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EMIGRATIONS AND ANTI-PREDATOR BEHAVIOR IN THE ANT GENUS *PHEIDOLE*

by

ROBERT DROUAL

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

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INTRODUCTION

The importance of predation in animals is reflected by the diverse anti-predator adaptations of prey. Animal defense mechanisms have been catalogued by Edmunds (1974) who followed a scheme first proposed by Robinson (1969) in dividing defense mechanisms into primary and secondary defenses. Primary defenses exist even in the absence of the predator and function to decrease the likelihood that an encounter will occur. These defenses include anachoresis (hiding in holes), crypsis, aposematism and Batesian mimicry. Secondary defenses, on the other hand, operate when an encounter with a predator has occurred and include flight, diematic behavior, thanatosis (feigning death), attack deflection and retaliation. Primary and secondary defenses often operate together in defensive systems. For example, many grasshoppers are cryptically colored to avoid detection but, when detection does occur, use their powerful legs to evade the predator (Edmunds 1974).

While some defense mechanisms are simple and straightfoward others can be quite complex and subtle. Some lizards dig special escape tunnels in their burrow systems for use when cornered underground by a predator (Pianka 1978). Termite workers guide nestmates to threatening stimuli by laying chemical trails, and when the stimulus is a breach in the wall of the nest, the recruited nestmates repair the wall (Stuart 1967). Animals often use subtle defense strategies to protect offspring from predators. Many birds use displays, such as broken wing displays, to distract predators from the nest (Armstrong 1947). The freshwater holostean fish *Amia* thrash about in the water feigning injury when a larger predatory fish approaches its young (Lagler et al. 1962). Digger wasps dig false burrows near the burrows in which they actually lay their eggs; since parasites lay eggs in both true and false burrows, the false burrows apparently function to reduce parasitism (Evans 1966).

Predators sometimes specialize on particular prey causing the evolution of enemy specific defenses. As the prey's defenses become more effective the predator may in turn evolve more effective attack strategies to overcome them. Thus predator-prey systems coevolve (Erlich and Raven 1964). The prevalence of coevolution is suggested by the many different animals that use enemy specific defenses. For example, gastropods typically defend against predators by withdrawing into their shells, however, when touched by a starfish which can extract them, *Nassarius* and *Struthiolaria* leap away by extending and flexing the foot (Feder 1972). A vertebrate example is the scorpion fish *Scorpaena guttata* which remains still and raises its protective spines when attacked by most predators but will flee from the octopus *Octopus bimaculatus*, a predator not deterred by the spines (Taylor and Chen 1969). Finally, the social wasp *Mishocyttarus drewseni* rubs a secretion from an abdominal gland onto the slender stalk of its comb nest which repels ants and thus helps prevent ants from reaching its immature offspring (Jeanne 1970).

To understand the selective forces shaping anti-predator behavior it is necessary to consider not only the advantages but the disadvantages of the behavior as well. The energy and time an animal invests in avoiding predation subtracts from that which could have been used for other activities. This tradeoff is clearly seen in animals like the ragworm Nereis and rabbits that remain in holes to avoid predators when they could be feeding instead (Broom 1981). This tradeoff is more subtle in other animals. For example, in animals that use chemicals to repel predators, such as lycid beetles which secrete a noxious fluid from glands in their hind femora when attacked by vertebrates (Linsley et al. 1961), the energy used to manufacture the chemicals must be diverted from other important functions such as reproduction. Batesian mimics exploit this situation by copying the aposematic coloration of the chemically repulsive species without incurring the synthetic costs of the chemicals themselves. This strategy is shown by cerambycid beetles that mimic the warning coloration of the lycid beetles without using the chemical defense themselves (Eisner et al. 1962). Defense mechanisms may also come into direct conflict with other essential systems. The West African lizard Agama agama is preyed upon by the shikra hawk Accipiter badius against which crypsis is advantageous. Although the female agamids are cryptically colored, the males, presumably influenced by sexual selection, are more brightly colored and are consequently more easily seen and caught by the hawk (Edmunds 1974).

Animals can decrease some of the costs associated with anti-predator behavior by forming social groups. For example, aposematically colored animals advertise their nasty properties to experienced predators but are conspicuously colored prey items to naive predators. This means that, unless the prey can demonstrate its noxious qualities before being fatally injured, a number of individuals will be killed in teaching the naive predator about the prey's inedibility. The naive predator may learn this faster when it encounters the prey in aggregations where the visual impact of the warning coloration is intensified (Edmunds 1974). Another, better documented, example concerns the relationship between the time devoted to feeding and that devoted to predator detection in the wood pigeon Columba palumbus. Murton (1968) found that birds in a flock spent a relatively larger proportion of their time feeding than isolated birds since they spent less time looking for predators. Hence, in groups the task of predator detection can be shared, and more time and energy devoted to other important activities.

Sociality also makes possible anti-predator strategies that are impossible to achieve on the individual level. When attacked by a predator individuals in a group will often suddenly scatter in random directions making it difficult for the predator to fixate on one. The predator hesitates and this provides more time for the prey to escape (Humphries and Drivers 1971). A cooperative defense can also be mounted by a group. In some social ungulates, such as the musk oxen Ovilos moschatus (Tener 1954), the eland Taurotragus oryx and the water buffalo Bubalus bubalis (Eisenberg and Lockhart 1972), the adults will interpose themselves between the young and a threatening predator. In chacma Papio ursinus and yellow P. cynocephalus baboon troops, dominant males bark to warn others in the troop of the presence of a predator and may approach it in a threatening manner (Hall 1960, Altmanns 1970). In this and many other examples (see Wilson 1975a) kin selection appears to operate, that is, the individuals that expose themselves to danger, do so to protect close relatives. Kin selection with its concomitant altruistic behavior reaches a pinnacle in social insects where the partial or complete sterility of the worker caste, combined with its high degree of relatedness to the reproductive caste, make extreme self-sacrifice in defense of the colony adaptive (Hamilton 1964).

Although the high degree of cooperation and self-sacrifice involved in colony defense in social insects has long been known, only recently has research begun to reveal some of its organizational complexities. Early research on defense behavior concentrated on the behavior of the worker subcaste specialized for defense (soldiers), and on the toxic and communicative properties of the contents of exocrine glands involved in defense (Wilson 1971). Except for the alarm-recruitment-construction defense of termites (Stuart 1967), colony defense in social insects was thought to be simply organized when compared to other behaviors such as foraging (Wilson 1971). Wilson's (1975b, 1976) discovery of the alarm-recruitment defense of *Pheidole dentata* changed this. In this defense minor workers guide nestmates, major workers in particular, to fire ant intruders by laying chemical trails. This constitutes an early phase of the defense in which an attempt is made to kill the fire ant scouts before they can recruit their own nestmates. If this fails, and more fire ants are recruited, nestmates continue to be recruited while the battle perimeter is drawn closer to the nest. Finally, if the *Pheidole* colony is about to be overwhelmed by the fire ants, the colony absconds from the nest. In this laboratory study it was further found that virtually only members of the fire ant genus *Solenopsis* elicited alarm-recruitment behavior. This led Wilson to hypothesize that selection pressure from competition with the native fire ant *S. geminata* caused the evolution of this complex defense.

Recently greater interest has been focused on how predation actually influences the organization of social insect societies. This research is notable in that, it tends to be conducted entirely in the field, and employs the comparative method. For example, Seeley et al. (1982) used a comparative approach to show how a wide array of colony characteristics including nest site, nest architecture, colony population size and worker defense behaviors can be seen as forming an adaptive complex for colony defense in three honeybee species *Apis florea*, *A. cerana* and *A. dorsata*. Jeanne (1975) also used a comparative approach to argue that ant predation is a major force in the evolution of nest structure in vespid wasps. To counter army ant predation, Chadab-Crepet and Rettenmeyer (1982) found that Neotropical polistine social wasps have evolved enemy specific alarm responses involving rapid nest evacuation. LaMon and Topoff (1981) related differences in colony defense strategies against army ants in three species of the ant genus *Camponotus* to differences in their worker caste polymorphism. In this thesis I present further evidence that army ant predation has exerted a considerable influence on colony organization in ants.

The primary focus of this study concerns the similar defensive systems used by *Pheidole desertorum* and *P. hyatti* against army ants of the genus *Neivamyrmex*, in particular *N. nigrescens*. The immediate alarm response of both *Pheidole* species to army ants is rapid nest evacuation. However, the overall defensive system is unique in that it implicates another behavior shared by *P. desertorum* and *P. hyatti*, frequent emigrations. Emigrations in social insects occur for a diversity of reasons (Smallwood and Culver 1979, Smallwood 1982), however, none has ever been related to an anti-predator function. This thesis presents evidence for such a function. To understand how emigrations can serve an anti-predator function it is first necessary to understand the peculiar characteristics of *P. desertorum* and *P. hyatti*'s emigrations and the complexity of their defense behavior. Consequently, this thesis is divided into three sections: the first section describes the temporal and spatial patterns of the emigrations; the second section describes and compares the nest-evacuation defenses used by both species against the army ant *N. nigrescens*; and the third section demonstrates how *P. desertorum*'s emigrations have an anti-predator function.

I. The Emigrations

Emigrations in ants are events typically caused by deteriorating conditions either within the nest, or in the territory of which the nest is a focal point (Wilson 1971). Because ant colonies usually inhabit durable nests in relatively stable habitats, emigrations should not occur frequently. Two groups of ants are exceptions to this generalization. One group occupies or constructs delicate or shallow nests, and when disturbed, quickly organize emigrations to other nests. These ants, which include Tapinoma melanocephalum, T. sessile, Paratrechina bourbonica and P. longicornis, have been characterized as "opportunistic nesters" (Hölldobler and Wilson 1977). In the other group, the legionary ants, frequent emigrations function to prevent the depletion of local food resources (Wilson 1971).

Neither P. desertorum or P. hyatti are opportunistic nesters or legionary ants but, as the following field study will show, nevertheless emigrate frequently. Furthermore, the spatial patterns in which these emigrations occur make them difficult to explain with any of the hypothesized causes for emigrations in ants. This section of the thesis presents data concerning the temporal and spatial parameters of these emigrations.

Methods

This study was conducted during June, July and August, 1980 at two different study sites. One site was an oak-juniper woodland on the grounds of the Southwestern Research Station of the American Museum of Natural History near Portal, Arizona (elev. 1646 m). The other site was a desert-grassland 8 km NW of Rodeo in Hidalgo Co., New Mexico (elev. 1250 m). At both sites winter (Dec., Jan., Feb. and March) and summer (June, July and Aug.) rainy seasons occur. On the oak-juniper woodland site, colonies of both P. desertorum and P. hyatti were marked; on the desert-grassland site only colonies of P. desertorum were marked. Colonies were identified according to the species (D - desertorum, H - hyatti), the date when found (Jn - June, Jl - July, A - August), and the order it was found on that date. For example, H-Jn18-2 is the second P. hyatti colony found on June 18.

Both species were active between 2000 and 0500 hr (MST). To document emigrations all colonies were inspected nightly between 2000 and 2400 hr. Days during which a colony either was raided by army ants or was still fragmented following an army ant raid were excluded. This was done in order not to confuse nest movements that were due to emigrations with those that were the result of nest evacuations (see Section III). About one-third of the emigrations were discovered in progress while in the remainder the colonies were found occupying a different nest. All nests were marked and the distances between them measured.

Results

Both P. desertorum and P. hyatti displayed considerable variation in their emigration frequencies (see Tables 1 and 2). Of the 26 P. desertorum and 24 P. hyatti colonies observed, one of each species (D-Jn11-2 and H-Jn17-1) never emigrated, while one P. desertorum colony (D-Jn20-1) emigrated 8 times, and one P. hyatti colony (H-Jn14-2) emigrated 16 times. However, both species emigrated at a surprisingly high frequency: the median emigrations per colony was 4 for P. desertorum and 6 for P. hyatti. When the percentages of days during which emigrations occurred were calculated for the colonies, and these percentages compared between species, no significant difference was found ($.1 > P > .05$, Wilcoxon two-sample test). The frequencies of days between emigrations for P. desertorum and P. hyatti are shown in Figures 1 and 2, respectively. As can be seen, both distributions are skewed strongly to the left with a surprisingly high number of emigrations occurring 1 to 2 days after the previous emigration. Again, no significant difference was found between the species with respect to these frequency distributions ($.4 > P > .2$, Wilcoxon two-sample test).

The emigration distances of both species were also variable. The mean emigration distance for P. desertorum was 2.5 ± 1.4 m (N = 102, range 0.4 - 6.9), and the mean emigration distance for P. hyatti was 1.8 ± 1.0 m (N = 137, range 0.3 - 4.9). The emigration distances of both species were well within their foraging distances. A posteriori estimates of foraging distances were obtained in two ways. First, distances between nests and peanut butter baits used to locate the nests were measured; this provided a rough estimate of the average foraging distance. For P. desertorum this distance was 5.6 ± 2.3 m (N = 15), and for P. hyatti, 3.2 ± 1.2 m (N = 15). Second, in P. hyatti preexisting recruitment trails were followed from the nest to the food source, and in P. desertorum, which appears to rely more on individual foraging along trunk trails, trunk trails were followed as far as possible. For P. desertorum the estimate obtained by this method was 10.5 ± 2.3 m (N = 8), and for P. hyatti, 5.3 ± 1.9 m (N = 5). The emigration distances were also considerably smaller than the distances between the nests of conspecifics. For P. desertorum the mean distance between nearest neighbors was 16.0 ± 2.7 m (N = 5), and for P. hyatti, 4.8 ± 1.0 m (N = 7). Despite the high emigration frequencies, colonies of neither species moved far from the nests at which they were first discovered: 49% of P. desertorum's emigrations, and 42% of P. hyatti's emigrations, were to former nests, and at the end of the study, 11 P. desertorum colonies and 5 P. hyatti colonies were at their first nests (Tables 1 and 2). This is also reflected in the crisscrossing patterns of emigrations in each species (Figs. 3 and 4).

A positive correlation was found between the daily ratios of colonies that emigrated to the total colonies observed and the daily rainfall for P. hyatti and P. desertorum in both habitats (P. hyatti: $r_s = .28$, $N = 66$, P. desertorum (oak-juniper woodland): $r_s = .25$, $N = 64$, P. desertorum (desert-grassland): $r_s = .32$, $N = 70$, Spearman rank correlation). The daily occurrence of emigrations and rainfall are shown graphically in Figures 5, 6 and 7. The effect of rainfall on emigration frequency can be most clearly seen with P. desertorum in the desert-grassland habitat (Fig. 7). During the 29 days before the first heavy rainfall on July 9 only three emigrations occurred, but within 9 days after this rainfall 29 emigrations occurred, and during this 9 day period 13 of the 15 colonies being observed on this site emigrated at least once. The sharp increase in emigration activity after the rain can possibly be explained by the effect of the rain upon the soil. Before the rains began the soil was very hard and compacted, but after the first heavy rainfall the soil loosened considerably. This undoubtedly made the excavation of new nests by the desert-grassland dwelling colonies much easier. The same reasoning can be extended to the oak-juniper woodland habitat. However, the greater amount of vegetation, the rockier soil and the generally moister conditions of this habitat probably account for the relatively higher emigration activity before the beginning of the rainy season.

During emigrations workers move in a column that connects the old nest with the new. The width of this column in P. hyatti was about 3 cm, while in P. desertorum this column was wider, reaching up to 15 cm. During observed emigrations the percentages of workers going to the new nest that carried brood were 33%, 46%, 47% and 52% in P. desertorum and 43%, 55% and 68% in P. hyatti. These percentages can be further broken down according to worker subcastes. Both species, as is typical in the genus Pheidole, have dimorphic worker castes. The larger, major workers have disproportionately large heads accomodating powerful adductor muscles for a pair of shearing mandibles. This subcaste has a greater propensity to engage in defense related tasks and is often referred to as the "soldier" caste (Wilson 1971)(For percentages of majors in worker populations see Table 5). The percentages of minors and majors that carried brood in these emigrations were, in P. desertorum, 28% - 55% (%minors - %majors), 51% - 28%, 47% - 46%, 53% - 41%, and in P. hyatti, 40% - 58%, 58% - 33% and 72% - 38%. Hence, the majors of both species participate considerably in the transport of brood. This contribution by the majors becomes particularly important when the colony contains female reproductive brood. In 5 P. desertorum emigrations 83 of 85 female reproductive pupae were carried by majors. Transport of these pupae require only one major as compared to 3 or 4 minors.
The queens of both species moved independently in the

emigrations although they were usually surrounded by a retinue of mostly minor workers who pulled them by the mandibles and antennae if they hesitated en route to the new nest. Alates also moved independently in the column although workers were sometimes observed carrying males. Both species therefore possess a number of behavioral adaptations that make their emigrations orderly and efficient.

A number of phenomena related to the high emigration frequency of these species were observed. One colony of each species (D-Jn20-1 and H-Jn19-2) performed what can be called aborted emigrations. In these cases, the colony was observed emigrating to a new nest but on the following night was still at the old nest. One P. desertorum colony (D-Jn25-1) appeared to perform two emigrations in one night: on Aug. 17 the colony was observed emigrating from nest 2 to nest 1, but on the following night was at nest 3 (Fig. 3). On a number of occasions an emigration could be predicted in advance by the colony's excavation activity at another site. For example, before colony D-Jn12-2 emigrated to its second nest on Aug. 17, workers excavated at the site for 13 days. However, two colonies of each species excavated at sites to which they did not emigrate although they emigrated later to other nests.

Discussion

The need to emigrate is a contingency all species of ants can be expected to face (Wilson 1971). However, only legionary ants (Wilson 1971) and opportunistic nesters are expected to emigrate frequently. Most ant species build or choose nest sites that are relatively long-lived and not easily disturbed. Among these species emigrations can be due to an abiotic factor such as shading (Brian 1956, Carlson and Gentry 1973), drought or frost (Brian 1952), or to some biotic factor such as inter- and intra-specific competition (Holldobler 1976, Waloff and Blackith 1962, Brian 1952, Brian et al. 1965). Because disturbances due to these factors are infrequent, emigrations caused by them should also be infrequent.

The view that emigrations occur infrequently among ants was challenged by Smallwood and Culver (1979). These investigators conducted a study in which they found that _Tapinoma_ _sessile_ and _Aphaenogaster_ _rudis_ emigrated frequently. Because _T. sessile_ and _A. rudis_ choose different nesting sites and have different life styles they further deduced that emigrations occur more frequently among ants than had been previously thought. However, the fact that _T. sessile_ is an opportunistic nester which is expected to emigrate frequently weakens their argument.

It is difficult to apply any of the known causes of emigrations in ants to explain the frequent emigrations of _P. desertorum_ and _P. hyatti_. The nests of both species are excavated in the soil to a depth of 30 to 40 cm (based on excavations in oak-juniper woodland), and hence are not easily disturbed. Shading is obviously not a factor in the desert-grassland habitat, and is negligible in the oak-juniper woodland where the canopy is not extensive. Permanent deterioration of the nest as a cause is eliminated by the fact that colonies return to former nests. Since both species emigrate in clumped patterns it is unlikely that the emigrations change foraging space. Moreover, the foraging distances of P. desertorum and P. hyatti are considerably longer than their emigration distances. It is also unlikely that the emigrations increase the efficiency of resource exploitation since both species exploit food sources that are unpredictable in time and space: although P. desertorum has been characterized as a seed eater (Davidson 1977) both species appear to prey and scavenge heavily upon a diversity of arthropods.

Although a precise analysis was not performed, both species appeared to be overdispersed in their distributions. This raises the possibility that the emigrations are due to intra-specific interactions. In P. desertorum, however, the mean distance between nearest neighbors was 6 times greater than the mean emigration distance, and large-scale aggressive interactions between neighboring colonies were never seen. In P. hyatti, on the other hand, the evidence for inter-colony interactions is somewhat more compelling. The mean distance between nearest neighbors was only 3 times greater than the mean emigration distance, and one P. hyatti colony actually emigrated 2.3 m into a nest that had been vacated four days before by a neighboring colony. However, again large-scale aggressive interactions were not observed, and in four cases where the change in the distance of the occupied nests of nearest neighbors was measured after an emigration, only once did the distance increase, and then by only about 0.1 m.

A possible anti-predator function for the emigrations is suggested by the defense behavior P. desertorum and P. hyatti use against army ants, especially N. nigrescens. Mirenda et al. (1980) found that P. desertorum and P. hyatti are among the prey species most frequently taken by N. nigrescens. Observations made during the course of this study confirm that N. nigrescens preys heavily upon both species (Tables 3 and 4). In fact, some P. desertorum colonies were raided repeatedly by the same N. nigrescens colony which entered the statary phase of its raiding cycle in a bivouac nearby. On two occasions a N. nigrescens colony bivouacked in the evacuated nest of a P. desertorum colony. One P. hyatti colony was raided by two species of Neivamyrmex. Of these colonies, only five appeared to be completely eliminated by the army ants. Part of the reason for this is the nest-evacuation defense P. desertorum and P. hyatti use against army ants. The organization of this defense will be discussed next.

II. The Nest-Evacuation Defense

Colony defense in social insects typically involves tactile, auditory or chemical signals that alert nestmates to the existence of threatening stimuli, and the alerted nestmates respond by either concentrating aggressively on the threat, or fleeing from it (Wilson 1971). However, as demonstrated by Pheidole dentata's alarm-recruitment defense (Wilson 1975b, 1976), colony defense can sometimes attain a high level of complexity. Moreover, the complexity of P. dentata's defense appears to be the result of selection pressure from competition and predation by the fire ant S. geminata (Wilson 1975b, 1976) and other members of the genus Solenopsis (Feener 1981). This suggests that the more complex defense systems in social insects may have evolved against their most frequent and important predators.

One of the most important predators of social insects are army ants of the subfamilies Dorylinae and Ecitoninae (Schneirla 1971, Wilson 1971). The impact of army ant predation is reflected in the anti-predator adaptations of prey which, among social insects, usually involve rapid-detection colony responses (Chadab 1979, LaMon and Topoff 1981). As already shown, army ants of the genus Neivamyrmex, particularly N. nigrescens, are important and frequent predators of P. desertorum and P. hyatti. N. nigrescens elicits similar nest-evacuation defenses from both Pheidole species exhibiting a degree of organization that merit them special consideration over the more simply organized panic-alarm defense systems of formicine ants (Regnier and Wilson 1969, Wilson and Regnier 1971).

The section concerns the organization of the nest-evacuation defense in _P. desertorum_ and _P. hyatti_. The results of experiments are presented that clarify, what cues are used for army ant detection, what signals are involved in alarm communication, and the nature of the trail-following behavior that occurs during nest evacuations. How the worker subcastes of each species contribute to the actual evacuation of brood is analyzed and compared, and related to differences between the two species in their nests, and the running speed and combat ability of their workers. Finally, the enemy specificity of the defenses are revealed by field and laboratory tests with different species of _Neivamyrmex_. Besides _P. desertorum_ and _P. hyatti_, the enemy specificity of the nest-evacuation defenses of two other species, _P. rugulosa_ and _Solenopsis xyloni_, are included.

Methods

This study was conducted during June, July and August, 1979, 1980 and 1981 at the same study sites mentioned in the previous section. All procedures and experiments were performed between 2000 and 0200 hrs (MST) using a headlamp fitted with a red filter when prolonged observation was necessary.

Brood carrying during nest evacuations was quantified by placing a plexiglass cylinder (Ø 30 x 21 cm) around the nest entrances of colonies in the field. A nest evacuation was elicited by releasing about 50 N. nigrescens workers within the cylinder. Because the inner wall of the cylinder was coated with Fluon®, the evacuating workers could not escape from the area enclosed by the cylinder, and the workers carrying and not carrying brood could be aspirated separately and counted.

Laboratory colonies, unless otherwise stated, were maintained in petri dish nests (Ø 15 cm) provided with a 4 mm base of moist dental stone. The nests were connected with plastic tubing (Ø 12 mm) to plexiglass foraging arenas (57 x 46 x 15 cm). The inner walls of the foraging arenas were coated with Fluon®, and the floors were covered with a sheet of filter paper. The colonies were fed termites and other arthropods.

The running speed of Pheidole minors was measured in the laboratory in the following manner. An emigration was induced by suddenly exposing a colony in a desiccated nest to light, and connecting it to a moist, dark nest by a plastic tube (Ø 13 mm). An emigration began quickly to the new nest, and the minors leaving the new nest to retrieve brood from the old nest were timed over a distance of 40 cm. Only runs that were continuous and unobstructed were timed to completion.

Combat trials were made by aspirating the workers into plastic vials (0 1.5 x 5.0 cm) that contained a small wad of moistened cotton. These vials were then laid on their sides, and survivorship was determined after 24 hrs. A worker was deemed to have survived if it could still move normally.

To perform enemy specification tests in the field, an empty and open vial was placed 10 cm from the nest entrance of the prey species, and a five minute baseline count was taken of the major workers that left the nest. The vial was then replaced with an open vial containing a specific number of Neivamyrmex workers. After a worker of the Pheidole species contacted an army ant, another 5 minute count was taken. If during this count 10 or more workers carrying brood left the nest the response was classified as "brood evacuation". If this did not occur, and the number of majors that left the nest were twice, and at least 10 greater than the baseline count, the response was classified as "majors leave the nest". If the response did not fall into either of the above two categories, it was classified as "no apparent response". With S. xyloni, since there is no distinct major worker subcaste, responses were placed in only the "brood evacuation" and "no apparent response" categories.

Laboratory enemy specificity tests were performed in a similar manner except that the counts were 15 minutes instead of 5. Because of the organization of nest evacuation in P. desertorum and P. hyatti (see below) in these tests the brood evacuation responses were divided into two more categories: when 10 or more workers carrying brood left the nest but did not go further than 10 cm from the nest entrance the response was classified as an "alert phase" of nest evacuation; when 10 or more workers carrying brood did go further than 10 cm from the nest entrance, the response was classified as an "evacuation phase" of nest evacuation. Since events in the nest were visible, the "no apparent response" category was changed to "no response".

Except for N. nigrescens, all the Neivamyrmex species were extremely hard to find, and because of this many of the sample sizes are small. To make statistical comparisons, the results of the enemy specificity tests were reduced to a 2 x 2 contingency table by grouping responses into brood evacuated and no brood evacuated categories, and grouping together tests done with different numbers of the same species, and then using Fisher's exact probability test. As will be noted, when there were large discrepancies in the number of workers used in the tests, some tests were excluded to make the comparison fairer. However, this was only done when the elimination of the data favored the null hypothesis.

Other statistical tests used in this section are Student's t-test, chi-square, anova and Student-Newman-Keuls tests. All data expressed as percentages were subjected to an arcsine transformation before statistical evaluation. The null hypothesis was rejected when $P < .05$. Further details concerning methods are given with the results.

Results

Organization of the Defense

P. desertorum and P. hyatti react to the presence of N. nigrescens by rapidly evacuating their nests. Hundreds of workers carrying brood, and sexuals, if present, rush out of the nest. Despite the rather sudden nature of this defense it can be divided into two distinct phases of intensity. In the weaker, or "alert" phase, the ants that leave the nest remain massed around the nest entrance in close contact with one another. Colonies of both Pheidole species were frequently seen in this phase of the defense in the field before a column of N. nigrescens was observed nearby. The mean distance of the army ant column from P. desertorum colonies in this phase was 4.8 m (range 2.4 - 9.1, SD = ± 2.2, N = 9). The alert phase appears to prepare a colony for a full scale evacuation without committing it to one while the army ants are still some distance from the nest. If the army ants do not discover the nest, the alert ends and the Pheidole reenter the nest. If the army ants do draw nearer to the nest so that a raid becomes imminent the stronger, or "evacuation" phase, of the defense occurs. In this phase many workers run from the nest. During this phase it was determined that in 5 P. desertorum colonies a mean of 2,214 (SD = ± 1,102) workers left the nest, while in 5 P. hyatti colonies a mean of 1,190 (SD = ± 1,207) workers left the nest. In 47 P. desertorum colonies where all the workers in the nest were collected by repeatedly causing nest evacuations, the mean number of workers in the nest was found to be 2,583 (SD = ± 1,441)(data collected in 1982). Hence, at least in P. desertorum, it appears that a considerable proportion of the workers leave the nest during this phase.

A considerable amount of the colony's brood may be left behind in the nest after an evacuation. For one colony of each species an accurate estimate of the percentage of brood remaining in the nest after an evacuation was obtained when the foragers that returned to the nest, and any workers that remained behind in the nest, began emigrating to another nest. The brood carried to the new nest was then counted. In P. desertorum 10%, and in P. hyatti 36% of the brood was left behind. Further estimates for four other P. desertorum colonies were obtained by inducing further evacuations after allowing the colonies to resettle. These estimates were 1%, 15%, 18% and 56%. Hence it appears that even if the Pheidole colony can successfully evacuate before a N. nigrescens raid, it is unlikely that the army ants will go away "empty handed".

The alarm communication that initiates the defense was observed in laboratory nests of both species. Upon entering the nest after contacting an army ant in the foraging arena, the minors flicked their gasters upward as they ran into their nestmates while rapidly palpating them with their antennae. Alarm appeared to follow in the wake of their erratic paths. To test if volatile alarm pheromones were being released by the minors the following experiment was performed.

Two rectangular red plexiglass tubes (17 x 1.5 x 1.5 cm) were assembled side by side (Fig. 8). The tubes were placed 4 mm apart and their adjacent walls were made only of fine wire mesh. The space between the wire mesh walls was closed off so that the diffusion of a volatile substance was restricted to the interior spaces of the adjacent tubes. Each tube served as a nest for a different <u>Pheidole</u> colony. An evacuation was elicited in one of the colonies (control colony) by releasing 50 <u>N. nigrescens</u> workers in its foraging arena. Five minutes after an evacuation began in the control colony the entrances of both colonies' nests were plugged and the workers carrying brood in each foraging arena were counted.

In these experiments workers carrying brood consistently left the nest of the control colony (<u>P. desertorum</u>: $\overline{X} = 139$, SD = ± 73, N = 6; <u>P. hyatti</u>: $\overline{X} = 78$, SD = ± 42, N = 6) but none ever left the nest of the experimental colony. Indeed, the experimental colonies never showed any signs of alarm. These results do not eliminate the possibility that short range alarm pheromones are being used with the tactile signals. However, it appears that alarm pheromones with the active spaces expected of panic-alarm pheromones (see Wilson 1971) are not being used alone to communicate alarm.

During an evacuation the ants do not run from the nest in random directions but appear to follow their own chemical recruitment trails. This hypothesis was tested in the field in the following manner.

Four plastic cylinders (Ø 18 x 5 cm) with notches (1 x 2 cm) cut in their bases were arranged 1 meter from the nest entrance so that their centers lay over imaginary perpendicular axes that intersected at the nest entrance. The cylinders were oriented so that the notches faced the nest entrance. The inner walls of the cylinders were coated with Fluon® to prevent escape from the cylinders except by means of the notches. The placement of the cylinders around the nest was chosen randomly from three possible arrangements: (1) at the four major compass points, (2) 30 degrees clockwise from the major compass points, (3) 60 degrees clockwise from the major compass points. One cylinder was chosen randomly to be the experimental cylinder. The deposition of a recruitment trail leading into this cylinder was induced with a peanut butter bait. The bait was then removed and 10 minutes later about 50 *N. nigrescens* workers were released near the nest to cause an evacuation. Ten minutes after the evacuation began the workers within the cylinders were aspirated and the number carrying brood counted.

The results of these experiments clearly show that both *Pheidole* species follow foraging trails during nest evacuations. For *P. desertorum* a mean of 122 workers with brood (SD = ± 57, N = 5) were aspirated from the experimental as compared to a mean of 15 workers with brood (SD = ± 16, N = 5) that were aspirated from the 3 control cylinders combined. For P. hyatti, a mean of 47 workers with brood (SD = ± 16, N = 5) were aspirated from the experimental cylinder while a mean of 3 workers with brood (SD = ± 3, N = 5) were aspirated from the control cylinders. Each replication was subjected to the chi-square test and the differences were found to be highly significant (P. desertorum: $\chi^2 \geq 147$, $P < .001$; P. hyatti: $\chi^2 \geq 91$, $P < .001$).

The source of recruitment trails in P. desertorum has been shown to be the poison gland (Holldobler and Moglich 1980). This was found to be true in P. hyatti also. To test whether evacuating Pheidole would follow artificial trails made with this gland, 10 poison glands were dissected from minor workers and crushed in 2 ml of ether. Twenty microliters of this extract was dispensed with a syringe along a 50 cm line beginning at the nest entrance. A control trail of pure ether was made in a symmetrical fashion. An evacuation was then induced by releasing 10 N. nigrescens workers into a container connected to the nest, and for a 5 minute period the workers carrying brood that followed each trail were counted. In P. desertorum a mean of 41 (SD = ± 24, N = 5), and in P. hyatti a mean of 35 (SD = ± 16, N = 5) workers carrying brood followed the experimental trail, while no workers of either species followed the control trail (P. desertorum: $t = 3.70$, $P < .01$; P. hyatti: $t = 4.89$, $P < .01$). Similar tests were done with the poison glands of majors (N = 4 for P. desertorum and N = 3 for P. hyatti) and the Dufour's glands and hindguts of minors (N = 2 for each gland and species) and yielded negative results.

One curious aspect of the organization of the defense is that the queen rarely leaves the nest. This remained true even with colonies in laboratory nests where the queen was not very far from the nest exit. During these evacuations the workers rapidly picked up brood and left the nest but virtually ignored the queen. However, in 3 out of 3 P. desertorum colonies and 1 out of 2 P. hyatti colonies that had been raided by N. nigrescens, a queen was either seen during an emigration, or collected when excavating the colony. Possibly the queens use tonic immobility or some other ploy to avoid being taken by the army ants.

Cues Involved in Army-Ant Detection

A single N. nigrescens worker detected near the nest is sufficient to cause nest evacuation in both Pheidole. The cues used in detecting the presence of N. nigrescens were investigated in the following series of experiments.

N. nigrescens uses mass chemical recruitment to conduct raids (Topoff et al. 1980). To test if the presence of a chemical trail laid by N. nigrescens would elicit a nest evacuation, a strip of filter paper was placed on the bottom of a tube (Ø 3.0 cm) connected to a box containing *Pheidole* brood (booty box). The open end of this tube was then connected to a box containing a *N. nigrescens* colony (nest box). The army ants quickly formed a raiding column over the strip into the booty box. Immediately after the army ants carried the *Pheidole* brood into its nest box, the strip was removed, any army ants still on the strip were shaken off, and the strip was placed directly in front of laboratory nest entrances in the path of *Pheidole* foragers. This procedure did not cause alarm or induce evacuations (N = 3 for each species).

To test if direct contact with the exocuticle of *N. nigrescens* alone would cause alarm, freshly killed (by freezing) *N. nigrescens* workers were placed within 10 cm of the nest entrance of field colonies. This procedure also failed to elicit colony alarm (N = 8 for *P. desertorum*, and N = 6 for *P. hyatti*). Freshly killed *N. nigrescens* workers introduced directly into laboratory nests were picked up and carried to refuse heaps by the workers (N = 5 for each species).

Another possibility was that the detection cues involved direct contact with moving army ants. To test this hypothesis in the field, a freshly killed *N. nigrescens* worker was held (with no. 5 watchmakers forceps) and moved laterally in front of *Pheidole* minors near the nest entrance. For each colony this procedure was repeated with at least 20 workers unless brood evacuation occurred. Brood evacuation was judged to have occurred if at least 10 workers carrying brood emerged from the nest. As a control the same procedure was followed with an empty pair of forceps. In 10 P. desertorum and 3 P. hyatti colonies tested, all except one P. desertorum colony evacuated brood with the experimental procedure. The control procedure did not cause brood evacuation. The same experiment was performed with majors of both species and yielded negative results (N = 5 for each species). The results remained negative even when a live N. nigrescens worker was used (N = 5 for each species). The majors tended to clamp onto the N. nigrescens worker, or to run around in excited loops, but even when the major did reenter the nest after contacting the army ant, brood evacuation did not follow. These results show that only minors can communicate the alarm that initiates nest evacuation.

Caste Polyethism During Nest Evacuations

During a nest evacuation there are primarily two tasks that workers can perform, brood evacuation, and combat with army ants. The proportions of each subcaste performing these tasks were determined in nest evacuations of both species. As expected, a high proportion of minors of both Pheidole species evacuated brood during these evacuations (Fig. 9), and no significant difference was found between the species in this respect (t = 1.20,

$.2 < P < .4$). However, the high proportion of majors that evacuated brood in both species was surprising. Virtually only majors evacuated the large and bulky female reproductive brood although majors also evacuated worker brood. A significantly higher proportion of P. desertorum majors than P. hyatti majors evacuated brood ($t = 3.81$, $P < .01$). The reason for this interesting difference is revealed by comparing the temporal organization of nest evacuations in each species.

P. hyatti's nest evacuations can be easily divided into two stages. During the first stage, which lasts about 20 seconds, the workers that leave the nest do not carry brood and include a high proportion of majors. During the second stage, the majority of workers that leave the nest carry brood. These stages also occur in P. desertorum, however the first stage is shorter, occurring within 10 seconds. This can be seen in the graphic representations of filmed evacuations shown in Figure 10. Note that in P. hyatti's evacuation 20 seconds passed before a minor carrying brood left the nest, while in P. desertorum's evacuation a major left the nest with brood within 3 seconds. The majors that leave the nest without brood run around in excited loops until they encounter army ants. In this way they establish a battle perimeter that gives their nestmates more time to evacuate. This tactic is apparently more important in P. hyatti than in P. desertorum. The reason for this is suggested by another comparison.

In *P. desertorum*'s evacuation 1,758 workers left the nest within 2 minutes and the evacuation virtually ended. In contrast, in *P. hyatti*'s evacuation, after almost 3 minutes, only 655 workers left the nest and the evacuation was still proceeding. Hence *P. desertorum*'s evacuations are faster than *P. hyatti*'s. For *P. hyatti*, during an actual army ant raid, the problem of getting as many workers and brood out of the nest before the army ants enter it is more acute so that a greater number of majors are sacrificed in detaining the army ants.

One of the reasons *P. hyatti*'s evacuations are slower may be due to differences in the subterranean nests of the two species. The nest entrances of *P. desertorum* are significantly larger than those of *P. hyatti* (Table 5). *P. hyatti*'s smaller nest entrance, in the very least, restricts the outward flow of traffic during an evacuation by a bottleneck effect and may reflect deeper differences in the structure of the nest that also decrease evacuation speed. Another reason *P. hyatti*'s evacuations are slower is simply due to the fact that *P. hyatti* workers run slower than *P. desertorum* workers (Table 5). This is not surprising since *P. desertorum* workers are larger and appear to have proportionately longer legs than *P. hyatti*.

The effectiveness of *P. hyatti*'s delaying tactic early in the evacuation depends upon the combat ability of its workers. Since both *Pheidole* species normally encounter *N. nigrescens* in large numbers, combat tests were done by pitting 10 workers of a specific subcaste against 10 N. nigrescens workers. It was found that all Pheidole subcastes differed significantly in their survivorship in these encounters ($P < .05$, Student-Newman-Keuls)(Table 6). When placed in the order of increasing survivorship the order is: P. desertorum minors < P. hyatti minors < P. desertorum majors < P. hyatti majors. The ability of the subcastes to inflict casualities on N. nigrescens was significantly different only between the subcastes, with the majors of both species inflicting higher casualities on N. nigrescens than the minors ($P < .05$, Student-Newman-Keuls). The inferior survivorship of P. desertorum workers may have been due to their larger size and proportionately longer appendages providing the army ants with a greater surface area to grasp and sting.

Enemy Specificity

In addition to P. desertorum and P. hyatti, field tests were done with P. rugulosa and Solenopsis xyloni. The results of these tests are presented in Table 7. The responses of each prey species will be discussed in turn.

For both P. desertorum and P. hyatti, the response to N. nigrescens serves as a standard against which the responses to other Neivamyrmex species can be compared with respect to brood evacuation since only one N. nigrescens worker is necessary to elicit brood evacuation. Both N.

fallax and *N. opacithorax* also elicited brood evacuation. However, even when tests with 100 *N. nigrescens* workers were excluded, *N. opacithorax* was found to be significantly less effective than *N. nigrescens* in eliciting brood evacuation ($P < .01$). Although *N. opacithorax* preys upon *P. hyatti* (see Table 4), because of its smaller size (worker length range, 2.3 - 4.6 mm, Borgmeier 1955) when compared to *N. nigrescens* (worker length range, 3.3 - 6.1, Schneirla 1971), *N. opacithorax* probably locates and raids *P. hyatti* nests less quickly than *N. nigrescens* and consequently is less of a threat.

Neither *N. harrisi* nor *N. texanus* caused brood evacuation. The differences between each of these species and *N. nigrescens* were significant (*N. harrisi*: $P < .01$; *N. texanus*, after tests with 100 *N. nigrescens* workers were excluded: $P < .001$). *N. harrisi* has been observed to prey only on *S. xyloni* (Mirenda et al. 1980), and did very poorly in combat tests with *P. hyatti* majors (Table 8). *N. texanus* and *N. nigrescens* are morphologically almost identical (Watkins 1976). However, they differ behaviorally in that *N. texanus* is more hypogaeic and is rarely seen on the surface. Hence it appears that neither *N. harrisi* nor *N. texanus* is a threat to *P. hyatti*.

All *Neivamyrmex* species caused brood evacuations with *P. desertorum*. However the sample sizes were not large enough to make meaningful comparisons except between *N. harrisi* and *N. nigrescens* where there was a significant difference ($P < .05$). The adaptive significance of this is similar to that with P. hyatti.

With P. rugulosa only N. fallax elicited brood evacuation. The difference between N. fallax and each of the other Neivamyrmex species were significant ($P < .01$). The difference between N. fallax and N. nigrescens is of particular interest since both prey on P. rugulosa but this ant defends differently against each. Against N. nigrescens, P. rugulosa majors try to prevent the raiders from entering the nest by blocking the small nest entrance with their heads. Only 2 to 3 N. nigrescens workers can squeeze through the small (1 to 2 mm) entrance at a time, but they nevertheless attempt to counter this strategy by pulling the majors out of the nest until the entrance is clear (Mirenda et al. 1980). N. fallax, like N. opacithorax, is smaller than N. nigrescens (worker length range, 2.3 - 4.6, N = 56) and this may make it better able to penetrate P. rugulosa's nest-blocking defense. Another possibility is that the small P. rugulosa workers (major length: 3.62 mm, minor length: 2.42 mm, Gregg 1958) can better outrun the smaller N. fallax workers and this makes the nest evacuation strategy more feasible against it. Because N. harrisi does not prey on P. rugulosa it is not possible to infer that P. rugulosa uses a nest blocking strategy against it.

N. harrisi elicited brood evacuation from S. xyloni but N. nigrescens elicited an aggressive response. This difference was significant ($P < .01$). S. xyloni workers effectively used their stings to attack and kill N. nigrescens workers. Of the four prey species used in this study only S. xyloni is not preyed upon by N. nigrescens. In fact, N. nigrescens actively avoids S. xyloni. For example, the release of S. xyloni workers near a N. nigrescens column caused the traffic in it to cease temporarily for more than a meter in both directions ($N = 5$). In contrast, the release of S. xyloni workers near a N. harrisi column caused the traffic in it to increase ($N = 3$). The difference in the behavior of these Neivamyrmex species to S. xyloni is underscored by the results of combat tests between them and S. xyloni (Table 8). The survivorship of N. nigrescens in these combat trials was significantly less than that of N. harrisi ($t = 7.70$, $P < .001$).

The results of laboratory tests with P. desertorum and P. hyatti are presented in Table 9. In P. hyatti the brood evacuation responses elicited by N. nigrescens were significantly different from those elicited by N. fallax ($P < .05$), N. harrisi ($P < .001$) and N. texanus ($P < .01$). In P. desertorum no significant difference was found between the brood evacuation responses elicited by N. nigrescens and N. harrisi ($P = .095$). With N. fallax and N. opacithorax the sample sizes of 1 are too small to make a meaningful test of significance possible.

Although the difference between P. desertorum and P. hyatti in the responses elicited by N. harrisi were not significant (P = .163), the results nevertheless suggest that an interesting difference does exist between them. With P. hyatti 3 of the 5 tests with 100 N. harrisi workers did not cause any response. In fact, in one of these tests, a N. harrisi worker actually entered the nest without causing great alarm. In contrast, with P. desertorum, when N. harrisi did not elicit brood evacuation it at least caused majors to leave the nest. Again, N. harrisi never elicited brood evacuation from P. hyatti in either field or laboratory tests while with P. desertorum it sometimes did.

Discussion

In social insects nest evacuation is an extreme and often costly form of colony defense. Social wasps that use it to avoid army ant predation are physically unable to fly with their brood and must abandon them (Chadab 1979, Young 1979). Ants can carry their brood out of the nest but the colony must then cope with the disorganization that follows. The workers, brood and alates that were safely concentrated in the chambers of the nest become scattered over the surface, exposed to environmental stresses and other predators. The various properties of the nest-evacuation defenses in P. desertorum and P. hyatti counter the disorder inherent in this form of defense.

Both phases of the nest-evacuation defense possess elements that increase colony cohesiveness. In the alert phase, the colony adopts a high state of readiness which increases the speed of the evacuation if it becomes necessary. However, because the workers do not stray far from the nest entrance, and remain in close contact with one another, they can also quickly reenter the nest if the danger passes. In the evacuation phase, the trail-following behavior of the ants also reduces disorder. By following trails, segments of the colony flee in the same direction and scatter within more limited areas. This results in a more clumped dispersion of the ants which facilitates communication among nestmates. Sometimes the trail is an emigration trail that guides the fleeing ants to their previous nest. Since there is no evidence that _N. nigrescens_ can follow _Pheidole_ chemical trails, a second raid on the alternate nest does not inevitably follow. After the army ants have withdrawn, the trails are used by the workers to return to the evacuated nest. The use of detection cues that in nature can only indicate the presence of live army ants enables the colony to return more quickly to the nest since other detection cues, such as army ant trails or cadavers, remain after the army ants have left.

The failure to demonstrate the use of volatile alarm pheromones in nest evacuations was at first perplexing. However, the biphasic organization of the defense can be better explained by a communication system that involves short range signals. To be successful a nest evacuation must occur rapidly. This could be achieved by the emission of volatile alarm pheromones but this would then make it less possible for the minors to modify the intensity of the alarm according to the extent of the threat, that is, the distance of the army ants from the nest. By using short range signals, either tactile alone, or tactile signals combined with short range alarm pheromones, the minors can vary the intensity of the alarm without greatly decreasing the speed of the communication.

The amount of brood that is saved during a nest evacuation is augmented by the considerable proportion of majors that evacuate brood in both species. Further, the majors are indispensable for the evacuation of the bulky female reproductive brood. The behavioral flexibility of the majors must be indicative of the great selection pressure on these species to increase the effectiveness of the defense. In P. hyatti, because of other constraints, the effectiveness of the defense is apparently increased by sacrificing a larger proportion of the majors in the early part of the evacuation in detaining the army ants.

The selection pressures exerted by army ants of the genus Neivamyrmex on P. desertorum and P. hyatti is also reflected in the enemy specificity of their nest-evacuation defenses. For both Pheidole species N. nigrescens is undoubtedly the most threatening Neivamyrmex species. This is reflected by the fact that only one N. nigrescens worker released near the nests of these species is sufficient to cause brood evacuation. N. fallax and N. opacithorax also elicit brood evacuation from these *Pheidole*, but less intensely, and with less consistency. Both *Neivamyrmex* species are smaller than *N. nigrescens* and may prey more heavily on the smaller *Pheidole* species, some of which appear to be more abundant than *P. desertorum* and *P. hyatti*. *N. harrisi* also elicited brood evacuation from *P. desertorum*, though less intensely than *N. nigrescens*. However, with *P. hyatti*, at most it only caused majors to leave the nest and attack it, and sometimes caused no alarm at all. In the desert-grassland site, *N. harrisi* was the second most frequently seen *Neivamyrmex* species and was observed to prey only on *S. xyloni* which is an abundant species in this habitat (Davidson 1977). Hence it appears that for both *Pheidole* species the ability to discriminate between *N. nigrescens* and *N. harrisi* has considerable adaptive value. Why, however, *P. desertorum* should react with more alarm to *N. harrisi* than *P. hyatti* is an intriguing question.

In *P. hyatti*, the difference in the responses elicited by *N. nigrescens* and *N. texanus* is not only another demonstration of this species ability to discriminate between a threatening and a nonthreatening species, but also suggests what sensory cues are involved in this discrimination. The detection of *N. nigrescens* by *P. hyatti* involves contact with the moving surface of a *N. nigrescens* worker. Since only the subtlest morphological characteristics differentiate *N. nigrescens* from *N. texanus* (Watkins

1976), it can be inferred that the discrimination is achieved through chemosensory organs. This suggests that both *P. desertorum* and *P. hyatti* have become particularly sensitive to chemicals on the exocuticle of *N. nigrescens* that are quantitatively or qualitatively unique to it. Differences between *P. desertorum* and *P. hyatti* in what chemicals are used for detection cues may explain differences between them in their ability to "recognize" non-threatening species like *N. harrisi*, particularly if there are only quantitative differences between *Neivamyrmex* species in the chemical cues on their surfaces.

Enemy specificity in the nest-evacuation defense of the other two prey species was even more marked. With *S. xyloni* there is a sharp difference not only in *S. xyloni*'s responses to *N. nigrescens* and *N. harrisi* but also in how these *Neivamyrmex* species respond to it: *N. nigrescens* avoids it while *N. harrisi* preys, perhaps exclusively, on it. This food niche separation between *N. nigrescens* and *N. harrisi* is reflected in the different combat abilities of these species with *S. xyloni*. The favored prey of *N. nigrescens* defend themselves mainly with shearing-type mandibles which may be used with chemical sprays. In contrast, *S. xyloni* defends itself mainly with a potent sting. *N. harrisi* can deal with this sting much more effectively than *N. nigrescens* but is hopelessly outmatched against the mandibles of *P. desertorum* and *P. hyatti* majors. Perhaps *N. harrisi* has evolved a hard, yet brittle, exocuticle that is less penetrable to stings but more vulnerable to the tensile pressures exerted by shearing mandibles. P. rugulosa exhibits the greatest flexibility in its defense behavior against Neivamyrmex species: not only can it discriminate between two different Neivamyrmex species but it also uses an entirely different defense strategy to deal with each.

The selectivity of these prey species in their defense response to different Neivamyrmex species however is probably not only a consequence of the predation pressure itself but also of the costly nature of the nest-evacuation defense. The inherently disruptive nature of this defense inflicts a considerable cost on the colony when it is used against a nonthreatening species. However, even when the defense is used only to evade a threatening species the colony still suffers from its disruptive effects. The next section will show how emigrations function to reduce the cost of these effects.

III. Emigrations and the Nest-Evacuation Defense

As was shown in the first section, both P. desertorum and P. hyatti emigrate frequently in patterns that result in a colony having a cluster of nests of which only one is occupied at a time. Although colonies excavate new nests, they also reuse old nests so that the colonies essentially shuttle back and forth between nests. In this section I present evidence that these multiple nests, and by extension the emigrations that created them, function to increase the effectiveness of the nest-evacuation defense. However, because nests of P. hyatti are less conspicuous, and are in areas with greater ground cover, I used only P. desertorum in this study.

A. Use of Multiple Nests

Methods

This part of the study was conducted during August 1980 in the desert-grassland site. Nest evacuations were induced by releasing 100 N. nigrescens workers within 10 cm of the occupied P. desertorum nest. Shortly after the start of the evacuation 5-min counts (separated by intervals of 1 min) were begun of the workers carrying brood that entered or left the unoccupied nests. When there was more than one unoccupied nest, the counts were taken at one, followed by the next nest, in a repeated, fixed sequence for a period of about 90 minutes. Immediately after this period, the N. nigrescens workers were removed, and a second period of counts was begun in which the evacuated nest was included. This second period of counts continued until workers ceased carrying brood into all the nests. This procedure was replicated with 6 different colonies, two had two nests, two had three nests, and two had four nests. After this procedure, the colonies were inspected nightly until they were again at only one nest.

Results

In all replications of the procedure a steady flow of workers began entering the unoccupied nests shortly after the evacuation began. During the first period of counting, which simulated an army ant raid lasting approximately 1.5 hours, a mean of 24.0 (SD = ± 15.2, N = 12) workers carrying brood entered the unoccupied nests per 5-min count. After the army ants were removed a mean of 22.6 (SD = ± 10.8, N = 6) workers carrying brood reentered the evacuated nest, while the mean workers carrying brood that entered the unoccupied nests decreased to 8.5 (SD = ± 6.1, N = 12) per 5-min count. Two representative examples of these results are shown in Figures 11 and 12.

During one replication, workers began transporting brood from one nest to another in an orderly column (Fig. 12). In this way, after becoming fragmented in the available nests, the colony reorganized. However, it took from one to seven days for the colony to reunite at one nest, with the interim inter-nest movements exhibiting great variability. For example, colony 3, which had three nests, occupied all three nests for the first two nights after the evacuation. During the next three nights the colony occupied two of the nests and for two of these nights workers carried brood back and forth between these nests. On the sixth night an actual army ant raid occurred, and on the following night the colony was only at the nest that had been raided. In four of the six replications the colony became reunited at the nest that had been evacuated.

These results suggest that the workers quickly find and enter all available nests after an evacuation. The manner in which many of the workers found the nests suggested that workers guide their nestmates to the nests by laying chemical trails. The fragmentation of the colony in more than one nest lasts a variable period of time during which brood is transported from one nest to another until the colony is again reunited in one nest.

B. Function of the Multiple Nests

Methods

To test if the presence of multiple nests increases survivorship after a nest evacuation I performed the following experiment during July and August 1982 in the same study site. Only the survivorship of the brood and alates were determined since, unlike the workers which leave the nest to forage, they remain stationary in the nest. However the alates like the workers evacuate the nest and return to it on their own.

The emigration activity of colonies was followed by nightly inspection until the locations of at least three nests for each colony were determined. The colonies were then collected by placing a plastic cylinder (Ø 30 x 21 cm) coated with Fluon® around the nest entrance, releasing N. nigrescens workers within it to cause a nest evacuation, and aspirating the ants as they came up on the surface. To collect all the brood and alates this procedure was repeated as many times as necessary after first permitting workers to reenter the nest. The brood and alates were then counted and replaced near the nest entrance within the cylinder until the alates reentered, and the workers carried the brood back into, the nest.

Previous to this the colonies had been randomly placed into one of two groups. In one group, the entrances of all unoccupied nests were sealed with soil. In addition any hole within 5 m of the nest that might serve as a nest was also sealed with soil. In the other group nothing was done. At 0200 (MST) on the night following the above censusing procedure, 100 N. nigrescens workers were released within 10 cm of the nest to again cause a nest evacuation, and at 0300 hrs the army ants were removed. In this way a one-hour army ant raid was simulated in which the colonies in the first group had access only to their evacuated nests, and the colonies in the second group had access to all their nests after the evacuation.

Early the next night the brood and alates in the nests were determined in the manner described above. To locate all possible nests a square grid of 16 food baits placed 2 m apart were set around the evacuated nest. For colonies meant to have access to only their evacuated nests this ascertained that no other nests were used, and for the other colonies, this revealed the location of any nests to which emigrations were not observed.

All percentages were subjected to an arcsine transformation before being statistically evaluated using Student's t-test.

Results

There was a significantly greater survivorship of both brood ($t = 2.55$, P .05) and alates ($t = 3.50$, P .01) in colonies with multiple nests than in colonies with only a single nest. The results are shown graphically in Figure 13. In both conditions, the greater survival of the alates may be explained by their greater ability to survive the higher surface temperatures that the beginning of the day brings; this provides them with more time to find nests. In the six colonies having multiple nests only 2 did not contain brood in all of their nests after the evacuation, and in only one of these did the evacuated nest not contain brood. This again demonstrated that these nests are found and used by the ants after an evacuation.

How well can a colony survive an actual army ant raid? After determining the brood and alates in the nest of one colony, it was raided by an actual N. nigrescens colony. For this reason it could not be included in the above experiment. However, the colony possessed a total of four nests, and 41% of the brood and 50% of the alates survived. This suggests that a considerable portion of the colony can survive both an army ant raid and the disruption caused by a nest evacuation.

Discussion

An anti-predator function has not been known for any of the emigrations that occur in ants, and it is difficult to conceive a priori how they might serve such a function. However, colony survival after a nest evacuation is enhanced by the multiple nests that are a consequence of the peculiar patterns of emigrations in P. desertorum. To understand why this is so it is necessary to consider both the predatory behavior of N. nigrescens and the costs associated with nest evacuation.

N. nigrescens is a column raiding army ant in which the end of a long raiding column branches into shorter raiding columns in a dendritic pattern (Mirenda et al. 1980). In this pattern of raiding many potential raiding sites are missed (Mirenda and Topoff 1980), and a N. nigrescens raiding column may pass within a couple of meters of a *Pheidole* nest without finding it (personal observations). Therefore, when the *Pheidole* ants begin entering their unoccupied nests shortly after a nest evacuation they are not necessarily going to be raided again in these nests. In fact, *N. nigrescens* will sometimes bivouac in the nest of a *P. desertorum* colony it had just raided while the *P. desertorum* colony survives by occupying its alternate nests. In the course of three summers I observed this happen to seven *P. desertorum* colonies, and to two of these more than once.

The "hit or miss" column raiding of *N. nigrescens* may increase the survival value of the multiple nests in another, more subtle way. The unoccupied nests very quickly become collection centers for the dispersed colony. Communication between the colony fragments that become settled in these nests aids in the colony becoming reunited in one of these nests. This process however takes a variable period of time and occurs when the colony is at great risk of being raided again either later the same night or on the following night, particularly if the army ant colony has entered the statary phase nearby. While fragmented, the smaller units of the colony may be able to conduct speedier and more successful nest evacuations against any subsequent raids. It also becomes less likely that the entire colony will be raided when the colony is fragmented.

Although *P. desertorum* may successfully evade *N. nigres-*

cens by evacuating, it still must face the considerable cost exacted by this defense. The workers, brood and alates that were concentrated in the chambers of the nest become scattered, exposed to predators and the fluctuating environment of the surface. In the arid habitat in which P. desertorum is found, the lack of leaf litter and other debris, combined with the high temperature and low humidity of the surface during the day, make holes excavated in the ground the only suitable type of nest. The multiple nests increase the availability of suitable microhabitats where the dispersed ants can find shelter after an evacuation, and in this way decrease the mortality that is a consequence of the disruptive nature of this form of defense.

Although the proximate cause of P. desertorum's emigrations is not known, it is not necessary that it relate directly to predation for the emigrations to serve an anti-predator function. Similar reasoning explains why, for example, the army ants' nomadic behavior can be explained as a way of avoiding food depletion although the proximate cause of the emigrations is brood stimulation (Schneirla 1971, Wilson 1971). A comparison can also be made to cryptic and aposematic coloration where the proximate physiological cause has no direct connection with the anti-predator function served by the effect. The possibility also exists that the emigrations have some other function in addition to their anti-predator function. However, even if this additional function were primary, the emigrations would still have to be considered as part of an adaptive suite (sensu Bartholomew 1972) of behaviors by which P. desertorum deals with army ant predation.

FINAL DISCUSSION

The avoidance of predation, important in any animal, is of particular importance in animals preyed upon by selective predators. Selective predators must be able to circumvent, penetrate or foil the general defenses of their prey, and this often causes the evolution of enemy specific defenses against them. Social insects are somewhat buffered from selective predation by the fact that the colony can sustain the loss of individuals as long as it continues to function as a unit. For example, the desert horned lizard *Phrynosoma platyrhinos* preys selectively on ants, especially the harvester ant *Pogonomyrmex*, however, it does not invade the nest but preys only on the foragers (Pianka and Parker 1975). Hence, although it may weaken the colony by reducing the number of foragers, its predation does not necessarily lead to the death of the colony as a reproductive unit. On the other hand, some ant species have evolved enemy specific defenses against what might be termed "invasive" predators. For example, *Pheidole dentata*, as discussed earlier, uses an enemy-specific alarm-recruitment defense against ants of the genus *Solenopsis*. The early phase of this complex defense is designed to quickly find and destroy exploratory units of rapidly recruiting *Solenopsis* colonies. If this early phase fails, and many *Solenopsis* workers are recruited to the *Pheidole* nest, the colony evacuates the nest to avoid being annihilated by the larger, more aggressive *Solenopsis* colony (Wilson 1975b, 1976).

Army ants are not only selective predators (Mirenda et al. 1980, Rettenmeyer 1963) but invasive predators of social insects as well. *N. nigrescens*, for example, preys mainly on *Pheidole* species relying on a rapid recruitment system to overwhelm its prey at their nests and capture their brood (Topoff et al. 1980). It is unlikely that *Pheidole* colonies could make a successful stationary defense against *N. nigrescens* since they are of intermediate size and their defensive capabilities tend to be concentrated in the major, or soldier, subcaste, which makes up only a small percentage of the worker population. However, even the larger, more aggressive harvester ants *Pogonomyrmex* sometimes fall prey to a numerically superior *N. nigrescens* colony when it is in the nomadic phase of its raiding cycle (Topoff 1982). Other examples are *N. harrisi*, which can overcome the aggressive defense of *S. xyloni*, and *N. fallax*, which can penetrate the nest-blocking defense of *P. rugulosa*. The most pervasive defense in social insects to a predator that can frequently and successfully invade the nest appears to be nest evacuation.

Nest evacuation in social insects illustrates particularly well the principle that defense mechanisms have costs as well as benefits. The hallmark of eusociality is the high degree of cooperation that is achieved among colony members. But this cooperation depends upon the cohesiveness that the physical proximity of colony members within the nest provides. The queen, brood and a large number of workers remain in the nest during most colony activities, even to a certain extent when the colony is changing its nest. Nest evacuation and the subsequent dispersal of the colony therefore constitutes a disruption to this cohesiveness. However, as shown above, the nest-evacuation defenses of P. desertorum and P. hyatti possess elements of organization that decrease the costs of this defense, and thereby increase its effectiveness.

The nest evacuation defense fits easily into the binary system of classifying defense mechanisms as a secondary defense since it occurs when the predator is encountered. However, classifying emigrations as a defense mechanism according to this scheme is problematical. First, it is not the emigrations, but the multiple nests that result from them, that have an important anti-predator function. Second, the multiple nests, as they fit into the overall defense system, have their effect only after the encounter with the predator has occurred, and don't function to decrease the chance that an encounter with a predator will occur so much as to ameliorate the conditions resulting from the defense itself. P. desertorum's emigrations and nest-evacuation defense therefore comprise an exceedingly intricate and subtle defense system.

Integrated defense systems in animals are typically conceived of as comprising an array of defense mechanisms for use against different predators, or as a sequence of defense mechanisms in which one defense is used if the previous one fails (Edmunds 1974). As an example of the former, the Ghanaian praying mantis *Tarachoda alzellii* is cryptically colored to resemble the bark on which it rests, but will run or fly (if it is a male), or present a diematic display, if it is discovered (Edmunds 1972). *P. desertorum*'s nest-evacuation defense and emigrations comprise an intergrated defense system in another sense: the emigrations result in the colony having accessory nests which decrease the cost of the nest-evacuation defense, and therefore play a supportive role. Perhaps then the concept of a defense system should be broadened to include those traits that increase the effectiveness of a defense without necessarily being directly anti-predatory in nature.

Before the discovery of *P. dentata*'s alarm-recruitment defense (Wilson 1975b, 1976) complexly organized defense systems in social insects were thought to occur only in termites (Wilson 1971). The termite alarm-recruitment-construction defense however is a general defense reaction to a broad range of threatening stimuli (Stuart 1967). In contrast, the alarm-recruitment and nest-evacuation defenses found in *Pheidole* species possess the additional feature of being enemy specific. This enemy specificity is reflected not only in qualitative differences in defense reactions to different predators, but in quantitative differences as well. This was demonstrated for example by the quantitative differences in P. hyatti's brood evacuation responses to N. nigrescens, N. fallax and N. opacithorax. This degree of enemy specificity is comparable to that shown by some vertebrates. For example, Thompson's gazelle's flight distance changes with different vertebrate predators, being greatest with wild dogs and least with jackals, with that for cheetahs, lions and hyaenas in between. These differences appear to correspond to differences in the capturing abilities of the predators since, for example, wild dogs have tremendous stamina and can chase gazelles for several miles while jackals can not run down an adult gazelle and rarely prey on them (Walther 1969). Finally, it should be noted that all four prey species used in this study displayed some degree of enemy specificity and also use a nest-evacuation defense against at least one Neivamyrmex species. Furthermore, the final phase of P. dentata's alarm-recruitment defense also involves nest evacuation. This suggests that the costs associated with nest evacuation increases selection pressure for the evolution of enemy specificity.

Army ant predation has an important impact on the structure of insect communities. Prey selection by Eciton burchelli, for example, has a significant influence on the patchiness and diversity of ant communities on the tropical rain forest floor (Franks and Bossert 1982). As shown above, army ant predation also has a considerable impact on the behavior of individual prey species. To gain a deeper insight into how insect communities function it is important to understand the complex anti-predator adaptations of prey. This is well illustrated by the discovery of _P. dentata_'s alarm-recruitment defense (Wilson 1975b, 1976): this led to the discovery that the parasitic phorid fly _Apocephalus_ influences competition between _P. dentata_ and _Solenopsis_ species by adversely affecting the behavior of majors during the execution of this defense (Feener 1981). The important effect of _Apocephalus_ would not have been understood if _P. dentata_'s alarm-recruitment defense had not been revealed. Now that complex defense systems are known to exist in ants, their further study should greatly enhance our understanding of insect community dynamics.

Table 1. Emigration characteristics of *P. desertorum*.

Colony	Days Observed	Number of Emigrations	Returns to a Former Nest	Distance Between First and Last Observed Nests (m)
D-Jn10-1a*	70	4	2	0.5
D-Jn11-1a	63	7	3	4.8
D-Jn11-2a	68	0	0	-
D-Jn12-1a	60	4	1	15.6
D-Jn12-2a	68	1	0	2.5
D-Jn12-3a	68	2	1	0.0
D-Jn12-4a	64	6	3	3.0
D-Jn12-5a	21	1	0	4.2
D-Jn13-1a	57	2	1	0.0
D-Jn14-1a	61	3	2	0.0
D-Jn15-1a	65	6	3	6.6
D-Jn15-2a	62	3	1	0.0
D-Jn16-1b	64	4	3	0.0
D-Jn17-1b	57	4	2	0.0
D-Jn17-2b	63	5	3	2.4
D-Jn18-1a	49	3	1	3.1
D-Jn20-1b	57	8	6	0.0
D-Jn25-1a	55	7	4	1.5
D-Jn28-1a	50	5	3	3.7
D-Jl01-1a	42	7	3	2.4
D-Jl13-1b	37	2	1	0.0
D-Jl13-2b	37	3	1	1.2
D-Jl15-1b	33	4	1	0.0
D-Jl30-1b	20	6	3	0.0
D-Jl30-2a	19	2	1	0.0
D-A 01-1a	18	2	0	4.0
Total	1,328	101	49	

*a-desert-grassland; b-oak-juniper woodland

Table 2. Emigration characteristics of *P. hyatti*.

Colony	Days Observed	Number of Emigrations	Returns to a Former Nest	Distance Between First and Last Observed Nests (m)
H-Jn14-1	66	6	3	4.2
H-Jn14-2	66	16	11	1.1
H-Jn14-3	66	8	2	5.4
H-Jn15-1	23	1	0	1.5
H-Jn15-2	63	7	3	0.0
H-Jn17-1	63	0	0	-
H-Jn17-2	63	6	2	0.8
H-Jn18-1	62	10	5	3.2
H-Jn18-2	55	7	2	6.8
H-Jn19-1	61	7	4	0.0
H-Jn19-2	57	4	1	0.0
H-Jn19-3	61	6	2	1.5
H-Jn19-4	60	5	2	0.0
H-Jn19-5	61	7	5	2.0
H-Jn21-1	59	3	0	2.6
H-Jn21-2	58	6	4	1.9
H-Jn21-3	57	4	2	0.0
H-Jn21-4	57	6	3	3.0
H-Jn23-1	53	2	0	0.8
H-Jn24-1	56	7	1	0.8
H-Jn26-1	51	5	1	2.5
H-Jn26-2	16	2	0	1.1
H-Jn27-1	46	8	2	0.4
H-Jn28-1	52	4	2	2.4
Total	1,332	137	57	

Table 3. Army ant raids on _P. desertorum_.

Colony	Dates of Raids	_Neivamyrmex_ sp.
D-Jn11-1	8/1-8/5	_N. nigrescens_
D-Jn11-2	7/9	"
D-Jn12-1	8/4, 8/6, 8/8	"
D-Jn12-4	7/4	"
D-Jn12-5	7/2*	"
D-Jn13-1	7/12, 8/10*	"
D-Jn14-1	8/5, 8/6, 8/12-8/15	"
D-Jn18-1	7/11, 7/12, 7/16, 7/25	"
	7/26, 7/28, 8/1	
D-Jn17-1	8/18	"
D-Jn25-1	8/28	"
D-Jl04-1	8/3, 8/5-8/7, 8/9	"
D-Jl30-2	8/13	"
D-Jl15-1	7/28	"

*Colony not seen afterwards.

Table 4. Army ant raids on _P. hyatti_.

Colony	Dates of Raids	_Neivamyrmex_ sp.
H-Jn15-1	7/7, 7/8*	_N. nigrescens_
H-Jn15-2	7/8	"
H-Jn19-4	7/28	"
H-Jn21-3	8/15	_N. opacithorax_
H-Jn21-4	8/17	_N. nigrescens_
H-Jn21-5	8/15	_N. opacithorax_
	8/18	_N. nigrescens_
H-Jn23-1	8/15*	_N. opacithorax_
H-Jn26-1	8/12	_N. nigrescens_
H-Jn27-1	8/12*	"

*Colony not seen afterwards.

Table 5. Comparisons between *Pheidole desertorum* and *P. hyatti*.

Character	*P. desertorum*	*P. hyatti*	Statistical Evaluation (t-test)
Length of minor (mm)	3.24 ± 0.23 (N=47)	2.61 ± 0.13 (N=60)	$P < .001$
Length of major (mm)	4.76 ± 0.19 (N=39)	4.05 ± 0.21 (N=66)	$P < .001$
Head width of minor (mm)	0.677 ± 0.034 (N=33)	0.586 ± 0.023 (N=60)	$P < .001$
Head width of major (mm)	1.393 ± 0.087 (N=53)	1.243 ± 0.054 (N=60)	$P < .001$
% of majors in worker population	17% ± 6% (N=8)	13% ± 5% (N=11)	$.1 < P < .2$
Diameter of nest entrance (cm)	5.8 ± 1.6 (N=10)	1.0 ± 0.5 (N=18)	$P < .001$
Running speed of minors (cm/sec)	2.10 ± 0.30 (N=89)	1.53 ± 0.22 (N=85)	$P < .001$

Table 6. Mean survivorship with standard deviation of combat encounters between 10 *Pheidole* and 10 *N. nigrescens* workers. N=30 for each pairing.

Combatant	*P. desertorum* minors vs. *N. nigrescens*	*P. hyatti* minors vs. *N. nigrescens*	*P. desertorum* majors vs. *N. nigrescens*	*P. hyatti* majors vs. *N. nigrescens*
Pheidole	1.3 ± 2.0	3.3 ± 3.1	4.5 ± 2.2	8.5 ± 1.2
Neivamyrmex	8.1 ± 2.4	8.4 ± 2.0	3.0 ± 3.3	3.7 ± 2.5

Table 7. Field tests of prey species' reactions to Neivamyrmex species.

prey species	*Neivamyrmex* species	no. of workers	N	brood evacuated	majors leave nest	no apparent response
P. hyatti	*N. fallax*	100	2	2	0	0
	N. harrisi	100	3	0	2	1
	N. nigrescens	1	13	11	0	2
	"	3	3	3	0	0
	"	10	5	5	0	0
	"	100	11	11	0	0
	N. opacithorax	1	1	0	1	0
	"	10	2	0	2	0
	"	30	5	2	2	1
	"	100	2	2	0	0
	N. texanus	1	2	0	0	2
	"	3	1	0	0	1
	"	5	1	0	1	0
	"	10	5	0	4	1
	"	20	1	0	1	0
P. desertorum	*N. fallax*	100	2	2	0	0
	N. harrisi	100	3	1	2	0
	N. nigrescens	1	5	5	0	0
	"	100	14	14	0	0
	N. opacithorax	100	1	1	0	0

Table 7. continued

prey species	*Neivamyrmex* species	no. of workers	N	brood evacuated	majors leave nest	no apparent response
P. rugulosa	*N. fallax*	100	6	6	0	0
	N. harrisi	100	5	0	0	5
	N. nigrescens	100	6	0	0	6
S. xyloni	*N. harrisi*	100	5	5	-	0
	N. nigrescens	100	5	0	-	5

Table 8. Survivorship in combat trials between 10 prey species workers and 10 *Neivamyrmex* workers. ($\bar{X} \pm$ SD, N = 15).

Combatant	*P. desertorum* majors vs. *N. harrisi*	*P. hyatti* majors vs. *N. harrisi*	*S. xyloni* vs. *N. harrisi*	*S. xyloni* vs. *N. nigrescens*
prey species	9.3 ± 1.2	9.3 ± 0.9	7.5 ± 1.5	8.9 ± 1.1
Neivamyrmex	0.1 ± 0.3	0.5 ± 0.9	8.7 ± 1.9	3.0 ± 2.1

Table 9. Laboratory tests of the reactions of *P. desertorum* and *P. hyatti* to *Neivamyrmex* sp.

prey species	*Neivamyrmex* species	no. of workers	N	evacuation phase	alert phase	majors leave nest	no response
P. hyatti	*N. fallax*	5	1	0	0	1	0
	"	10	2	0	2	0	0
	"	50	1	0	0	1	0
	"	100	2	1	0	1	0
	N. harrisi	100	5	0	0	2	3
	N. nigrescens	1	5	3	2	0	0
	"	10	5	5	0	0	0
	N. opacithorax	10	1	0	0	1	0
	N. texanus	1	1	0	0	1	0
	"	5	2	0	0	2	0
P. desertorum	*N. fallax*	100	1	0	1	0	0
	N. harrisi	10	2	0	1	1	0
	"	100	5	2	1	2	0
	"	500	1	0	0	1	0
	N. nigrescens	1	5	2	2	1	0
	"	5	2	2	0	0	0
	"	10	5	5	0	0	0
	N. opacithorax	100	1	0	0	1	0

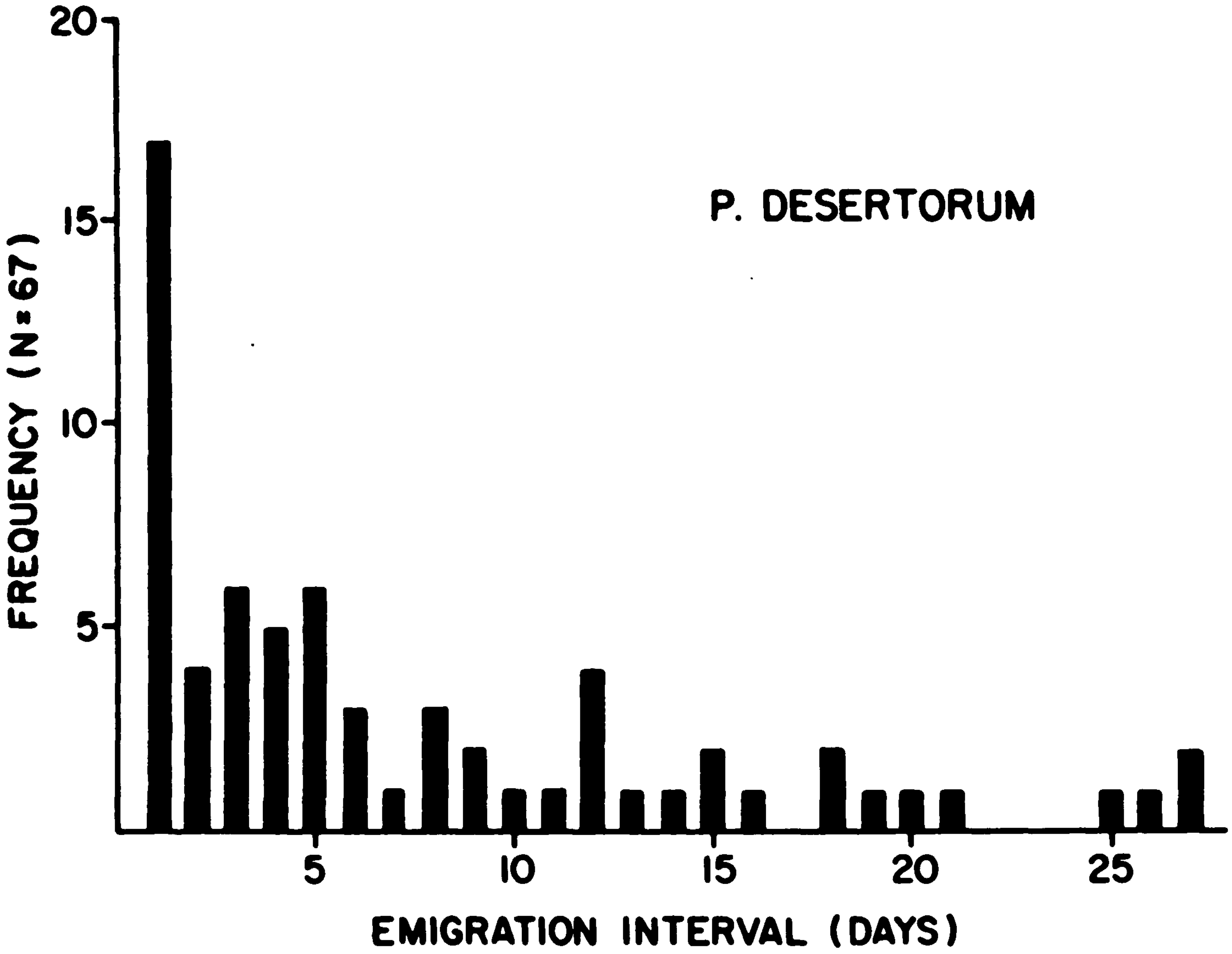


Figure 1. Frequency of days between emigrations for P. desertorum.

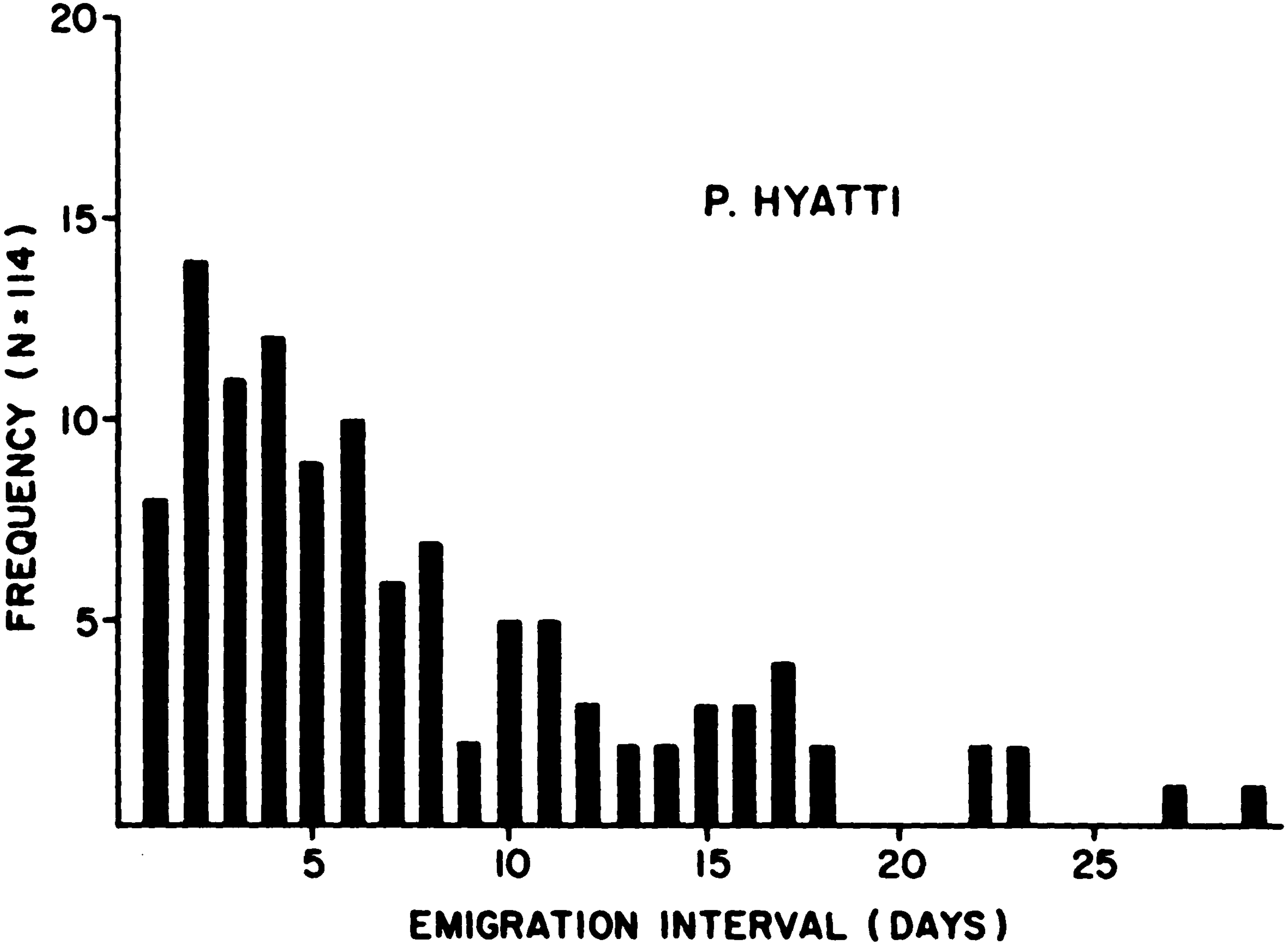
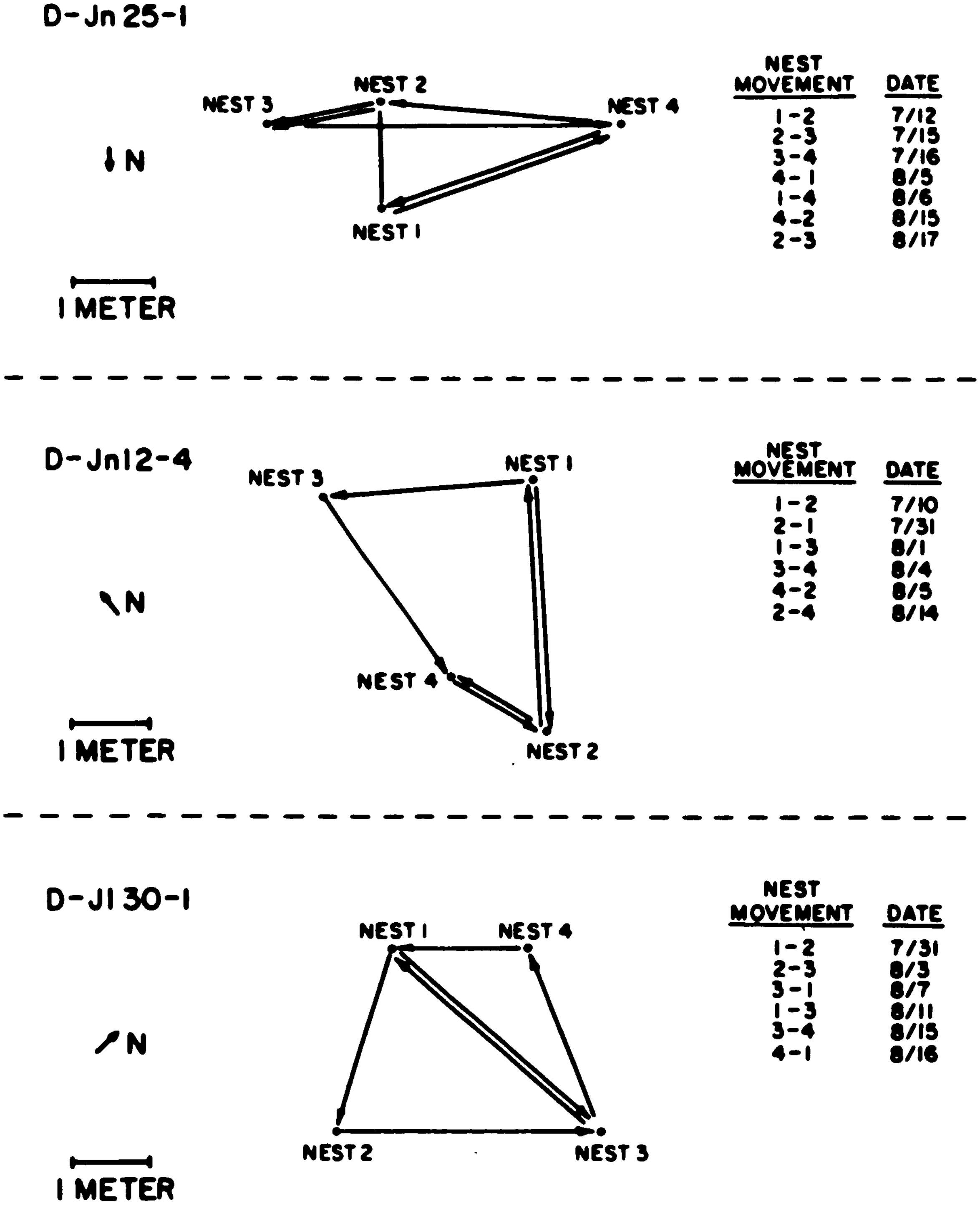


Figure 2. Frequency of days between emigrations for *P. hyatti*.



D-Jn 25-1

NEST MOVEMENT	DATE
1-2	7/12
2-3	7/15
3-4	7/16
4-1	8/5
1-4	8/6
4-2	8/15
2-3	8/17

D-Jn12-4

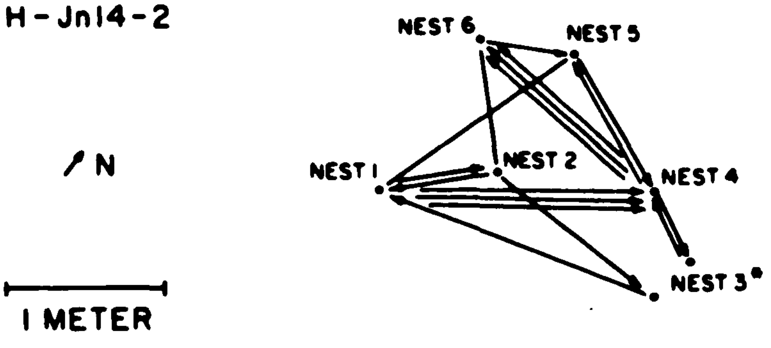
NEST MOVEMENT	DATE
1-2	7/10
2-1	7/31
1-3	8/1
3-4	8/4
4-2	8/5
2-4	8/14

D-Jl 30-1

NEST MOVEMENT	DATE
1-2	7/31
2-3	8/3
3-1	8/7
1-3	8/11
3-4	8/15
4-1	8/16

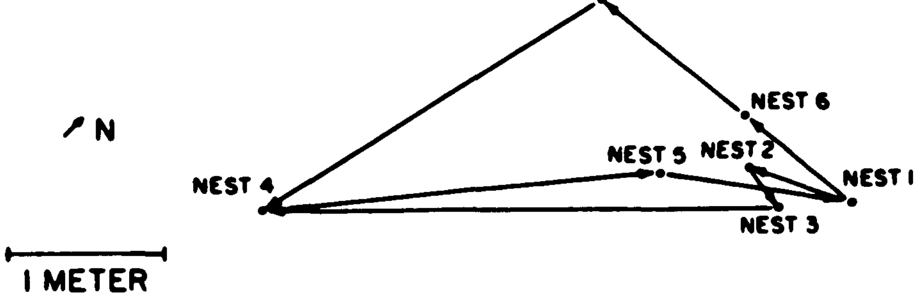
Figure 3. Patterns of emigrations in P. *desertorum*. Dates of emigrations are shown on the right.

H-Jn14-2



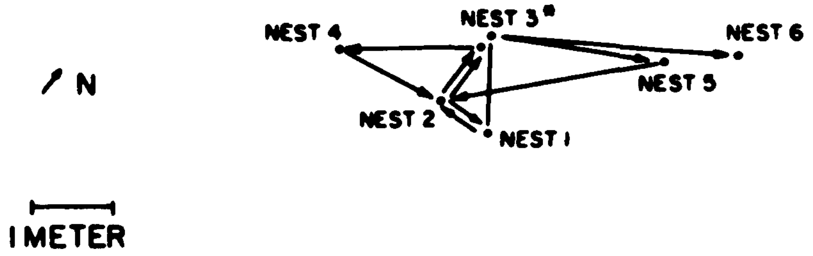
NEST MOVEMENT	DATE
1-2	6/15
2-3	7/2
3-1	7/7
1-4	7/9
4-3	7/15
3-4	7/18
4-5	7/22
5-1	7/27
1-4	7/30
4-6	7/31
6-5	8/3
5-4	8/5
4-6	8/6
6-2	8/11
2-1	8/13
1-4	8/15
4-6	8/17

H-Jn14-3



NEST MOVEMENT	DATE
1-2	6/18
2-3	6/22
3-4	7/10
4-5	7/20
5-1	7/27
1-6	8/1
6-7	8/11
7 4	8/14

H-Jn18-1



NEST MOVEMENT	DATE
1-2	7/1
2-3	7/5
3-4	7/11
4-2	7/17
2-3	7/21
3-5	7/29
5-2	8/4
2-1	8/5
1-3	8/8
3-6	8/13

Figure 4. Patterns of emigrations in *P. hyatti*. Dates of emigrations are shown on the right. *Nest with two entrances.

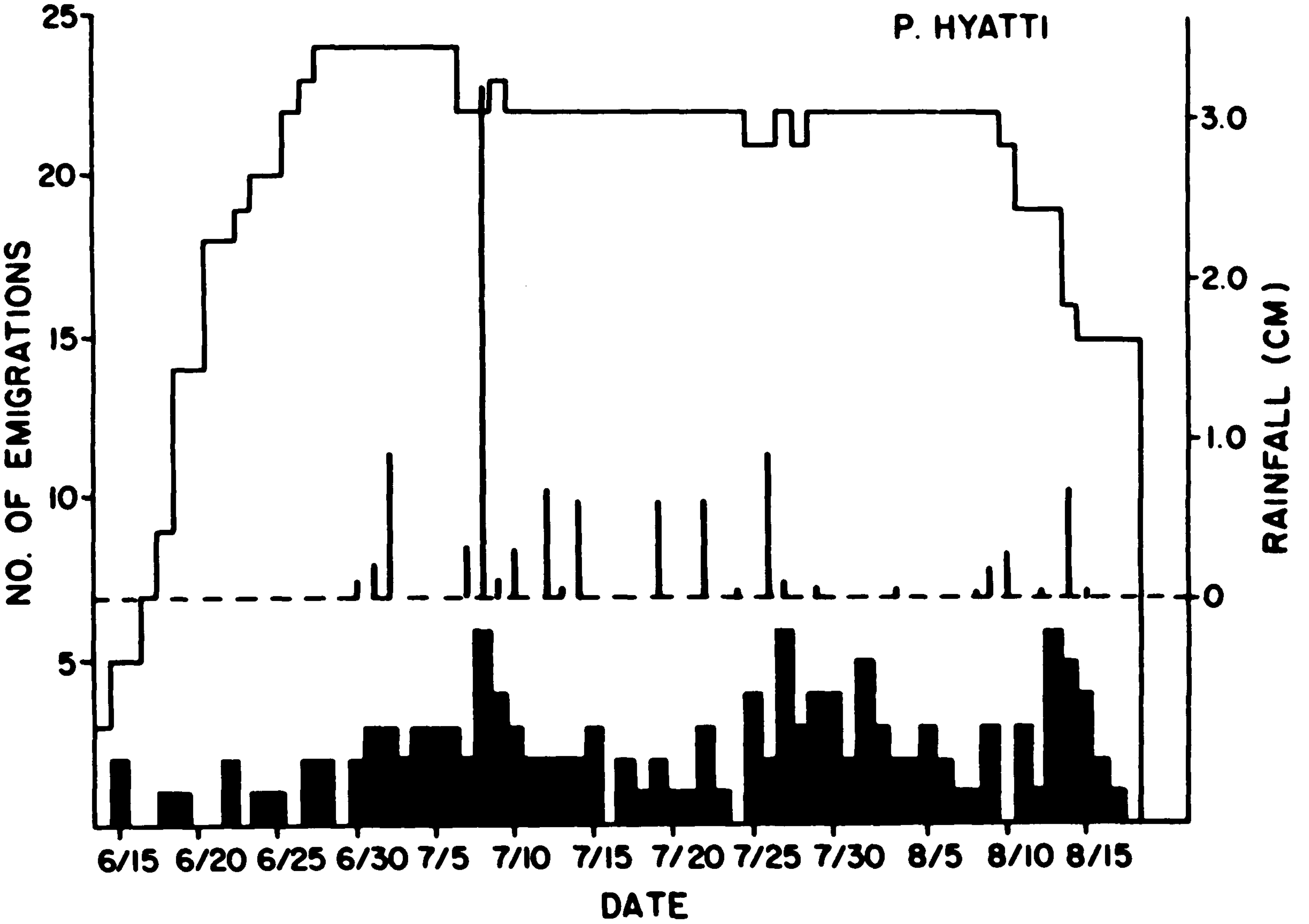


Figure 5. Daily occurrence of emigrations in P. hyatti. Upper line outlines the number of colonies included in the sample each night.

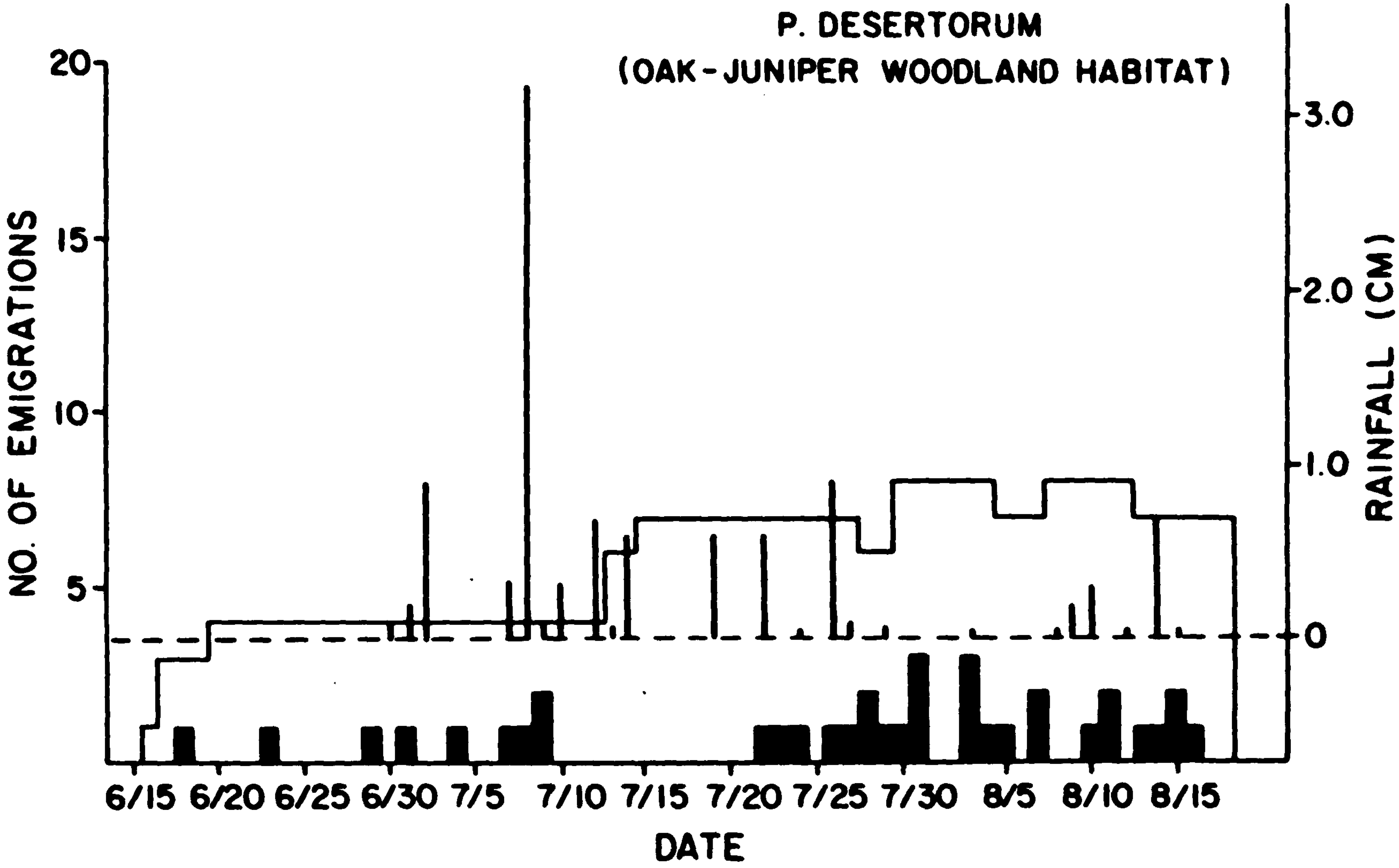


Figure 6. Daily occurrence of emigrations in *P. desertorum* in oak-juniper woodland.

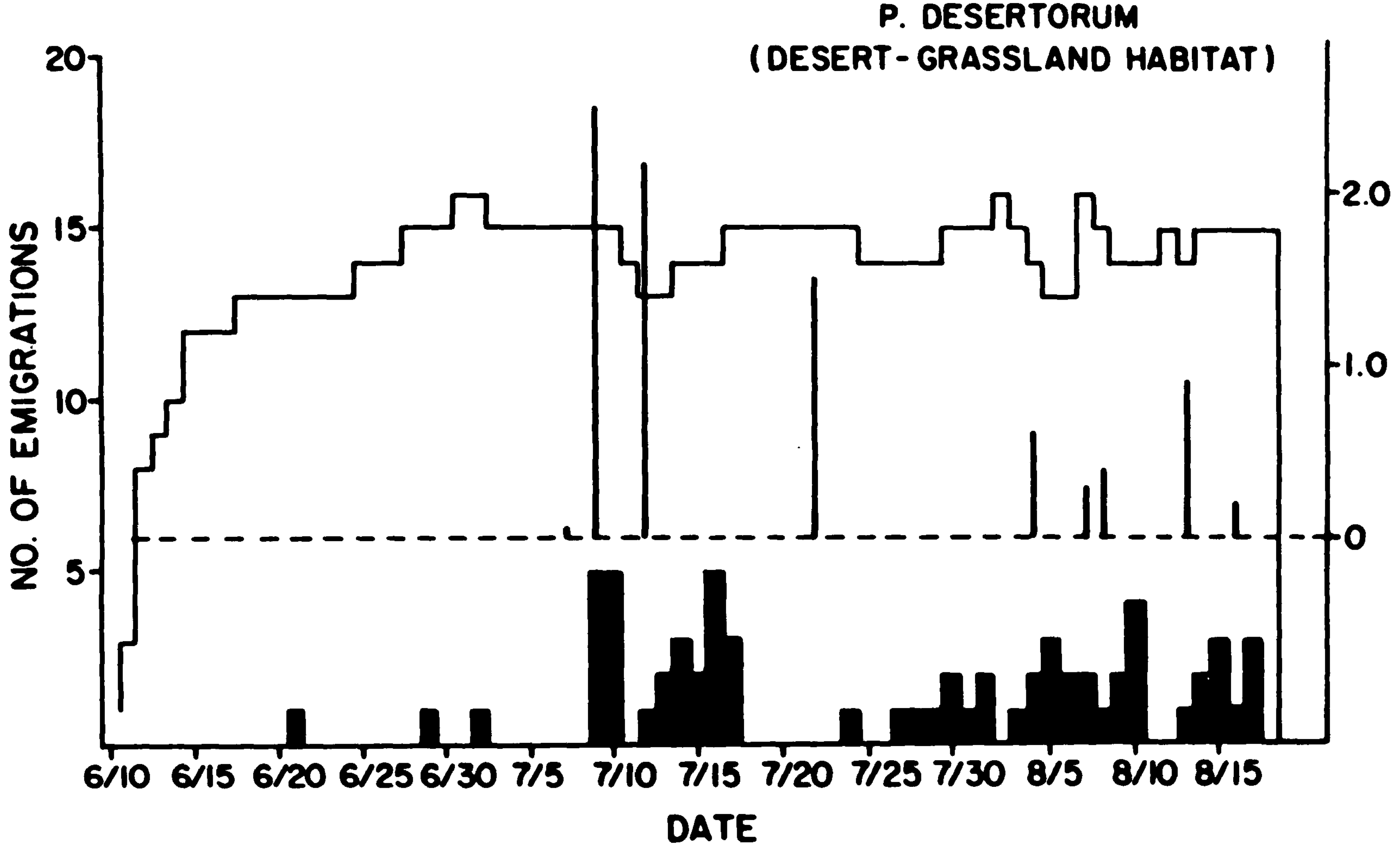


Figure 7. Daily occurrence of emigrations in *P. desertorum* in desert-grassland.

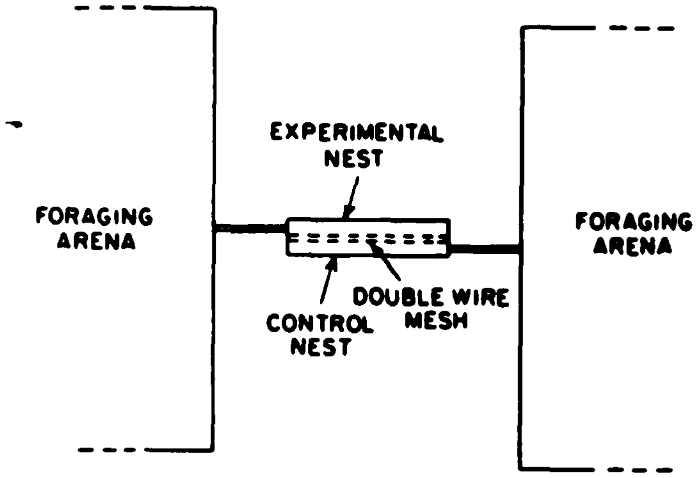


Figure 8. Laboratory arrangement for the alarm pheromone experiment.

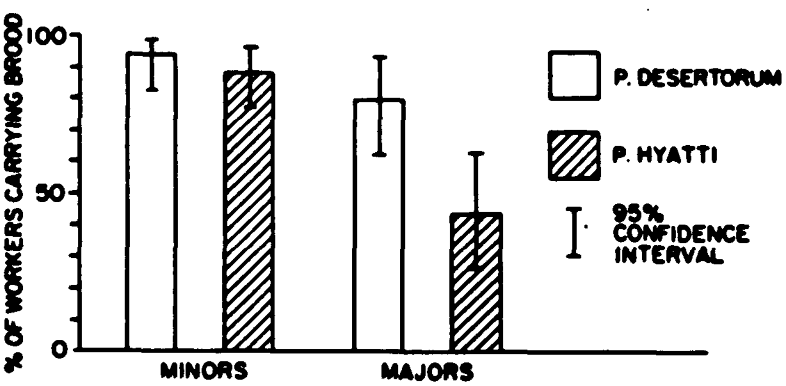


Figure 9. Percentages of workers of each subcaste that carried brood during evacuations in *P. desertorum* and *P. hyatti*. (N = 5).

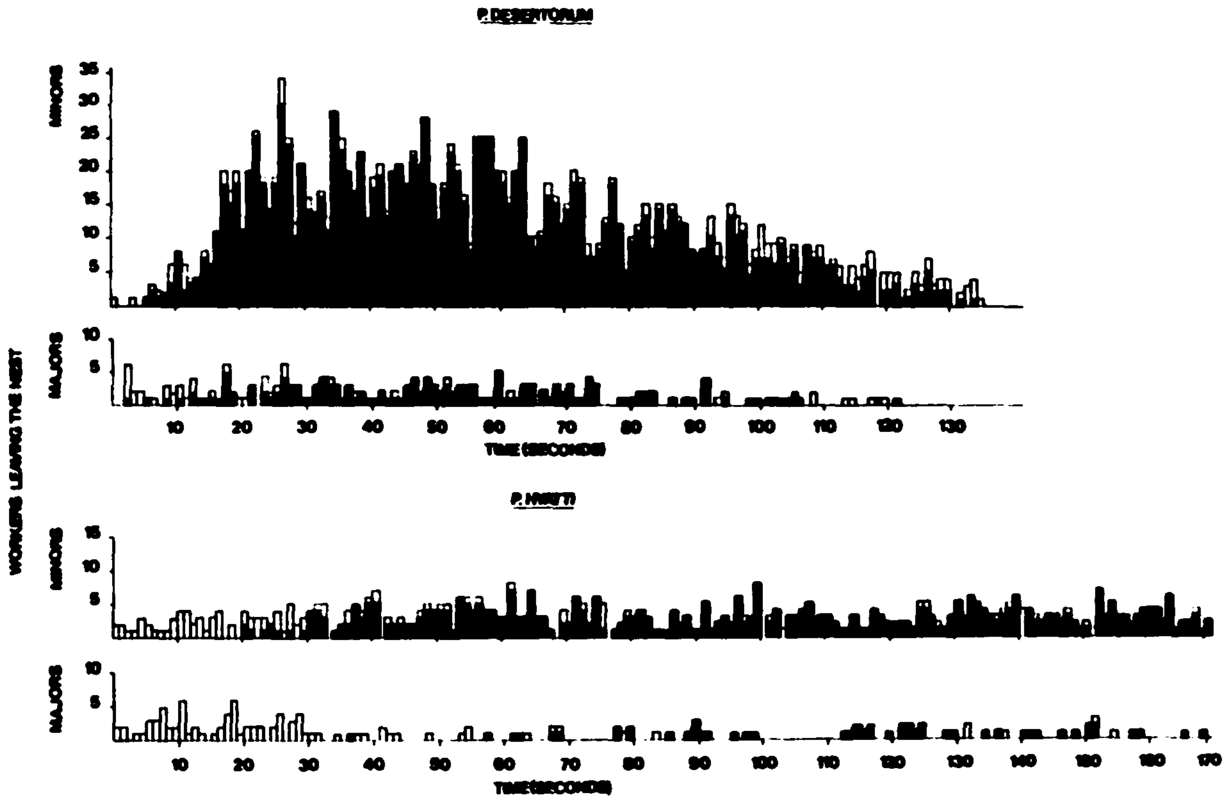


Figure 10. Representative evacuations for P. desertorum and P. hyatti derived from filmed evacuations. The bars indicate one-second counts. The darkened portion of each bar indicates the number of workers that carried brood.

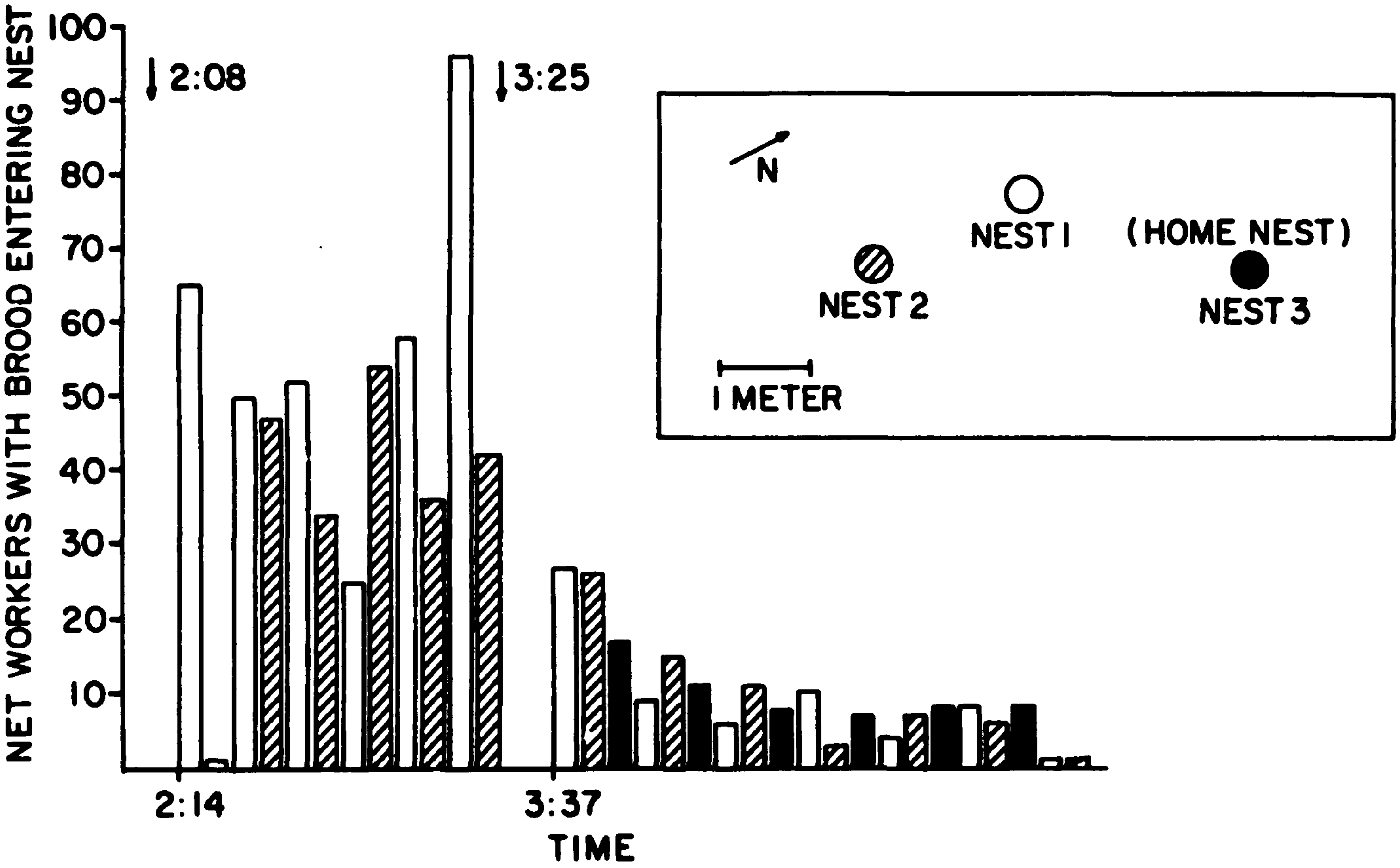
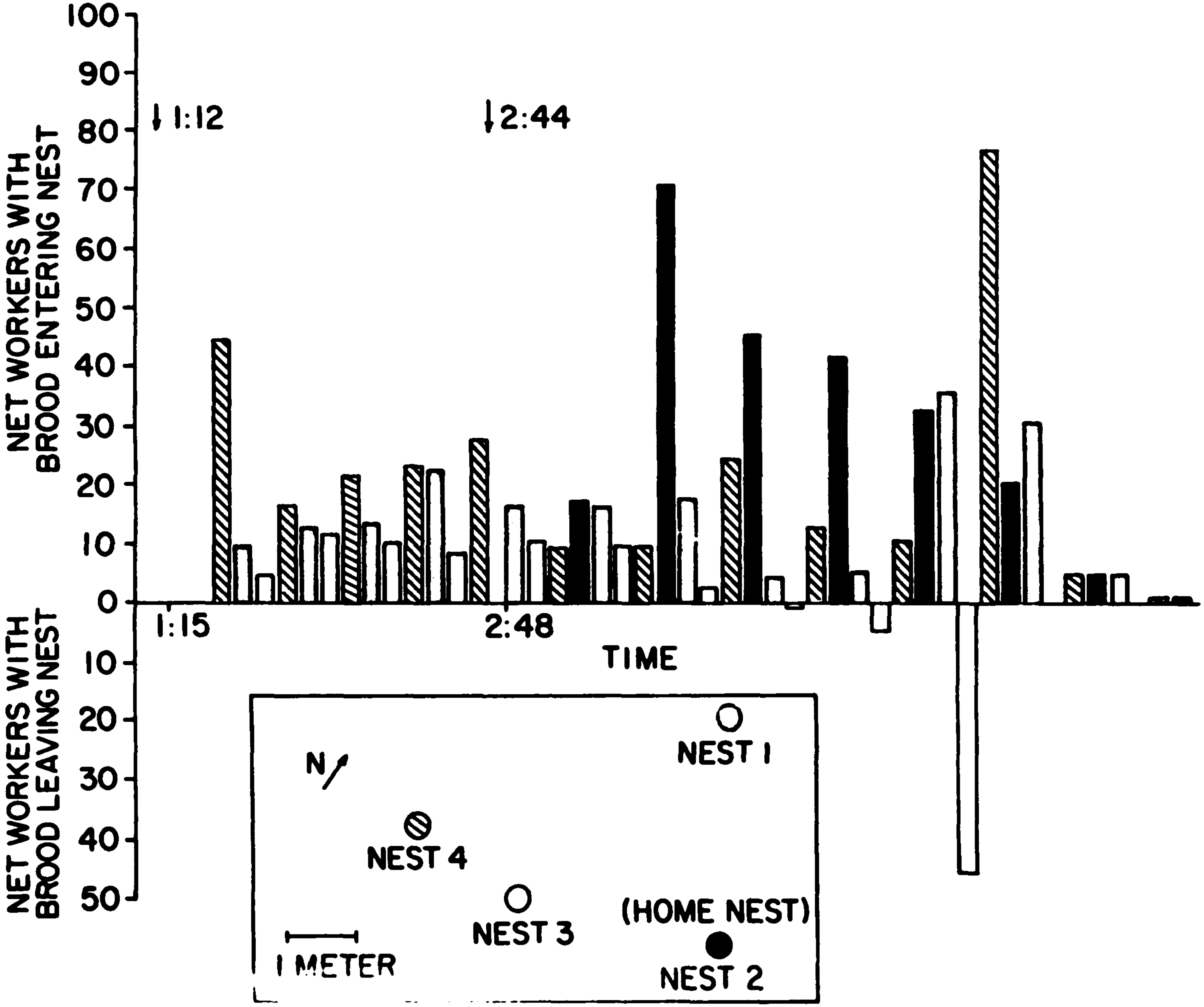


Figure 11. Results of the procedure testing for the use of multipe nests for a colony with 3 nests. Inset shows the disposition of the nests. The nest occupied before the evacuation is indicated as "home nest". The arrows indicate the times the army ants were released and removed, and the times on the x-axis indicate the starts of the first and second periods of counting.

Figure 12 (next page). Results of the procedure testing for the use of multiple nests in a colony with 4 nests. (see Figure 11).



NET WORKERS WITH BROOD ENTERING NEST
NET WORKERS WITH BROOD LEAVING NEST
100
90
80
70
60
50
40
30
20
10
0
10
20
30
40
50
1:12
2:44
1:15
2:48
TIME
N
NEST 1
NEST 4
NEST 3
(HOME NEST)
NEST 2
1 METER

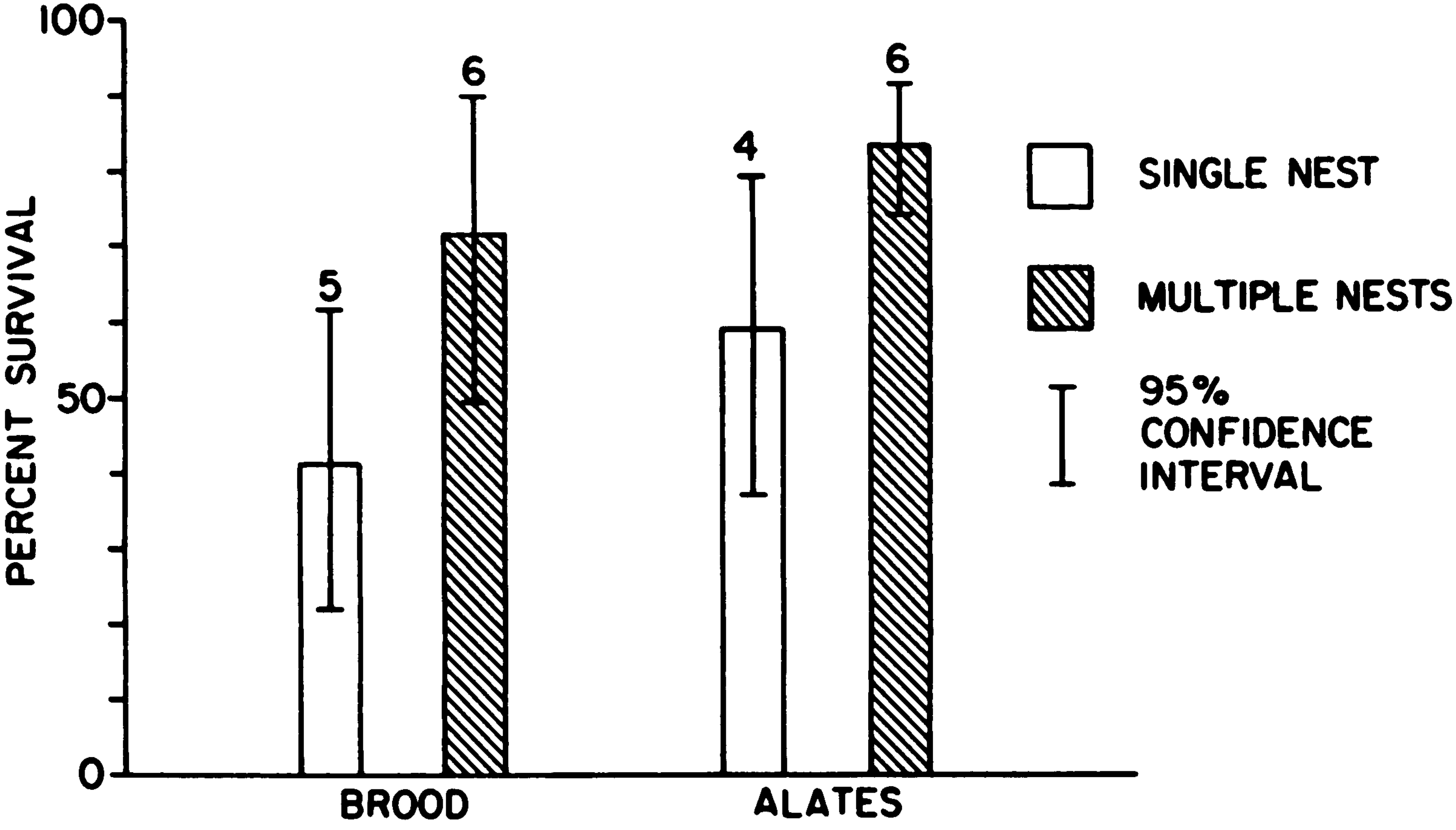


Figure 13. Percent survival of brood and alates after a nest evacuation. The numbers above each bar indicate the number of replications.

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