constituted a miniscule portion of the total prey intake.

The greatest portion of prey items were immature stages of other ant species. The booty intake of colony 76N-3 (Table 2) was composed of 30% larval, 46% pupal, and 11% adult ants. Termite workers composed 13% of the prey. Similarly, the booty intake of colony 76N-8 (Table 2) was composed of 17% larval, 32% pupal, and 11% adult ants, with termites

Table 3. Prey of two colonies of *N. nigrescens* in July and August 1977

Prey species	Colony 77N-1A		Colony 77N-5		Combined	
	Nests raided	% of total	Nests raided	% of total	Nests raided	% of total
Pheidole desertorum	18	31.0	26	18.4	44	22.1
Pheidole sciophila	5	8.6	16	11.3	21	10.5
Pheidole rugulosa	0	0.0	20	14.2	20	10.1
Pheidole hyatti	5	8.6	13	9.2	18	9.0
Pheidole xerophila	0	0.0	5	3.5	5	2.5
Pheidole sitarches	0	0.0	2	1.4	2	1.0
Unidentified *Pheidole* sps.	2	3.4	11	7.8	13	6.5
Leptothorax sp.	4	6.9	1	0.7	5	2.5
Conomyrma insana	4	6.9	2	1.4	6	3.0
Paratrechina melanderi	2	3.4	0	0.0	2	1.0
Aphaenogaster huachucana	1	1.7	1	0.7	2	1.0
Pogonomyrmex californicus	1	1.7	1	0.7	2	1.0
Myrmecocystus mimicus	0	0.0	1	0.7	1	0.5
Camponotus festinatus	1	1.7	0	0.0	1	0.5
Unidentified ants	6	10.3	18	12.8	24	12.1
Gnathamitermes sp.	9	15.5	24	17.9	33	16.6
Totals	58		141		199	

accounting for the remaining 40% of prey items.

Termites and several species of ants were preyed upon much more frequently than the remaining prey shown in Table 3. For instance, colonies of *Pheidole* accounted for 51.6% of the nests raided by 77N-1A and 65.8% of the nests raided by 77N-5. Much evidence supports the contention that *N. nigrescens* is selecting certain species of ants to raid in preference to others. Table 4 shows the density and relative abundance of the seven most common ant genera on a bajada near the study area (Davidson 1977a and personal communication) and the relative frequency of predation on each genus (considering only those genera). *Pheidole* is the most abundant genus, but it is preyed upon more than twice as frequently as would be expected if it were raided in proportion to its density. Raiding on most other genera is much less frequent than expected by chance encounters in the field. The overall difference between the observed and expected frequency of predation on each genus is significant ($\chi^2 = 147.2$, $df = 6$, $P < 0.001$).

There is probably further selection of prey within the genus *Pheidole*, but estimates of density for all sympatric species are not available. However, if we consider two species, *Ph. desertorum* and *Ph. xerophila*, for which both density and predation frequency during July 1977 are known, the selectivity of *N. nigrescens* is evident. Colonies of *Ph. xerophila* are at least ten times those of *Ph. desertorum*, yet the latter is preyed upon almost ten times as frequently (Table 3).

Table 4. Density and frequency of predation on the seven most common ant genera in the study area (July–August 1977)

Genus	Colonies/ ha[a]	Relative density	Colonies raided	Proportion of colonies raided
Pheidole	1,338	0.455	123	0.932
Solenopsis	862	0.293	0	0.000
Conomyrma	396	0.135	6	0.045
Iridomyrmex	184	0.062	0	0.000
Myrmecocystus	134	0.045	1	0.007
Pogonomyrmex	19	0.006	2	0.015
Novomessor	10	0.003	0	0.000

[a] From Davidson (1977a and personal communication)

The prey selection of *N. harrisi* stands in sharp contrast to that of *N. nigrescens*. Twelve raids from six colonies of *N. harrisi* were observed. Some of these raids were in close proximity to those of *N. nigrescens*, but in every case *N. harrisis* was raiding *Solenopsis xyloni*. This ant is abundant on the study site (Table 4), but was never raided by *N. nigrescens* during our study. The raiding columns of *N. harrisi* extended for an average of only 5 m on the surface.

Predator-Prey Interactions

By following raid columns as they developed, we were frequently present at a raid site just as it was discovered by army ants, and were able to observe the initial interactions that took place between predator and prey. Different species reacted very differently to approach by army ants; in those differences may lie the key to success or failure in avoiding predation.

Subterranean termites foraged in small groups near the surface. When discovered by *N. nigrescens*, they offered no resistance and were plucked singly from their column. The army ants did not recruit heavily to these spots or pursue the termites through their tunnels (which may have been too small), but they took all termites available. Several such pockets were usually found within a small area.

Species of *Pheidole*, though heavily preyed upon, were not as easily captured as termites. Two types of predation avoidance were seen in this genus. The first was flight behavior. The larger, faster-moving species *Ph. desertorum* and *Ph. hyatti* may have anticipated the raids through signals from foragers extending from their own nest to the army ant column. On such occasions, the *Pheidole* massed around their nest holes, each worker holding a piece of brood. When the army ants approached within a few centimeters of the nest, the mass dispersed – sometimes in all directions, sometimes uniformly away from the raiders. Captured workers were easily overcome, but many escaped the raid. Two colonies that took flight sufficiently early escaped entirely. Workers of both *Pheidole* species also climbed nearby vegetation; *N. nigrescens* rarely followed upward. After the raiding subsided, *Pheidole* returned to their nest. As we never observed a queen fleeing the nest, it is possible that queens were normally defended in underground chambers.

The second predation-avoidance behavior was nest defense. The smaller, slower-moving species – *Ph. xerophila, Ph. rugulosa, Ph. sciophila,* and *Ph. sitarches* – did not attempt to outrun the army ants, nor were they conspicuous around their nest openings when the raid approached. Their nest openings were usually not discernible until attention was drawn to them by the army ant swarm. Army ants entered the narrow opening singly and later emerged backward, pulling on a *Pheidole* soldier, who typically had a vice-grip on the army ant's foreleg or antenna. This process continued until the passageway was cleared, indicated by a smoother flow of army ants into and out of the hole. Shortly after the 'breakthrough', the army ants emerged from the hole carrying *Pheidole* brood. These *Pheidole* workers were also subdued easily by individual army ants once their strategem had been overcome.

Army ants had a more difficult time with ants larger than themselves. For example, nests of *Novomessor cockerelli*, a nocturnally active forager, were abundant on our site and frequently encountered by raid columns, but during the period of our most thorough observations (July–August 1976 and 1977) not one nest was raided. When raid columns approached these nests, the *Novomessor* workers would approach the column and engage the army ants. It took 5–10 raiders to subdue one of these ants and 2–4 raiders to lug it back to the bivouac. Many *Novomessor* workers were killed, but the tide of the raid was always stemmed. However, in September 1977, two colonies of *N. nigrescens* raided *N. cockerelli* consistently for two weeks. The implications of this abrupt shift in prey selection will be examined below.

Workers of *Pogonomyrmex*, also larger than army ant workers, were more difficult to subdue than *N. cockerelli*. *P. barbatus* workers foraging at dawn often walked through raid columns. The army ants attacked the intruders, but were generally unable to subdue them, even when ten or more workers combined in the effort. On one occasion, we observed *P. barbatus* workers break up an army ant emigration and a raid column that 'trespassed' on their mound. The harvesters simply walked into each column in a mass resembling a football huddle, and scattered army ants in all directions. The emigration re-formed later, over a new route that gave the mound a wide berth. Not one *P. barbatus* worker was killed in this encounter. *P. californicus* fared less well; some small colonies of this species were raided (Table 3).

Army ants appeared to avoid *Myrmecocystus* sps. and *Iridomyrmex pruniosum*. Raiders would approach these nests and even palpate the ants, but the raid never progressed further. *Myrmecocystus* did not react noticeably to these encounters, but *I. pruniosum* climbed over the raiders, which stood motionless. In both cases, the raiders ran back along their column and did not return.

Discussion

Characteristics of Raiding Behavior Related to Cyclic Behavior and Colony Size

Several measures of raiding activity indicate a vast difference in colony arousal between the NP and SP. First, raids occur on virtually every ND, but not on some SDs. Second, NP raids are more intense. Schneirla (1971) quantified this phenomenon in *Eciton* by comparing the traffic (ants/min) on raid columns on selected NDs and SDs. We have shown here that NP raids of *N. nigrescens* start earlier in the evening, last longer, and yield greater amounts of booty than SP raids.

The same relationship undoubtedly holds for other aspects of raiding (e.g., number of raid columns, raid sites, and area covered), since all of these measures are closely related and probably result from common causal factors. Not every measure of raid activity is a reliable indicator of phase differences, however. Schneirla (1971) noted that strong, NP raids of *E. hamatum* may move as little as 40 m from the bivouac while weaker, SP raids sometimes move up to 350 m. We have noted a similar phenomenon in *N. nigrescens*, whose raids may vary from 5 to 40 m in the SP and from 5 to 60 m in the NP. The variability in raid distance may depend more on external factors, such as terrain or the richness and distribution of raid sites, than do other measures of raid behavior.

Schneirla (1957, 1971) attributed between-phase differences in colony behavior to stimulation from the brood (Schneirla's brood-stimulative theory). He did not demonstrate the exact nature of the signals by which the larval and pupal brood stimulate workers to raid and emigrate (for a critical review, see Wilson 1971), and subsequent work (Rettenmeyer 1963) could only confirm the existence of the nomadic-statary cycle in other species and the correlation of phases with brood condition. The present study confirms the sharp contrast in the behavior of *N. nigrescens* as correlated with brood condition (Schneirla 1958) and shows in greater detail how phase differences in colony arousal are expressed in raids, but these results do not support or refute the mechanistic aspects of Schneirla's theory of proximate causation. His theory is not totally without experimental support, however. In a recent study (Topoff et al. to be published, b), the signals inciting the onset of the NP are shown to arise from the newly eclosed callow workers.

Schneirla (1949, 1971) stated also that raiding intensity varied systematically *within* each phase, and related those changes to his theory: raids at the end of the NP were said to be larger as a result of the increasingly potent stimulus arising from the maturing larval brood; similarly, raids were larger at the end of the SP because of the movements and secretions of pupae about to eclose. We can confirm only the SP changes in raid intensity. Though one of our colonies raided most heavily at the end of its NP, the colony also failed to emigrate during this period, a result not easily explained with brood-stimulative theory, as heavy raids and emigrations should go together. Emigrations sometimes hindered raiding in some colonies (Mirenda 1978; ms in preparation). In any case, there was no systematic change in NP raid intensity. It seems likely that the buildup in raid intensity at the end of the SP is due to stimulation from the eclosing pupal brood, since a similar buildup was seen in the experimental colonies of Topoff et al. (to be published, b) in which there were no larvae.

Another factor that accounts for variation in raid intensity is colony size. Within one phase, larger colonies have more raid columns, cover more area, discover more prey sites, and gather more booty. Larger colonies also raid more efficiently, covering more area and gathering more booty than do smaller colonies in the same amount of time. The differences are no doubt due to the greater number of raiders, and reflect on the adaptive significance of large colony size. The ability of group predatory ants to utilize large arthropods and social insects as prey may depend upon colony size, while specialization on this type of prey may have been a major factor in the evolution of large colonies in army ants (Wilson 1958). The greater efficiency of large colonies of *N. nigrescens* in raiding supports this hypothesis and also indicates a basis on which natural selection may currently operate to maintain large colonies in army ant populations. Colony size must now be correlated with more direct measures of fitness (e.g., production of sexual forms) to verify this hypothesis.

It should be noted, however, that most of the colonies we encountered were considerably smaller than any previously reported for this species. Schneirla (1958, 1971), working in a canyon near our study site, reported the size range for *N. nigrescens* as 80,000–140,000 adults, with a mean of about 100,000.Our colonies ranged from 9,500 to 100,000 adults with a mean of about 30,000 (Mirenda 1978). Perhaps differences in prey abundance in the two habitats account for the difference in colony size. Alternatively, since most previous estimates are based on crude measures, it may be that colony size has been uniformly overestimated in army ants. Size determinations in the field, employing the more rigorous methods outlined here, will have to be made in several habitats to resolve this issue. It seems clear in any case that the success of army ants as predators is not solely dependent on the use of overwhelming numbers of raiders in their forays; just as important in the evolution of their predatory habits are the behavioral characteristics of individual raiders and the judicious selection of prey.

Prey Selection

Both Schneirla (1971) and Rettenmeyer (1963) recognize differences in the prey taken by species of New

World army ants. The swarm-raider *E. burchelli* takes the greatest variety of food items (including wasps, orthopterans, and spiders) but still kills more ants than any other prey. *E. burchelli* is also the most likely species to raid ant colonies in trees. *E. hamatum* takes immature stages of wasps and other species of ants most often, and adults of other insects much more rarely. Other species of *Eciton, Neivamyrmex, Nomamyrmex*, and *Labidus* feed primarily on ants.

There are some notable differences in predation on selected species of ants and termites. Of all the *Eciton* species studied by Rettenmeyer (1963), only *E. quadriglume* attacks *Atta* and other leaf-cutters in the tropics, though *N. nigrescens* frequently raids *Trachymyrmex* in the mountains of southern Arizona (Schneirla 1958, 1971; personal observation). Similarly, only *E. burchelli* and *E. dulcius* prey upon *Paraponera clavata*. The epigaeic *E. burchelli* and *E. hamatum* take no termites (Rettenmeyer 1963; Schneirla 1971) while the more hypogaeic genera *Neivamyrmex, Nomamyrmex*, and *Labidus* are termitophagous (Borgmeier 1955; Pullen 1963). Finally, *N. nigrescens* and *N. harrisi* exhibit sharp food preferences and nonoverlapping distributions of prey types under the conditions of the present study.

Factors like time and energy for search, pursuit, and handling of prey, as well as nutritive value, should affect the range and the proportion of different items found in the diet of any animal (MacArthur and Pianka 1966; Pianka 1974; Schoener 1971). The narrow range of prey selection in *N. nigrescens* is probably closely related to the costs and benefits of foraging. *N. nigrescens* preys upon the most abundant genus, *Pheidole*, but availability is not the sole determinant of predation frequency. Species of *Pheidole* lack defensive weapons powerful enough to repel or discourage army ant raids, nor can they avoid attacks consistently by leaving their nests. *Pheidole* thus make easy prey when compared to other species of ants in the study area. *Novomessor* and *Pogonomyrmex*, due to their size and strength, are difficult for *N. nigrescens* to subdue, while *Myrmecocystus* and *Iridomyrmex*, with powerful alarm-defense secretions (Wilson 1971), seem to be avoided by army ants or are perhaps not recognized as potential prey. *N. nigrescens* might suffer damaging losses if these ants were routinely raided.

It would be interesting to know the sensory/perceptual mechanisms on which this prey discrimination is based. *N. nigrescens* is blind and nocturnal, and relies heavily on tactile and chemical stimuli for orientation (Topoff and Lawson 1979). Foragers of many desert ants leave the nest via 'trunk trails' (Hölldobler 1976; Davidson 1977b), which could provide the physical and/or chemical cues by which *N. nigrescens* orients toward or away from each species. Perhaps *N. nigrescens* has an olfactory 'search image' (Croze 1970) for *Pheidole*.

The increase in predation on *N. cockerelli* by some colonies in September indicates that the mechanisms of prey selection are complex. Davidson (1977b) and Whitford (1978) have shown that the activity of these *Pheidole* species in arid habitats is strongly related to rainfall and forage availability. During 1977, rainfall on the site decreased from 13.8 cm in July to 6.0 cm in August to 2.2 cm in September (U.S. Weather Bureau – Rodeo, New Mexico station). Under dry conditions, many *Pheidole* colonies (and probably other small ants) become inactive and seal their nest openings, making detection and attack by army ants impossible. The increased predation on *N. cockerelli* may thus have resulted from the decreased availability of *Pheidole*. The prey preferences of *N. nigrescens* and other army ants can be expected to change according to the structure of the ant community in space and time.

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