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Social organization and foraging success in *Lasius neoniger* (Hymenoptera: Formicidae): behavioral and ecological aspects of recruitment communication

James F.A. Traniello
Harvard University, Museum of Comparative Zoology Laboratories, Cambridge, MA 02138, USA

Summary. Live, moribund, or dead arthropods are gathered by *Lasius neoniger* through individual and social retrieval. 85% of the total biomass of prey (fresh weight) in the diet is cooperatively retrieved by groups of workers. Short- and long-range chemical recruitment signals coordinate cooperative foraging. Stort-range recruitment of workers to assist in the retrieval or defense of prey is achieved by simultaneous discharge of hindgut material and poison gland secretion. In long-range recruitment, workers discovering prey deposit a trail of hindgut material while returning to the nest. Hindgut pheromone both stimulates nestmates to leave the nest and orients them to the food source. Colony response is adjusted according to prey weight. Group retrieval of prey follows after a sufficient number of foragers have been recruited to move the prey. Rapid prey movement decreases the exposure of food sources to neighboring conspecific and interspecific competitors. The ability to move prey rapidly is limited to prey on the order of 130 mg or less in weight. The probability of interference during foraging and resource loss to competitors increases with increasing prey size, but the probability of loss is significantly less than the probability of interference for intermediate size prey (~20 mg), which can be moved quickly. The foraging and recruitment behaviors of *Lasius neoniger* appear to have a prey size-dependent effectiveness which results in greater foraging success on prey of a relatively narrow size range above those prey that can be retrieved by solitary foragers.

Introduction

In social species such as ants it is difficult to separate foraging ethology from foraging ecology because of the importance of cooperative behavior in resource acquisition. Underlying cooperative foraging systems are communication signals that integrate the activities of individuals. Recently, there has been a change in the focus of research on communication during foraging organization from mechanistically analyzing recruitment signals to studying their ecological significance. Hölldobler et al. (1978) demonstrated that in *Novomessor cockerelli* and *N. albesitosus* chemical and vibrational stimuli mediate group retrieval of prey, a social process that reduces food resource losses to interspecific competitors. Workers of *Monomorium minimum* are recruited to arthropod prey along potent trails composed of Dufour's gland secretion, and while dissecting prey, employ a chemical defense to prevent interference from sympatric ant species (Adams and Traniello 1981). *Iridomyrmex pruinosum* employs a similar strategy; a pygidial gland repellent is effective in deterring foraging by *Myrmecocystus* (Hölldobler 1982). Other aspects of foraging such as territorial strategy also involve communication systems (Hölldobler and Wilson 1978; Hölldobler and Lumsden 1980).

Cooperative foraging systems are social adaptations to ecological factors such as resource distribution patterns and intensity of competition. Typically, cooperative foraging is chemically coordinated. Although considerable variation in chemical communication systems has been described (Wilson 1971; Hölldobler 1978), this variation has on few occassions been correlated with the ecology of the species. In this paper I describe the ecology and ethology of foraging in the ant *Lasius neoniger*, and present an experimental analysis of the chemical signals involved in the social organization of foraging and their role in interspecific competition and foraging success.

Materials and methods

Field studies

Lasius neoniger is perhaps the most conspicuous and abundant ant species in North America (Wilson 1955). It is the dominant ant species in open habitats in the northeastern United States, commonly occuring sympatrically with *Formica lasioides, F. schaufussi, Myrmica americana, Monomorium minimum, Tetramorium caespitum* and *Solenopsis molesta* (Talbot 1953; Goldstein 1973; Traniello 1980a). *L. neoniger* occurs in dense populations, and as many as five distinct, polydomous colonies have been recorded in a square meter (Traniello 1980a). Workers tend subterranean aphids for carbohydrate secretions, and forage epigaei-

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Present Address: Boston University, Department of Biology, 2 Cummington Street, Boston, MA 02215, USA

cally for protein foods, chiefly dead or dying arthropods, or arthropod fragments. Field studies were conducted at three sites in Massachusetts, one in the Estabrook Woods, Concord, and two in Westford. The study sites in Westford, which were visited most frequently, were each roughly a hectare in area and were abandoned pastures which had not been in use for 25–30 years. The dominant vegetation at the sites included the grass *Digitaria*, dandelion *Taraxicum officinale*, buttercup *Ranunculus*, and clover *Trifollium pratense*. Observations and experiments were conducted from April to October, 1977–1981, principally from 6 to 11 AM. Surface temperature ranged from 15–40° C.

Laboratory studies

Laboratory colonies composed of groups of 300–500 workers were housed in test tubes fitted with cotton plugs and placed in plastic containers (24 cm × 30 cm), the walls of which were treated with fluon to prevent escape. Ants were fed on honey water, freshly killed insects, and artificial diet.

For recruitment signal analysis, extracts of the mandibular gland, the poison gland, the Dufour's gland, and the hindgut were prepared from *L. neoniger* workers in the laboratory. Whole glands were removed, washed in distilled water or ethanol, and homogenized in 10 μg of 100% ethanol per gland in a Kontes extract vial. Aliquots of the solution were dispensed with a 10 μl microsyringe (Hamilton No. 701-N).. Bioassays were performed in the field. Artificial trails (5 μl extract/25 cm) were drawn out on pieces of chromatography paper, or glandular secretions (1 gland/5 μl ethanol) were offered on a one cm^2 piece of filter paper.

Statistical evaluations were based on Student's t-test, Mann-Whitney U-test, and Wilcoxon two-sample test for ranked observations. Comparisons of the significance of differences between probabilities of interference and loss of experimental prey were based on a test for the equality of two percentages using arcsin transformation (Sokal and Rohlf 1969). The null hypothesis was rejected when $P < 0.05$. Additional methodological details will be presented with the descriptions of individual experiments.

Results

1. The importance of social retrieval in resource acquisition

The food habits of *L. neoniger* are quite generalized. Workers opportunistically forage for prey of various types (Wilson 1955; Traniello 1980a). Common prey include representatives of the insect orders Lepidoptera, Orthoptera, Hymenoptera, Homoptera, Hemiptera, and Coleoptera. Nearly one-half of all forage items collected were insect fragments. Each item collected in the field was identified (generally to family or genus for insects), weighed (fresh weight), and its body length was measured and recorded. In addition, the retrieval method employed was recorded. Workers employ four foraging techniques: 1) individual retrieval, 2) cooperative retrieval by workers foraging in the same area, 3) cooperative retrieval by a group of workers recruited from the nest, and 4) mass recruitment of workers to immovable prey. Combined forage sample data, representing a quantification of protein food habits, is given in Fig. 1. Numerically, the majority of prey in the diet are individually retrieved. However, the majority of items in the diet that contribute most to the total biomass are retrieved socially through the recruitment of nestmates. 85% of the total prey biomass is retrieved cooperatively.

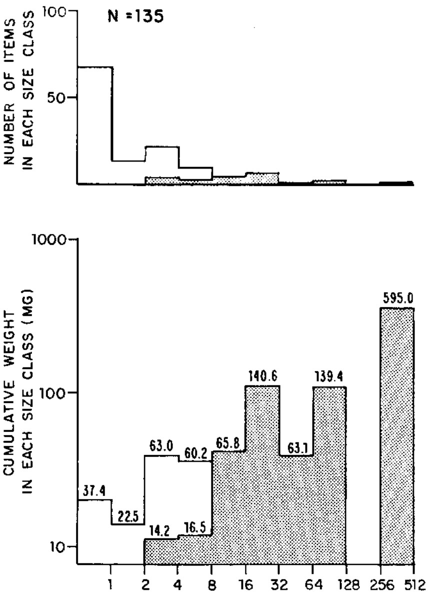

Fig. 1. Dietary profile of *Lasius neoniger*. In the upper figure the y-axis indicates the number of items in each size class, whereas in the lower figure by y-axis indicates the cumulative weight of the items in a size class. In both figures the x-axis is a $\log_2$ transformation of the weight ranges of each size class, which permits the inclusion of large, rare items. □ = individual retrieval; ▨ = social retrieval. N = sample size

2. The social organization of foraging

Short-range recruitment. Two pheromonally-mediated communication systems are involved in cooperative foraging. The first system is imployed to summon nearby workers to assist in retrieval. The first worker to discover food attempts to carry it homeward; after 10–20 sec of attempted retrieval, the behavior changes to circling, dotting the gaster tip, or rotating and dragging the gaster around the prey. If workers are nearby (within approximately a 5 cm radius) they orient toward the location of the prey and assist in its retrieval or defense. Retaining the terminology of Hölldober (1978), I term this behavior short-range recruitment.

Observations of workers that first discover prey suggest that an attractant is emitted by scouts which allows nearby workers to orient to the point of discharge, thereby attracting nestmates to aid in prey transport or defense. This hypothesis was supported by the following experiment. Small roaches (~ 8 mg) were placed in an area foraged by a colony of *L. neoniger* and the time required for three workers to locate the bait was recorded when the first two workers 1) were aspirated as soon as they contacted the food, and 2) were allowed to remain at the bait. The results (Table 1) indicate a significant difference in the time required to assemble this small consort of workers. Based on this result and ethogram data, I assumed that the attractive stimuli were emanating from the worker that discovered the prey and not the odor of the prey itself. Because the behaviors

Table 1. Differences in the amount of time (in sec) required for three *Lasius neoniger* workers to contact a bait under two circumstances. In condition A, the first two workers to contact the bait were immediately aspirated. In conditions B, they were allowed to remain on the bait. The differences are statistically significant (ts = 2.98, $0.001 < P < 0.01$, Wilcoxon statistic)

Trial	Condition		Trial	Condition	
	A	B		A	B
1	95.0	38.0	15	160.0	101.0
2	39.0	7.2	16	37.8	41.2
3	18.0	6.0	17	12.0	3.8
4	18.2	4.8	18	150.0	110.0
5	29.8	7.2	19	41.0	7.0
6	21.4	44.4	20	242.0	80.0
7	32.0	45.8	21	42.4	23.4
8	100.0	31.4	22	25.0	14.5
9	95.0	20.0	23	123.0	98.2
10	174.0	24.4	24	71.0	30.4
11	23.2	11.0	25	175.0	67.0
12	8.4	3.0	26	27.0	15.0
13	38.2	35.0	27	67.0	20.8
14	33.0	22.6			

of workers after prey discovery were suggestive of pheromonal emission, the possibility of chemical signals was examined.

The response to gland extracts was recorded as the number of approaches made by workers during the first two min after the extracts were offered. Individuals which appeared to move randomly toward the filter paper were discounted.

Initial results were somewhat inconclusive (Table 2a). The response of workers to extracts of the poison gland, and the hindgut were significantly different from controls (hindgut/control: $0.02 < P < 0.05$; poison gland/control: $0.01 < P < 0.02$), but were not different from each other ($0.5 < P < 0.6$). The secretion of the poison gland is formic acid, which is known to function as an attractant or excitant in combination with hindgut material in some formicine species (Ayre and Blum 1971; Hölldobler 1971). It is quite possible that the two substances are discharged simultaneously during short-range recruitment. To test this hypothesis, I offered mixtures of gland extracts (hindgut material and poison gland secretion) in competition with extracts of either gland alone by placing contaminated pieces of filter paper 5 cm apart. Counts of workers attracted were taken in a 3 min period. The positions of the two odor dummies were exchanged at 1.5 min. Secretions offered together were more attractive than either secretion alone. The results (Table 2b) suggest that poison gland secretion (formic acid) and hindgut material are simultaneously discharged and mediate worker attraction. The contents of the mandibular gland (in part, presumably citral and/or citronellal, personal olfaction) and the Dufour's gland (undecane and other hydrocarbons) probably function during the communication of alarm and do not seem to be involved in recruitment (see for example Bergström and Löfquist 1970).

Table 2. Attraction of workers of *L. neoniger* to extracts of glandular substances offered on a filter paper square placed 5 cm upwind of groups of foragers. Eight replicates were performed. The response of workers to extracts of the poison gland and the hindgut were significantly different from controls (hindgut/control: ts = 2.7, $P < 0.05$; poison gland/control: ts = 3.1, $0.01 < P < 0.02$) but were not different from each other (ts = 0.77, $0.5 < P < 0.6$). In a series of experiments in which either poison gland secretion or hindgut material was offered in competition with mixtures of equal volume of hindgut material and poison gland secretion, the combination of the two secretions was significantly more effective in attracting workers (1b). Statistics based on Student's *t*-test. The volume of the combined extracts was equivalent to the volume of either extract alone (0.5 µl)

a)	Extract tested				
	Mandibular gland	Dufour's gland	Poison gland	Hindgut	Control
Total no. of ants responding	8	51	81	111	11
Mean response	1.4 ±1.5	7.3 ±7.1	11.6 ±8.5	15.9 ±14.4	1.6 ±1.7

b)	Extract tested			
	Hindgut	Hindgut – Poison gland	Poison gland	Hindgut – Poison gland
Total no. of ants responding	19	50	22	77
Mean (±sd)	3.2 ±1.9	8.3 ±4.2	3.7 ±2.0	12.8 ±6.5
Range	1–6	4–15	1–6	4–23
	$0.02 < P < 0.05$		$0.01 < P < 0.02$	

Table 3. Response of *Lasius neoniger* workers to 30 cm long artificial trails prepared from extracts of various glands. Six replicates were carried out in the field. A response was defined as continuous following for at least 5 cm

	Hindgut	Poison gland	Dufour's gland
Total number of ants respondings	70	11	9
Mean number of ants following 5 cm (±sd)	11.7±7.7	1.8±1.5	1.5±1.5
Mean following response (cm) (±sd)	23.2±9.3	13.1±7.3	9.2±1.9

Long-range recruitment. If the number of foragers attracted to prey by short-range recruitment is insufficient to cooperatively carry the item, one or more individuals may return to the nest in trail-laying posture. A trail-laying individual periodically dots the tip of the gaster on the substrate. Soon after her return to the nest, workers arrive at the food source. When artificial trails composed of extracts of the poison gland, the Dufour's gland, and the hindgut were offered to foraging workers in the field, hindgut trails were consistently effective as orienting signals (Table 3), as is true in *Lasius fuliginosus* (Hangartner 1967).

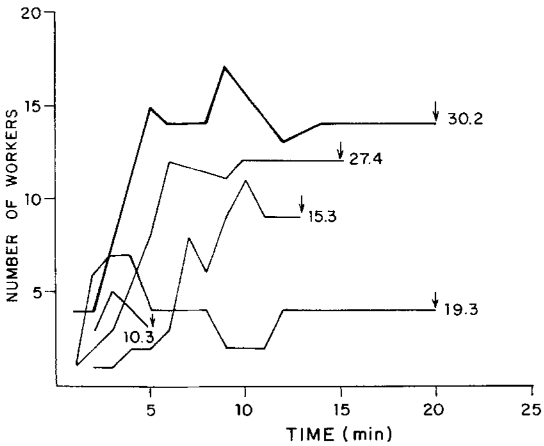

Fig. 2. Representative group retrieval processes. The weight of the item retrieved is given with the time required for transport to the nest (arrow)

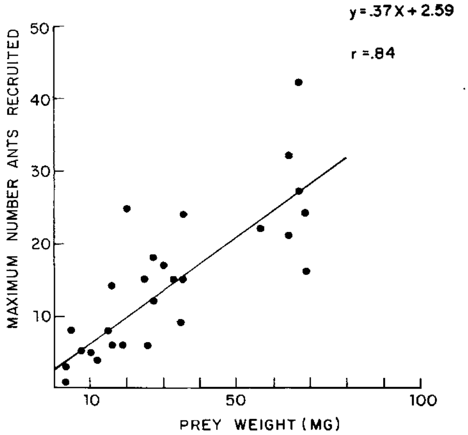

Fig. 3. Relationship between prey weight and recruitment response. Twenty-seven prey of different sizes were offered to a single colony, and the maximum number of workers recruited during the retrieval process was recorded for each item. The correlation between prey weight and the size of the recruited group is significant $(0.2 < P < 0.05)$

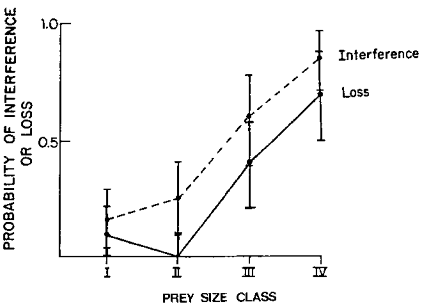

Fig. 4. Relationship of foraging success to prey size in *Lasius neoniger*. Vertical bars represent 95% confidence limits. Mean weights of size classes: *I* 8.04 mg; *II* 21.48 mg; *III* 131.56 mg; *IV* 498.82 mg. (See also Table 5)

After dead or crippled insects on the order of 60 mg or less are located by scout ants, dependent upon the weight of the item and the presence of nearby workers, either immediate cooperative retrieval by 2–5 workers follows or one worker returns to the nest to summon assistance. In either case, the concerted carrying efforts of the workers results in the rapid removal of the item. Several representative cooperative retrievals are illustrated in Fig. 2. The economy of cooperative retrieval is illustrated by the ability of recruiting ants to assess the size of a food item and adjust the number of workers necessary for its retrieval accordingly. This was observed in a series of field experiments in which prey of different size were offered to a colony. To control for factors affecting the resistance to retrieval other than prey weight such as microtopography, the items were offered 15 cm away on a flat surface placed adjacent to the nest. The maximum number of workers recruited to assist in the cooperative retrieval of the 27 items was recorded. As the results presented in Fig. 3 indicate, prey size is significantly correlated with the maximum number of workers recruited. Of course, there is an upper limit to prey size above which the recruitment response levels off and remains constant in spite of large increases in prey weight. However, for items on the order of 60 mg or less the relationship holds. In the field, large prey items were consistently recruited to *en masse* by *L. neoniger* workers. This long-range recruitment strategy mobilized individuals from the nest which follow a hindgut odor trail to the food. In addition to its use in exploiting large immovable items it is used to secure any prey that offer a degree of resistance to retrieval that cannot be overcome by the short-range recruitment of foragers.

3. Interspecific competition, prey size, and foraging success

Lasius neoniger strongly overlaps in nest site preference, diurnal foraging periodicity, seasonal foraging activity, and prey type and size with the sympatric species *Myrmica americana, Monomorium minimum, Formica schaufussi*, and the imported species *Tetramorium caespitum*, among other minor components of the ant fauna (Talbot 1953; Goldstein 1973; Traniello 1980a). These species affect resource utilization indirectly by *L. neoniger* by removing food items before they can be found, and directly through aggressive or chemical interference and competitive displacement (Traniello 1980a; Adams and Traniello 1981). Interactions between *Lasius* and one or more other species were frequently observed at naturally occurring and experimentally offered prey. The ability to mobilize nestmates to a new food find and successfully defend it from competitors are important parameters in foraging success. Of 425 roach baits (~250 mg each) offered along a 75 m transect across the center of one study site, workers of *L. neoniger* first discovered and recruited to 39.8% of these experimental prey; 17.6% of baits occupied initially by *Lasius* were lost to competitors through interference and subsequent displacement. Resource loss, however, is not only caused by direct interference mechanisms. For example, workers of *Formica schaufussi* are able to individually retrieve a wide range of prey sizes (up to ~80 mg) and often abscond with prey initially located by *Lasius* while the latter species is in the process of recruiting nestmates to assist in retrieval.

Our observations of species interactions at naturally occurring insect prey and at baits suggested that prey size strongly influences foraging success. Large, immovable prey were usually lost to competitors even if occupied first by

Table 4. The mean (x), standard deviation, (sd), and range of item sizes in prey classes I–IV offered at 10 cm from colonies of *Lasius neoniger*

Class I	$x=8.035$ mg sd $=0.802$ range $=7.1$–10.0	Class III	$x=131.56$ mg sd $=15.07$ range $=111.4$–156.5
Class II	$x=21.475$ mg sd $=1.066$ range $=20.1$–23.9	Class IV	$x=498.82$ mg sd $=29.837$ range $=461.7$–543.5

L. neoniger. Prey size in the diet of *L. neoniger* ranges from 0.1–595 mg. I next considered whether *L. neoniger* was more effective at securing prey of some sizes than others. In other words, do the foraging and recruitment systems have a prey size dependent effect on foraging success?

To answer this question, four size classes of standardized baits (nymphs of the cockroach *Nauphoeta cinerea*) were used as experimental prey. The different weights of items in each size class offered required that different retrieval strategies be deployed ranging from individual retrieval or small group recruitment (2–10 workers) (Class I) to mass recruitment and dissection (Class IV). The weight characteristics of the baits are presented in Table 4. In the field, 20 baits of each size class were placed at a distance of 10 cm from a *Lasius* nest entrance. For each bait, the retrieval time (if possible), or the period of occupation, and the presence of interference from competitors, was recorded. Prey movement rates are given in Table 5. Interference was defined as any interaction potentially or actual causing loss of prey or worker injury. The entire observation period for the large, immovable baits was three hours, and if baits were removed or usurped by other species during this time, they were considered to have been lost. Many confrontations with competitors did not result in succession, although as many as four species challenged *Lasius* for the possession of one bait. The results of the study are presented in Fig. 4.

As envisaged by Oster and Wilson (1978), the relationship between prey size and the probability of interference was somewhat sigmoidal. Items in the smallest size class were retrieved with relatively high success, and with increasing prey size, the probability of loss increased to a level beyond which an increase in size did not further increase either interference or loss. The probabilities of interference and loss for size class I prey, which were carried by single foragers or small groups of workers, were low and not significantly different. This indicates that small prey are rarely lost to competitors. For prey approximately 20 mg in weight (class II) the probability of interference (0.25) was significantly different ($P<0.001$) from the probability of loss (O). Probabilities of interference and loss for items in size classes III and IV were not significantly different. It is reasonable to assume that as prey size increases over the 20–130 mg range (class II to III), the ability to successfully retrieve prey decreases because the difference between interference and loss probabilities that were significant for class II prey become insignificant over this increase in size. Therefore, the chance that prey are successfully taken decreases for items between roughly 20 and 130 mg in weight. The diet of *L. neoniger*, which is modified by competitive interactions, may include prey in this size range, but foraging success decreases as prey size increases. Prey movement rates decrease significantly as prey size increases (Table 5), thereby increasing the time in which the food source is accessible to competitors. This correlation appears to explain why prey on the order of 130 mg or more are likely to be lost to other and species.

Discussion

The size range of prey acquired by *Lasius neoniger* is expanded by social mechanisms beyond the relatively small range (0.1–∼8 mg) that individual foragers can retrieve. The dead or dying arthropods and the occasional live prey which are retrieved vary in spatial and temporal location and in caloric value. Sweep samples of arthropods taken to assess resource distribution indicate a 2,000 fold potential difference in prey weight (<1 mg–2 g). *Lasius neoniger* has a monomorphic workers caste and appears to have adapted to this prey size variability behaviorally rather than through caste polymorphism (Oster and Wilson 1978). Cooperative foraging enables workers of *L. neoniger* to exploit energetically valuable prey. If the standard deviation of mean prey weight collected by individual foraging alone and by cooperative retrieval in addition to individual foraging is taken as an indicator of dietary breadth, then dietary breath is increased approximately 33 fold (1.6 vs 62.9 for individually retrieved and combined individual and social foraging, respectively). Foraging costs associated with cooperative retrieval appear to be lower than those of solitary foraging. The mean fresh weight of forage taken from single workers was 1.5 ± 1.6 mg, amounting to a total of 154.4 mg for 95 workers trips. The same prey weight, in the form of 2–3 single items could be retrieved in concert by approximately 30–40 workers, depending upon is resistance to retrieval. There appears to be an energetic advantage to cooperative foraging, reflected in reduced search and retrieval costs. The behavioral flexibility of social foraging also permits *L. neoniger* to utilize resources that have different "packaging", such as single, large prey, or large numbers of small prey. The plasticity of recruitment communication

Table 5. Comparison of prey movement rates for size classes I, II, and III (prey in size class IV were immovable). N = number of prey in each size class for which retrieval times were recorded. There is a significant decrease in prey movement rate as prey size increases. Statistical evaluation based on Mann-Whitney U-test

Prey size class	Mean prey weight (mg)	N	Range of retrieval times (sec)	Mean prey movement rate (cm/sec) ± standard deviation	P
I	8.04	18	25–390	0.088 ± 0.089	$0.02<p<0.5$
II	21.48	20	102–583	0.045 ± 0.026	$p<0.002$
III	131.56	9	575–4,605	0.005 ± 0.005	

therefore allows this species to acquire patchily distributed resources that occur in units of different sizes.

Oster and Wilson (1978) hypothesized that as prey size increases, so does the probability of interference competition. Clearly this relationship holds for *L. neoniger*. They also note that the main disadvantage to recruitment is the time that the process consumes, during which competitive interactions and/or predation on workers may occur. Species such as *L. neoniger*, which utilize prey that are large relative to the body size of workers, can be expected to evolve methods to decrease losses due to interference during recruitment. In *L. neoniger*, short-range recruitment appears to serve the function of decreasing the time during which a food item is unoccupied and therefore accessible to intra- and interspecific competitors. Prey movement is also critical. As is the case in *Novomessor*, prey must be moved before aggressive competitors or "repellent strategists" (small bodied, mass-recruiting species such as *Monomorium minimum* and *Iridomyrmex pruinosus*) arrive (Hölldobler 1973, 1982).

Although food resources are lost primarily to neighboring colonies of *Monomorium minimum, Myrmica americana, Tetramorium caespitum* and *Formica* schaufussi, losses also occur to conspecifics. The chemical signals of short-range recruitment that attract nearby workers do not appear to have any specificity. The hindgut trail pheromone of *L. neoniger* is colony-specific, but the specificity lies in the persistent component of the pheromone (Traniello 1980b). The ephemeral constituent(s) that regulate(s) recruitment attract(s) workers from any colony. Also, poison gland secretion (formic acid) mediates attraction and alarm in most formicine ants. Given the high density of *L. neoniger* colonies in a population, one might question why such a short-range system has evolved, since emitting non-specific attractants may have the effect of recruiting an individual from a neighboring colony, and hostility or prey loss may ensue. The answer to this question becomes apparent when the spatial patterning of foraging of *L. neoniger* colonies is considered. Workers travel along trunk trails which rarely intersect the trail systems of other colonies, and are usually divergent (Traniello 1980a). Therefore, it is likely that workers from the same nest will be in the vicinity of an individual discharging short-range recruitment pheromones. Loss of prey and worker injury or mortality primarily result from interspecific interactions. Of 80 prey offered, 49 attempts at usurpation were made by workers of *Myrmica, Tetramorium, Monomorium,* and *Formica*; 23 of these attempts (46.9%) were successful.

Workers of the sympatric endemic species *Formica schaufussi, Myrmica americana,* and *Monomorium minimum* are monomorphic, and although body size varies considerably among species (0.47–1.50 mm headwidth), differences in body size alone cannot adequately explain prey selection and food resource partitioning. I hypothesize that in the case of these generalist, opportunistic ant species, partitioning may be behavioral, based at least in part on differences in social methods of foraging. We have previously demonstrated the importance of recruitment behavior and prey defense in foraging success in *Monomorium minimum* (Adams and Traniello 1981). This species, which is the smallest bodied species in the guild, successfully utilized resources that are either very small (< 1 mg) or very large (> 500 mg). Here I report that the foraging behavior of *L. neoniger* (rapid recruitment/retrieval) also has a prey size dependent effectiveness. The social organization of foraging in these two species is quite different (recruitment of relatively small retrieval groups and cooperative carrying in the case of *Lasius*, mass recruitment and prey dissection in *Monomorium*). The resulting contrast in utilization mechanisms is striking: *Lasius* cannot rapidly dissect prey, and *Monomorium* cannot move prey, independent of prey sizes larger than the minute particles that single workers can retrieve. In these species protein food is channeled to the developing sexual brood (Wilson 1971), therefore increasing protein intake can increase the reproductive output of a colony. Interspecific competition for arthropod prey appears to be an important selective agent in the evolution of social behaviors associated with foraging. Cooperative foraging has been postulated or demonstrated to be important in ant community structure (Carroll and Janzen 1973; Culver 1974; Davidson 1977a, b). Among generalist ant species, social organization appears to play a primary role in resource acquisition.

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