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MIRENDA, JOHN THOMAS
FIELD STUDIES OF RAIDING AND EMIGRATION IN
THE ARMY ANT, NEIVAMYRMEX NIGRESCENS.

CITY UNIVERSITY OF NEW YORK, PH.D., 1978

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FIELD STUDIES OF RAIDING AND EMIGRATION IN THE ARMY ANT, *NEIVAMYRMEX NIGRESCENS*

by

John T. Mirenda

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

1978

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

FIELD STUDIES OF RAIDING AND EMIGRATION IN THE ARMY ANT, NEIVAMYRMEX NIGRESCENS

by

John T. Mirenda

Adviser: Professor Howard Topoff

A field study of the behavior of the nearctic army ant, Neivamyrmex nigrescens, was conducted to provide a quantitative description of raiding and emigration characteristics, and to examine the relationship between these complex social behaviors.

There was a vast difference in raiding activity between the nomadic and statary phases, but colony size also affected the intensity and success of raiding. Hence the amount of food gathered per individual in the colony was relatively constant within one behavioral phase. Emigration directions and distances varied widely and unsystematically over the course of the nomadic phase, and there was a small probability of a failure to emigrate on any nomadic day. There was also much variability in emigration onset and duration times, which was primarily due to success or failure to find a suitable nest site before the emigration started. Colony size also affected emigration duration.

Emigrations were usually preceded by raiding, proceeded over a successful raid column, and terminated in or near a group of raid sites. However, recruitment to food was not a necessary precondition for emigrations, nor did emigrations always move into areas of heavy raiding. The new nest was not usually formed in a site where food was also obtained, and there was a short latency from the time these sites were first discovered to the start of the emigration. The direction, distance, and timing of emigrations were affected more directly by the discovery of a suitable nest location than by any aspect of raiding success. Nevertheless, both raiding and emigration activity were eliminated by artificially overfeeding colonies; therefore these behaviors share a common motivating factor, which is most probably brood stimulation.

Social organization during raids and emigrations is maintained by the interplay between general arousal from the brood and recruitment to specific stimuli. Different recruitment systems to prey and to nest sites promote efficient use of surface activity time, and prevent exposure of the queen and brood before another nest is available. The tendency to emigrate into an area where there has been heavy raiding results from the discovery of a nest site in or near the raid sites, and probably allows the colonies to follow their food supply.

Acknowledgements

I wish to thank Dr. Howard Topoff, the principal sponsor of this research, for introducing me to army ants, and for the intellectual stimulation, thoughtful guidance and encouragement he provided at every point in my graduate career. Drs. David Miller, Carl W. Rettenmeyer, Carol A. Simon and Gerald Turkewitz also read this manuscript and made helpful comments. I am especially indebted to Doug Eakins, Lisa Franz, Karen Gravelle, Susan Herrick and John diMatteo for their indispensable assistance on many long nights in the desert. Favors by many people helped significantly during the preparation of this paper, and I particularly want to thank Kevin Kearney, Mark Jacquin and Patricia Mirenda for stimulating discussion and encouragement, Pat Levitt for preparing many of the figures, and Rosemary Cicchetti for typing the manuscript.

This research was supported by PHS Grant 1T32MH14280-03 to the Training Program in Animal Behavior-Biopsychology, jointly sponsored by the City University of New York and the American Museum of Natural History; and by NSF Grant BNS76-17366 to Howard Topoff.

This paper is dedicated to the memory of Auguste Forel and T. C. Schneirla.

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INTRODUCTION

Army ants first came to prominence through the descriptions of naturalists in the American tropics (Bates, 1863; Sumichrast, 1868; Belt, 1874), who were fascinated with the ants' large-scale predatory forays, their frequent changes of nest location, and the high degree of coordination between individuals that allowed the expression of these complex behaviors. To the present day their distinctive behavioral traits--group-predation and nomadism--and the processes underlying them have stimulated considerable scientific interest and research on the army ants.

T. C. Schneirla made the first detailed inquiry of army ant behavior in a series of studies in Panama in the 1930's. At this time the dominant explanation of their nomadism was that the movements were caused by exhaustion of the food supply after a colony had resided in and raided over an area for a long period of time (Vosseler, 1905). The colony, in response to a depleted food environment, would move off in search of more fertile feeding grounds. Schneirla's first field observations convinced him of the incorrectness of this hypothesis because colonies moved out of areas that still contained much potential prey. Other external environmental factors (weather, lunar cycle) were ruled out because colonies in the same area were at very different points in their behavioral cycle.

Schneirla (1938, 1940) found instead that the behavior of two species of *Eciton* in Panama alternated between two contrasting phases: in the statary phase (SP) a colony maintained a single nesting site for 18 to 22 days from which it foraged irregularly for food; in the nomadic phase, which lasted between 15 and 18 days, the colony changed its nest almost nightly and foraged more frequently and intensively for food.

Perhaps the most significant finding was that the behavioral phases of *Eciton* were correlated with the condition of the colony's brood (Schneirla, 1938, 1940, 1949; Schneirla and Brown, 1950). When the brood was in the pupal stage the colony was statary. The queen became physogastric midway through this phase and produced another brood. When the pupal brood emerged and the recently laid eggs were hatching into larvae the queen became contracted and the colony became nomadic.

To explain this nomadic-statary cycle (NSC) and its correlation with particular stages of the brood's development Schneirla (1938) proposed brood-stimulative theory:

> Briefly, as each statary phase ends, the colony is aroused by high-level stimulation from an emerging callow brood and begins a nomadic phase. As the callow arousal effect wanes, the nomadic phase is maintained by the stimulative effect of a developing larval brood. When these larvae become mature the colony lapses into reduced function, and a

> statary phase then runs its course under low-level stimulation from this brood in its pre-pupal and pupal stages.

According to Schneirla, this theory accounts for the regularity in timing and the duration of the phases of cyclic behavior in other species of *Eciton* (Rettenmeyer, 1963) as well as in *Neivamyrmex nigrescens* (Schneirla, 1958), *Aenictus laeviceps* and *A. gracilis* (Schneirla and Reyes, 1966, 1969). Cyclic behavior is more variable in *Dorylus* (*Anomma*) *wilverthi* (Raignier and van Boven, 1955) but even in this species the transition from the SP to the NP is correlated with the emergence of a massive callow brood. Brood synchronization and the degree of coordination between broods are both less pronounced in *Dorylus* than in the genera considered above; thus the stimulation from the brood is a less potent factor, which accounts for the lesser degree of regularity and precision in *Dorylus*' cyclic behavior.

The evidence for cyclic behavior in *Labidus*, *Nomamyrmex*, *Cheliomyrmex*, and other species of *Neivamyrmex* is much less complete. The main difficulty in evaluating the nomadism of these army ants is the infrequency of their surface activity. Although it seems likely that cyclic behavior is less highly developed in the more hypogaeic species, nearly all the emigrations seen in these genera have nevertheless been accompanied by the presence of callows or a synchronized larval brood (Rettenmeyer, 1963). Brood-stimulative theory thus remains a powerful tool for understanding the different patterns of nomadism exhibited by army ants.

Schneirla also used the factor of brood-stimulation to explain variation in behavioral characteristics <u>within</u> each phase:

1. The transition from raiding to emigration on any nomadic day (ND) is triggered by brood stimulation (Schneirla, 1971: 105):

> ...at dusk with environmental influences greatly reduced in variety and potency, three types of stimuli assume control. These are brood or booty to carry, a chemical trail to follow, and nestmates as sources of sensory influences on running. We may postulate this effect: the great brood, responding to day's end changes in its own condition and in worker behavior, undergoes an increased excitation that causes workers to pick up the larvae and carry them forth.

2. Colonies do not emigrate on every night of the NP, however. Schneirla and Brown (1950) reported that failures to emigrate are most likely between ND 2 and 6. This is the interval between the maximum callow arousal effect and the maximum larval arousal effect (Schneirla, 1944, 1957, 1971: 159).

3. Emigrations are longer and raids are larger at the end of a NP than at the beginning because the larval brood presents an increasingly potent stimulus as it matures (Schneirla, 1944, 1971).

4. Army ant colonies raid more intensively as the SP comes to a close. This increased activity is supposedly due to the movements and secretions of pupae about to eclose (Schneirla, 1971, Ch.6).

Schneirla (1971) also stated that emigrations begin earlier in the day in the early part of the NP and that emigration durations increase as the NP proceeds. Though he did not explicitly relate emigration onset or duration to his theory of brood stimulation, we may assume that these characteristics are also affected by the level of brood stimulation in the colony. Emigrations should therefore begin earlier and last longer when brood stimulation is at its highest (i.e. at the very beginning of the NP when the callow arousal effect is at its maximum, and at the end of the NP when the larval brood stimulation is at its maximum).

There is little quantitative data to support any of these contentions, and Rettenmeyer (1963) has furthermore shown that the longest emigrations of _E_. _hamatum_ and _N_. _nigrescens_ occur in the middle of the NP. It may be that brood-stimulative theory has been applied inappropriately to the characteristics of raids and emigrations within the NP and SP, or that brood-stimulation is not related to this aspect of army-ant behavior. The first purpose of this paper is to test the statements of Schneirla regarding variations in the characteristics of raids and emigrations within a behavioral phase. To do this I have provided a quantitative description of emigrations and raids throughout the NSC of a representative army ant, _N_. _nigrescens_.

In his review of the behavior of the New World army ants, Rettenmeyer (1963) basically agreed with Schneirla that brood-stimulation was the major factor underlying behavioral phase differences, but he saw more room for other factors to influence raids and emigrations. His position is summarized in the passage that follows (p. 456):

> I agree with Schneirla's main theory that the brood or broods are the primary stimulus inducing raiding and emigrating; however, I believe he has gone too far in discounting the influence of the amount of booty on the activity of the ants. The amount of booty in an area affects the direction, distance, and duration of raids and emigrations. Although it has not been demonstrated, it would appear that the amount of food within bivouacs must influence the amount of activity of the larvae, and thus, their stimulation of the adults.

Army-ant colonies are quite large and consume a considerable amount of arthropod prey (Rettenmeyer, 1963; Schneirla, 1971). Colonies become nomadic when their food-consuming capacity is greatest--with a larval and callow adult brood present in the nest (Schneirla, 1971). For these reasons army-ant nomadism has been viewed as an adaptation which allows colonies to move to new feeding grounds

(Schneirla, 1949, 1957).

Wilson (1958, 1971) has further suggested that nomadism evolved as a result of specialization on large arthropods and social insects for prey. Since the evolution of behavior cannot be traced directly, the reconstruction of historical "steps" depends upon circumstantial evidence derived from comparisons with living species. Nevertheless, Wilson's account is plausible: first comes group raiding, an adaptation that makes the exploitation of large arthropods and social insects possible; second, nomadism arises to facilitate shifting the colony's "trophophoric field". Periodic shifting is needed because large arthropods and social insects are "more widely distributed than other types of prey".

Wilson (1958) may also have provided some insight into the early stages of army-ant behavior. He reported that two species of the ponerine tribe Amblyoponini, Amblyopone pallipes and Myopopone castanea, recruit colony members and carry their larvae to large prey items, by which the colonies may sometimes change their nests. The adaptive result of this behavior may be to bring the colony to a micro-habitat where abundant and/or preferred food is located, or to facilitate the exploitation of the food already found.

Army-ant emigrations typically progress over previously established raiding trails, and recruitment to food may form a necessary link in a chain of events leading to an emigration. In the course of raiding Eciton forms caches of booty along the trails (Schneirla, 1971: Chaps. 3, 5; Rettenmeyer, 1963). I suggest that these caches have two effects: 1) they increase the effectiveness of foraging since raiding ants can leave the food safely without having to travel back to the bivouac; 2) they increase the recruitment of other workers to areas of the raiding trail system where caches are formed.

Using chemical trail substances and tactile cues, army-ant foragers who have discovered prey can recruit hundreds of other workers to the site within minutes of its discovery (Chadab and Rettenmeyer, 1975). The ants are normally recruited from adjacent positions of the raiding columns, but Topoff (in preparation) has shown in the laboratory that the signals can persist long enough to recruit workers from the nest. The emigration may result from a sustained recruitment of first other raiders, and then brood-tending workers and their charges to the raid sites. Emigrations of the fire ant Solenopsis saevissima (F. Smith) were induced in the laboratory with massive doses of extracted trail substance normally used to direct nestmates to food (Wilson, 1962).

The recruitment-to-food mechanism might also allow the colony to keep emigrating in the direction of the greatest food supply. I showed above that Rettenmeyer (1963) believed that the location and amount of captured food exercised a strong influence on the course of army-ant emigrations. Unfortunately, he provided no quantitative evidence on this point. Schneirla (1938) once stated that the colony emigrated along the heaviest raiding route of the day, though he did not provide any quantitative evidence either. In his later writings Schneirla abandoned this idea altogether, and implied that the location and size of food sites outside the bivouac played only an incidental role in determining the route of the emigration (i.e., they helped to determine the path of least resistance). He cited the case of an _E_. _burchelli_ exodus which was forcibly diverted from the major raiding path of the day by heavy incoming (toward the bivouac) traffice, and which eventually emigrated over another route (Schneirla, 1971, Figure 5.1 and pp. 104-105).

When a colony sends out two or more raiding columns prior to an emigration, opportunities to make a direction "decision" should arise. Each raiding column may find some food, but that column which has found the largest source of the best booty should have the most numerous and vigorous recruiters "advertising" it to nestmates; hence the colony should always emigrate towards the area of their greatest raiding success. A similar resolution to this type of conflict occurs during honeybee swarming (Lindauer, 1961).

Even the probability of emigration occurrence may depend upon the location and abundance of the raiding sites. If abundant food is found close to the nest, it should be exploited fully before moving on. The food will be carried back to the bivouac, increasing the food supply there. No cache will form; recruitment out of the nest will wane; no emigration will occur. If food is found farther from the nest the likelihood of cache formation is greater and so is the likelihood of emigration. The farther the ants must go to find food, then, the greater the chance that an emigration will occur. This hypothetical mechanism serves to take the ants out of an area inadequate in food and to keep them in areas where a "windfall" occurs.

The recruitment-to-food theory of army-ant nomadism generates several hypotheses that I have tested with observations and experiments on _N. nigrescens_:

1. A colony will recruit to food before an emigration.
2. A colony will sample different areas around the bivouac for food prior to the emigration.
3. Raiding ants will form a booty cache in or near the future nest before the emigration starts; this cache will serve as a focus of recruitment from the nest that will gradually lead to an emigration.
4. A colony will recruit most heavily to and then emigrate

toward the area of greatest raiding success; frequently the emigration should proceed into a raid or cache site where much booty has been captured or stored.

5. The colony will emigrate short distances or not at all when abundant food is found close to the old bivouac.
6. The colony will not emigrate whenever the booty store inside the current bivouac is high.

Hypotheses 1-4 were tested simply by observing the sequence of events from the time that the colony becomes active in the early evening, through the time when the emigration begins. It is necessary to cover all raiding columns thoroughly, taking the following measurements on each: number and location of raid and cache sites, the times during which those sites are used by the ants, the amount of booty captured (or some other measure of raiding success).

Hypothesis 5 was tested in the same way as 1-4 but also by experimentally adding food close to the bivouac at the onset of the colony's surface activity period.

A test of Hypothesis 6 required counts of the entire booty intake of a colony from each of a consecutive series of nomadic days (NDs) and was also tested by experimentally increasing the colony's booty supply.

METHODS

Observations and data were obtained between July and September in 1976 and 1977.

The Study Site

The study area was located 5 miles NW of Rodeo, in southwestern New Mexico (Hidalgo County). At an elevation of 1253 meters this desert-grassland community (Lowe, 1964) receives about 287 mm of rain annually, and has mixed vegetational cover (Table 1). Several shrubs dominate the landscape for most of the year--*Prosopis glandulosa*, *Ephedra* sps., *Acacia greggi*, and *Gutierrezia* sps.; however, following heavy rains in July grasses (*Hilaria mutica* and and *Bouteloua* sps.) and a great variety of annual flowering plants come to predominate in this ungrazed portion of flat valley bottomland. Parts of the study area are flooded for several hours following the summer cloudbursts.

Surface soil temperatures on the site averaged 50^{o} C at 15:00 hours throughout the summer and 17^{o} C at 02:00 hours. Considerable variation in temperature is introduced by the type and percent of cloud and vegetational cover. There is less variability in these factors on my site than in the nearby canyon where Schneirla (1958, 1961, 1963) studied *N. nigrescens*. This relative stability and the greater aridity (see Table 1) provided an advantage which contributed greatly to the efficacy of the research.

Since the ants did not begin their surface activities until approximately 19:00 hours on most days it was possible to be at their nest sites before they became active and chart their surface activities as they developed. On some days we arrived soon after their emergence from the subterranean nest and found their raiding fronts only a few meters from the nest opening.

A second important advantage provided by this site was the excellent view of the ants' surface activities. Approximately 70% of the flat, pavement-like substrate lies exposed and unsheltered by surface vegetation in July. This proportion gradually shrinks to about 30% by the middle of September as grasses and annuals reach their culmination. Even in late summer the ground cover did not, except in rare cases, obscure more than a meter or two of the length of an army ant column. At times the cover hindered examination of portions of the column, but at no time did it render unobservable more than 10% of the total area which any colony was exploring. Nevertheless, to avoid visibility problems, we made the natural observations in the early part of the summer, and conducted experiments that did not require an extensive clear field later in the summer.

Finding, Identifying, and Maintaining Colonies in the Field

Colonies of army ants were found by walking through the study area in the early evening while visually scanning the ground. Illumination was provided during this early stage with a double-mantled Coleman gas lantern.

Three species of army ants were found in this study area: *Neivamyrmex nigrescens*, *N. harrisi*, and *N. fallax*. *N. nigrescens* was the most frequently encountered species. Its conspicuousness was largely due to the extent of its activities on the surface, including raids and emigrations, but colonies were also numerous throughout the summer months, averaging about one colony/hectare. In contrast, only once in two summers was *N. harrisi* seen emigrating, though this species was frequently encountered raiding for short distances on the surface, sometimes in very close proximity to *N. nigrescens*. *N. fallax* was seen least frequently and was never encountered on an emigration. Individual workers of *N. nigrescens* also appeared darker and slimmer-bodied than their sympatric congenerics, but we always confirmed species' identifications using the taxonomic criteria of Watkins (1972, 1976).

Each colony of *Neivamyrmex* encountered was given a designation consisting of three parts: year, species, and colony number. For example, the designation 76N-3 refers to the third colony of *N. nigrescens* encountered in 1976.

The colonies were observed at close range with miner's cap lamps powered by rechargeable lead-acid batteries worn around the belt (Minespot Safety Appliance Co., Pittsburgh). These units provided a long-lasting, moderately powerful, and focusable beam of light which did not disturb the ants when used properly. It was necessary to refrain from long periods of observation at a single point on the column and from bringing the light too close. At a viewing distance of about 0.5 meters the illumination was sufficient to easily distinguish the behavior of individual ants and yet was not disturbing to them. When the ants were particularly sensitive (during emigrations and on windy nights) it was necessary to outfit the cap lamps with red filters, which made observations more difficult but prevented disturbances caused by the unfiltered beam.

Visual inspection of the emigration column of a newly encountered colony was sufficient to indicate the approximate position of the colony in its NP. Both Schneirla (1949, 1961) and Rettenmeyer (1963) have shown that larval size increases steadily during the NP. Because of the shorter developmental period of the larvae in this study I constructed larval growth curves from several colonies studied (Figure 1). Between 100 and 200 workers carrying larvae were collected from several sections of the emigration column. In the lab the workers and larvae were separated (within 12 hours of collection) and the length of the ten largest and ten smallest larvae in the sample were measured under a microscope. I repeated this procedure on successive NDs for several colonies. Though no series of measurements from one colony spans the entire NP, series from different colonies overlap and show good concordance (particularly in the growth of the small larvae). Using Figure 1 it was possible to make a good estimate of the ND of any colony encountered on an emigration simply by sampling 100-200 larvae and determining the sizes of the largest and smallest larvae. These curves were used to determine the maximal point in the NP of colonies 76N-8 and 77N-5, as they were encountered after the onset of their NPs. Measuring larvae on successive NDs also served as a check on colony identity and health.

The presence and distinctiveness of the newly eclosed adults, or _callows_, usually reinforced the conclusion based on information from the larvae. At the onset of the NP the callows were extremely pale (some may even be carried by adults on the emigration), but grow less discriminable from the darkly pigmented mature adults as the NP proceeds.

It was sometimes possible to estimate the position of colonies encountered in the course of the SP. _N. nigrescens_ does not go through full-scale emigrations during this phase, but workers occasionally move the brood (in the pupal stage) for short distances across the surface to nearby holes. These statary shifts expose the brood to examination. Throughout most of the SP the pupae are strikingly white, but pigmentation develops rapidly during the last few days before eclosion.

Employing these signs, certain colonies were selected for intensive study. Table 2 gives the designations and dates of study of these colonies. In the early summer my assistants and I observed a colony in the early part of the NP, or late part of the SP, and studied it through the completion of its NP. It was checked and observed periodically during the SP while attention was focussed on another colony that had meanwhile become nomadic. When the second colony was completing its NP, the first colony was just becoming nomadic again, and we would shift back to it; and so forth throughout the summer. It was also possible, through brief checks of other colonies, to acquire data from them for comparison with that on colonies observed or experimented with.

Colonies were not marked, and bivouac location was the main key to colony identity from one ND to the next. Hence, colonies in or near the NP were checked at least once between the hours of 02:00-05:00, since emigrations sometimes started in this interval. On the few occasions when the colony was not found at the previous ND's bivouac site, it was located a few meters away in the direction of the previous ND's heaviest raiding. On the next emigration larvae were sampled and measured to confirm colony identity.

Observations of Raids and Emigrations

In 1976 we observed events at the basal portion of raiding columns. A raiding column was defined as any trail of ants that had a separate connection with the next opening, that was used for at least 15 minutes and extended at least 5 meters from the nest. On each such column an observer was stationed alongside a clearly exposed section within 5 meters of the nest and, lying prone with headlamp trained on the column, counted the number of ants leaving the nest and the number of ants returning to the nest with booty. The counts were made for periods of 5 minutes at intervals beginning every 15 minutes. During the 10-minute break between counts the observer sampled prey items, which were weighed within 12 hours and then preserved for future identification. These observations usually began at the onset of raiding at dusk and continued on many nights through any or all emigrations until the raiding and other activity ceased at dawn.

In the early part of 1977 colonies were observed to determine the nature of events at the periphery of the raiding nexus. We recorded the number and distribution of raid sites, caches, other potential nest sites, and major landmarks of the raiding nexus (trail-junctions, bends, etc.). Also recorded were the duration of raiding at each site, the types of prey attacked, and the defensive behavior of the prey. Counts of booty were occasionally taken, but with less regularity than in 1976. These observations were carried out for the most part from the onset of raiding at dusk until the first emigration of the evening began.

A raid site was defined as any hole in the ground along a column where the army ants entered empty-mouthed and re-emerged carrying a piece of booty. A cache site was defined as any location (on or below the surface) along a column which the ants entered with booty but re-emerged from empty-mouthed. Also recorded were locations of holes other than raid or cache sites which the ants explored for more than a few minutes; these might have become the next nest for the colony when it emigrated.

The observer measured the direction and distance from the nest to each site. Direction was measured with a pocket compass (North=0°) and distance with a measuring wheel. Direction and distance from one nest site to another on successive emigrations was measured in the same way. The raiding and emigration routes were sketched roughly as they developed, then recorded permanently the next morning in maps incorporating the location of the important sites on each column.

An emigration provided the ideal time to estimate the size of the colony. _N_. _nigrescens_ tended to send out only one raiding column before the emigration started (see Figure 43). This enabled us to obtain a count of the complete colony. Before the emigration began one observer counted the number of ants leaving the bivouac; the second observer counted the number of ants returning with booty (these two measures are shown in Figure 36); the third observer counted the ants returning without booty. When the emigration began the first observer continued to count ants moving outward carrying larvae; the second counted ants moving outward without larvae; the third counted ants returning to the nest (who were all unladen). Counts were made simultaneously during 2-minute periods at intervals beginning every 6 minutes. There was a constant rate of traffic in both directions within these brief time intervals (spot checks were made of the column between counting periods). Integration of the three counts yielded total number of workers and total number of larvae in the colony. Table 2 shows the number and sizes of colonies studied during several behavioral phases, and whether the sizes are based on complete counts or on estimates based on partial counts of the colony.

Feeding Experiments

These experiments were conducted on three colonies on a total of 20 NDs (see Table 14).

The first prerequisite was to collect the right type and amount of food. Though some species of army ant may eat various kinds of plant materials along with their normal animal prey (Borgmeier, 1955; Rettenmeyer, 1963), _N_. _nigrescens_ is known to be strictly carnivorous (Rettenmeyer, 1963; Schneirla, 1958). Our observations of raiding confirmed this finding and also the preference this species has for termites and ant brood.

Because the nests of desert-dwelling ants require difficult excavation before brood chambers are reached, food was collected only in the riparian deciduous woodlands. As a result, most of the food we collected was from species upon which our colonies did not predate. However, _N_. _nigrescens_ colonies in the riparian forests do prey upon those species that we collected (personal observation). In any case, our colonies avidly took all fresh ant brood or termites offered to them, regardless of species.

Food was usually collected in the morning and afternoon preceding the night of the experiment by turning over rocks and logs, then removing a large proportion of the brood inevitably exposed. It should be noted that we did not collect the entire colony, excavate the nest, or remove any queens; only the brood available on the surface was collected. This procedure protected the vast majority of workers as well as the queen. Any surface cover that we disturbed to expose the brood was carefully replaced after the collection.

When luck was good we collected enough food for up to two days' experiments in one search. The unused portion was kept dry and chilled during the day. Food stored in this way was attractive to the ants up to three days from the time of collection.

The counts of booty gathering during 1976 (see Tables 5 and 7) indicated that we had to provide approximately .40 mg of booty/ND/larva on the average to equal a normal night's foraging. We estimated the size of the larval brood during the first emigrations of the NP, then collected an amount of booty sufficient to equal or surpass the above mentioned ratio. Subsequent counting of the colonies confirmed that we administered more than an average night's booty in 17 out of the 20 experimental nights, and came extremely close to that amount on the other 3 nights (see Table 14). Due to an overestimation of colony 77N-8's brood we tended to overfeed them by a factor greater than 2.0.

We began the experiments early in the NPs of colonies 77N1-A and 77N-8, but inclement weather forced a delay in the onset of the experiment with 76N-3 until ND 9. The experiment was conducted on NDs 9-13 with 76N-3, on NDs 3-6 and 8-12 (postponed on ND 7 because of inclement weather) with 77N-8, and on NDs 2-5 and 10-11 with 77N-1A. The break in the experiment with 77N-1A occurred because its activity level became so low that we feared for the colony's health, and gave it a few days to recover before resuming the experiment.

On a typical experimental night my assistants and I arrived at the colony's nest site well before sunset and awaited the first stir of activity from the nest. As the ants formed a sustained column we placed the wooden feeding box (30x30x1.5 cm, with plexiglas top) in a clear area alongside the column between 3 and 5m from the nest opening. We next built a ramp with moist dirt leading from the ground to the box entry hole. A few termites or other booty were then scattered in front of the advancing column; these were quickly seized by the ants who were led in this manner into the vicinity of the box entry point. The box was then loaded with booty through holes in the plexiglas top. The ants quickly discovered this "windfall" and recruited their nestmates to it. Soon the inside of the box was covered with swarms of army ant workers.

As the ants entered the box an observer determined the rate of recruitment (ants/minute) to it and the rate at which booty was carried out of it. These counts were taken at the box entry hole for 30 seconds at intervals beginning every five minutes; they were continued until activity at the box ceased. These counts showed us the responsiveness of the colony to food and also served as a check on the quantity of food delivered.

In order to maximize the rate of recruitment to the box and booty capture, the box was kept full of food at all times. A typical experiment only took about two hours to complete and thus did not restrict the colony's activity to the area around the box for a long time. This intensive feeding allowed us to evaluate the effects of a rapid increase in the colony's food supply on subsequent behavior.

RESULTS

Cyclic Behavior in *N. nigrescens* and its Correlates

A. Length of Behavioral Phases and Cycle

Table 2 shows the duration of the behavioral phases of the colonies studied. Eight complete NSCs, starting with the first day of a SP and continuing to the last day of the subsequent NP, from 5 colonies averaged 30.3 days in length. Nine complete NPs averaged 13.1 days in length. The addition of 2 more NPs which we did not observe from their onset but for which we have maximum estimates of their length (based on sizes of larvae) brings the average to 13.2 days. Nine complete SPs averaged 16.9 days in length. The variation in phase lengths between colonies is low.

B. Sizes and Growth of Individuals and Colonies

All-worker broods were raised during the NPs described above. Figure 1 charts the growth of these worker larvae over the course of the NP. There are two sets of points in the figure: one showing the average length of the ten largest larvae and one for the average length of the ten smallest larvae. When the NP begins some of the larvae have already reached 2.0 mm in length--these probably go on to become major workers between 5.0 and 6.0 mm. The minor workers average approximately 0.5 mm when the NP begins and attain a length of 2.5-2.75 mm. Both groups reach their full length by ND 14.

We counted several colonies during emigrations, and some of these in successive NPs, and are thus able to describe the growth of colonies (see Table 2). First, larval brood sizes ranged between 20,000 and 30,000 individuals. Second, many colonies started out their summer's surface activities with an adult:brood ratio considerably less than 1.0. Third, the worker population of all colonies increased over the course of the summer. By the second NP of the summer the adult:brood ratio always exceeded 1.0. This was true even for colony 77N-1A, whose first NP (7/23-8/4) was with a callow queen and only a few thousand of her mother's worker larvae (all males had gone with the mother colony). When that queen produced her first brood (during the SP of 8/4-8/22) the result was to bring the ratio below 1.0 again. However, upon the eclosion of her first brood, the ratio undoubtedly exceeded 1.0 again.

Observations of Raids

A. Onset and Duration

The colonies were completely inactive on the surface during the day. Unless it was an unusually cool or cloudy day the colonies did not become active on the surface until sometime after sunset (between 18:00 and 19:00 hours during the summer.

Table 3 shows the starting and ending times of raids in the NP and SP of two colonies in 1976. In the NP the colonies raided almost continuously from dusk to dawn, except for intervals during the emigrations (see Effects of Emigration on Raiding). Raiding activity was more variable in the SP. On the first two statary days (SDs) raiding began early in the evening but ended after a few hours. Between SD 3 and 10 very little raiding occurred, and raids that did occur began late in the evening and lasted only a short time. From SD 11 onwards raiding was more frequent, lasted longer, and started earlier in the evening.

B. Discovery of Raid Sites

In 1977 we observed events at the periphery of raid columns of nomadic colonies, locating raid sites as they were discovered by the ants. These observations also began at the onset of raiding at dusk but were continued for a variable time afterwards. Typical raid patterns for colony 77N-1A are shown in Figures 2 and 37; for colony 77N-5 in Figures 3, 4, and 38; and for colony 77N-7 in Figure 5. The figures do not show the full area that a colony covers in the course of raiding. For every branch of the columns shown in these figures, there were many more which formed from the main trail but did not persist long enough to find raid sites (perhaps they did not persist <u>because</u> they did not find raid sites). Nevertheless, an approximate measure of the area covered by each column was obtained by treating the raiding patterns in these figures as points on a plane surface, and forming a polygon with the nest and the outermost raid sites on each column as the vertices.

Table 4 presents a summary of the following characteristics of these raids on several NDs: number of columns, area covered by them, number of sites raided; also shown are the hours of observation on each ND and rates of area covered and of discovery of raid sites.

First, there does not appear to be any increase in the magnitude of these characteristics as the NP progresses. Second, though each colony was observed for about the same number of NDs and total hours, 77N-5's raiding statistics are about twice those of 77N-1A. These differences are most certainly due to colony size. Colony 77N-1A only had 9500 workers while 77N-5 had at least twice that number (Table 2). For further comparison, the raiding activity of colony 77N-7, whose worker force was estimated at over 80,000 during this NP, is presented in Table 4. This colony exceeded the average m^2/hr and raid sites/hr of the other colonies, though this was only an average ND's raiding for 77N-7. This colony was too large for even three observers to handle and we did not continue these observations with it on subsequent NDs.

Ant nests were extremely abundant and diffusely distributed in the study area, and all colonies found prey close to their nest within a few minutes of the start of their activity on the surface. Differences between the colonies in the latency from the beginning of activity of their columns to the discovery of the first raid site were not significant (77N-1A: M = 9.4 m, S.D. = 7.4m; 77N-5: M = 6.2m, S.D. = 4.4 m; t = 1.67, df = 38, $p > .05$). The pooled data shows that an average raid column found its first prey in 20.3 min from the time it first became active (S.D. = 16.9 min) and that this site was found at 7.4 m from the nest (S.D. = 5.8 m).

Subsequent raid sites were not far off in space or time. Figure 6 shows the average time of discovery and the average distance from the nest of the first several raid sites for all columns of 77N-1A and 77N-5. The discovery of raid sites in this habitat was a linear function of both the time active and the distance travelled from the nest. The average column discovered a new raid site every 22 minutes at 2 m increments travelled from the nest. Despite the almost continuous discovery of new raid sites, most raiding columns missed many nests of preferred prey types.

C. Booty Intake

In 1976 counts of booty brought back to the nest were made throughout a NSC of two colonies. A total of 147 hours of raiding was observed on 18 NDs, which represents 90% of the hours these colonies were active on those NDs and 60% of the total estimated time the colonies were raiding on

26 NDs. In the SP, 61.25 hours of raiding were observed on 28 SDs, which represents 92% of the hours these colonies raided on those days and 70% of the total estimated time the colonies were raiding on 34 SDs.

Figures 7-22 show the number of pieces of booty brought back to the nest in fifteen-minute blocks on selected NDs. Most of the figures are broken into three time periods: before, during, and after the emigration. On those graphs not so divided, there was no emigration that ND. Figures 7-14 show the booty intake of colony 76N-3 on 8 NDs between 8/5-8/18. Figures 15-22 show comparable data for colony 76N-8 between 7/30-8/8. On most NDs the flow of booty to the nest started within minutes after the colony began to raid and continued until the colony ceased its activity at dawn. The level of booty flow fluctuated greatly from one time interval to another and from one ND to the next. The gaps in booty flow that occurred during emigrations are discussed below (see Effects of Emigration on Raiding).

The booty counts from each day were summed and multiplied by the weight of the booty to determine the colony's gram intake on each day. Tables 5 and 6 show the amount of booty in grams gathered by colony 76N-3 during a NP and SP. Tables 7 and 8 show the intake of colony 76N-8 during its NP and SP. During intervals when no direct counts were made gram intake was estimated. To do this the estimated hours the colony was active were multiplied by one of two quantities: the rate of intake at the time the counts left off that evening (76N-3: NDs 3, 11; 76N-8: NDs 8, 12) or the average rate of intake for the entire counting period (all the remaining estimates). Counts and estimates were summed to arrive at the totals for each colony in each phase.

A nomadic colony raided for about 10 hours and collected a substantial amount of booty each ND. The only exception to this rule occurred with colony 76N-3 on ND 12, when heavy rains and wind kept the colony inactive all night. Visual inspection of the amounts and rates of booty intake in Tables 5 and 7 indicates that booty intake did not increase as the NP progressed.

During the SP the colonies were not active on the surface every night and raided for an average of only 3.7 hours on those nights when they were active. Colonies gathered much less booty in the SP, which was due both to less hours of raiding and lower rates of booty intake. The amount of booty captured began to increase toward the end of the SP, when the hours spent raiding and the rates of booty intake were similar to those of the NP.

For ease of comparison between colonies and phases, the total grams, hours and rates of booty intake in Tables 5-8 are presented in Table 9. Clearly there is more booty captured in the NP than in the SP. Colony 76N-3 gathered more booty in its NP than 76N-8, and gathered it at a higher rate. These differences are also related to colony size. During these NPs 76N-3 had 23,320 workers while 76N-8 had about half that number (Table 2). However, 76N-3 also had more larvae to feed (33,160 vs 22,300) and when this factor is taken into accout the booty intake is more comparable. Colony 76N-3 gathered 0.44 mg/larva/ND; colony 76N-8 gathered 0.41 mg/larva/ND. The foragers of 76N-8 actually worked more efficiently to keep that pace than those of 76N-3, gathering 0.77 mg/worker/ND against 0.62 mg/worker/ND for 76N-3.

In the SP 76N-8 gathered more food than 76N-3 despite the fact that 76N-3's SP was two days longer. Again the difference is related to colony size, and disappears when this factor is taken into account. Colony 76N-8 gathered .11 mg/SD for each of its approximately 33,000 adults while 76N-3 gathered 0.10 mg/SD for each of its 23,000 adults.

Observations of Emigrations

Several important features of the emigration are reported here: frequency, onset time, duration, direction, distance. The summary is based on observations of 8 NPs from the 6 colonies listed in Table 10. The observations do not include any emigrations during a NP in which the feeding experiments were conducted (see Table 2).

A. Emigration Frequency

At least one emigration occurred on 83 of the 94 NDs (88.3%) we observed (see Table 10). On many NDs there was more than one emigration (i.e. colonies moved in sequence to two or more nests, each of which was occupied for at least a half-hour before the next emigration began), which brings the total number of emigrations to 116. Our colonies thus averaged 1.24 emigrations/ND and 1.63 emigrations on every ND on which at least one emigration occurred.

There were no emigrations on 11 NDs. Both the failures to emigrate and the NDs with more than one emigration were evenly distributed among the colonies (Table 10) and occurred at all points during the NP (Table 11). Only one of the failures to emigrate can be attributed to bad weather: on ND 12 for colony 76N-3, the rain was so heavy and protracted that the colony did not venture out of its nest all night. There thus seems to be a small probability of no-emigration on any given ND. The estimate of this probability should be based on a sample of NDs which does not include any first or last NDs since, by definition of the NP, an emigration must occur on those days. The corrected sample of NDs is 81 (94 NDs observed minus 13 first and last NDs) and the estimate of the probability of no-emigration on any ND is .14.

On 3 NDs there were abortive emigrations (i.e., the adults carried larvae out of the nest onto a surface column for a few minutes but later returned them to the old nest). One abortive emigration occurred after a night of heavy rain when the nest had probably been disturbed by flooding; two other instances occurred during normal circumstances and, following the abortive emigration, another emigration began later in the evening and was completed.

B. Emigration Onset and Duration

Figure 23 shows that emigrations usually began between 18:00-24:00 hours: only rarely did an emigration begin outside this time interval. Figure 24 shows the onset times of the 72 emigrations in Figure 23 plotted against ND. Onset times varied unsystematically through the NP, though there may be a tendency for emigrations to begin earlier in the last few NDs. The latest onset times occurred between NDs 5 and 11.

Emigrations averaged 4.2 hours in duration (S.D. = 1.7 hours, n = 29). Figure 25 shows the distribution of these emigration durations and Figure 25 shows emigration duration as a function of ND. It is evident from both these figures that emigration durations vary widely. Though there may be a tendency for durations to increase as the NP progresses, the variance in duration is not strongly related to ND. A Kruskal-Wallis one-way analysis of variance (Siegel, 1956) shows that emigration durations vary significantly between colonies (H_c = 2103, df = 5, $p < .001$). A rank-order correlation shows that average emigration duration is perfectly correlated with colony size (r_s = 1.0, n = 6, $p < .01$).

C. Emigration Distance and Direction

Table 10 shows the total distance emigrated during the NP, the average distance moved/ND and the average distance moved/emigration for each NP observed. The differences between the NPs in m/ND are significant (H_c = 14.76, df - 7, $p < .05$) while differences in m/emigration are not (H_c = 9.78, df = 7, $p > .05$). Thus, any differences in the total distance covered by a colony result more from differences in the number of emigrations than to longer emigrations. The rank-order correlation between number of emigrations per NP and total distance moved for the 8 NPs in the sample is .86 ($p < .05$). Larger colonies tended to emigrate farther during the NP than smaller colonies, (r_s = .71, N = 7, p =.05).

Figure 4 shows the distribution of emigration distances on the 83 NDs on which an emigration occurred. Figure 28 shows these distances as a function of ND. As with onset and duration time it is clear that the distance emigrated is variable but does not increase as the NP progresses. In fact, the longest emigrations occurred in the middle of the NP, between NDs 4 and 10.

For each NP an index of directionality was calculated from the direction of all the emigrations that occurred in that NP (i.e. degree readings, with North = 0^{o}, from nest 1 to nest 2, from nest 2 to nest 3, etc. to all nests occupied in the NP). This index is an empirical mean vector (Batschelet, 1965) and has 2 components: θ, the mean direction in degrees (North = 0^{o}) of the emigrations, and r, the strength of movement toward that direction, which varies from 0 to 1.0. These measures are also presented in Table 10. The significance of r is assessed with the Raleigh test (Batschelet, 1965). According to this test, only during two NPs was there a significant concentration around θ. During the other six NPs the distribution of emigration directions does not differ significantly from a uniform distribution.

Figures 29-34 are maps of the colonies' movements that we have been considering. The variation from ND to ND in direction and distance moved is apparent in all the maps. Only the movements of colony 77N-7 (second NP in Figure 33) and of colony 77N-8 (Figure 34) show a consistent directional preference. Nevertheless the colonies did usually move away from areas recently occupied. They accomplished this by holding a very general heading for two or three NDs, then changing that heading for the next few NDs, and so on. The heading changes were rarely so dramatic as to bring a colony back to an area just vacated, nor were the changes so regular as to bring the colony in a circle by the end of the NP, though this almost happened to colony 77N-5 (Figure 32).

Relationship of Raiding and Emigration

In this section observations are presented which bear on the hypotheses of the recruitment-to-food theory. All observations were made during the NPs listed in Table 2 and include all NDs except those on which feeding experiments were conducted. The number of cases reported varies from one type of observation to another. This is because some characteristics of activity (e.g. whether raiding precedes an emigration) are easier to observe with certainty than others (e.g. whether a cache forms somewhere along the raiding nexus).

A. The Raiding-Emigration Transition

Workers usually form and maintain surface columns, encounter prey, recruit nestmates to the raid sites, and bring booty back to the nest for some time prior to the onset of the emigration. Some degree of raiding preceded 89.5% (77/86) of all emigrations observed. Figure 39 shows the frequency distribution of time intervals between the onset of raiding and the onset of the emigration. Of the 77 emigrations in the sample, 53 (68.8%) began within 4 hours after the onset of raiding. A very few emigrations began extremely late in the evening (Figure 22); these are the emigrations which began between 6-10 hours after the onset of raiding in Figure 39.

The activity of colony 77N-8 on ND 1 is typical of the sequence of events leading from raiding to emigration from an observation point at the base of the raid column. The activity is shown in Figure 36. The colony became active on the surface at 18:05 as workers poured out of the nest in a wave. Outgoing traffic began to wane after 15 minutes as ants began to return to the nest with booty (the figure does not show the number of ants returning to the nest without booty). The booty-laden traffic peaked at 18:40, then dropped off considerably. A second wave of outgoing traffic occurred at 19:00, dropped off in 20 minutes, and was followed by a higher peak of booty return. Outgoing traffic peaked again at about 19:40 but fell off rapidly. At 20:00 the greatest amount of booty-laden traffic yet returned to the nest. This wave of returning traffic waned by 20:30; meanwhile outgoing traffic increased again and at 20:50 callows carrying larvae were in the outgoing traffic: the emigration had begun. Booty-laden traffic continued to the nest for a few minutes more, but by 21:00 this traffic had been totally reversed by the steadily increasing exodus of callows and adult workers carrying egg masses, microlarvae and booty outwards.

The activity of colony 77N-1A on ND 6 is illustrative of events as they unfold at the periphery of the raid column, and is shown in Figure 37. The colony became active on the surface at 19:00, as a column left the nest and proceeded to the West. This column discovered 3 raid sites and over the next 2.5 hours brought the booty captured from those sites back to the nest. At 19:20 a second column left the nest heading South. The ants found prey at sites 4-7 in Figure 37. Raiding continued along this column for the next 3.0 hours, during which time all the booty captured at those 4 raid sites was carried back to the nest. Between 22:30 and 23:00 there was an activity lull, but then another exodus took place along the column and prey was discovered at sites 8 and 9 in the figure. At 23:20 a group of ants extended a segment of the raiding column into a small hole under an Ephedra bush near raid site 8. No booty was obtained at this site, but by 23:40 the emigration had begun from the old nest and proceeded directly to that hole (nest 2 in Figure 37).

Less typical, but no less important for our hypotheses about the raiding-emigration relationship, is the activity of colony 77N-5 on ND 11, shown in Figure 38. The colony began raiding in the early evening of 7/15, sending columns to the North, East, and West of the nest. These columns found numerous raid sites all around the nest. After raiding for two hours, and carrying all the captured booty back to the nest, a branch of the East-going column headed off to the South and came upon a large hole in the ground (possibly a rodent hole). Within 20 minutes of this discovery an emigration began from the old nest and proceeded directly to the hole (nest 2 in Figure 38).

Note that in both cases no booty cache formed in or near the new nest site prior to the start of the emigration. Booty caches formed prior to only 21.2% of the emigrations (7/33), a surprisingly low percentage. Five of those caches formed in underground chambers into which a colony eventually emigrated. In the other two instances the cache was formed on the surface within 3 m of the new nest. The ants forming these caches did not carry any of the stored food into the new nest until workers carrying larvae on the emigration trail had passed the cache point. The ants forming thses caches were clearly directed to the new nest (though only a few meters from it) rather than recruiting nestmates to it.

Though colonies did not often emigrate into cache sites, workers usually established and maintained a trail leading up and into the subsurface chamber(s) into which the colony eventually emigrated. The new nest was discovered in this way before 35 of 43 emigrations started from the old nest (81.4%). A one-sample χ^2 test (Siegel, 1956) shows that this difference is significant ($\chi^2 = 14.5$, df = 1, $p < .01$). Most of the occasions on which an emigration started with no new nest to go to were associated with nest disturbances and are discussed below. On the remaining occasion the possible causes were not so obvious. Workers were raiding normally when this emigration began. The workers carried brood in an orderly fashion over a previously established raiding trail, but soon signs of confusion and disorder appeared: reversal of brood-laden traffic, shifting of traffic from one branch of the column to another, formation of brood caches. The column finally encountered and emigrated into a rodent mound.

Of the 35 instances when the nest was established before the emigration began, 9 nests were in raid sites (nests of ant colonies just raided) while 26 nests were formed in non-raided sites. This difference is also significant ($\chi^2 = 8.24$, df = 1, $p < .01$).

There was usually a very brief time interval between the discovery of these sites by the ants and the subsequent start of the emigration from the old nest, but a few latencies were very long. The median latency for 117 emigrations was 30 minutes; the mode was also 30 minutes. The range of latencies was quite wide (5-320 minutes) and the variance is strongly related to the factor of raiding. The range of latencies for emigrating into a non-raid site was only 5-60 minutes; the median of the 13 cases is 30 minutes. In contrast, the latency range for emigrations to raid sites was 50-320 minutes with a median of 80 minutes for the 4 cases.

A few emigrations (9/86) occurred with no prior raiding. The circumstances surrounding these movements were unusual and a summary of my field notes follows to illustrate the abnormalities and their possible causes.

During a NP in September, colony 76N-3 emigrated twice with no prior raiding. The pattern of activity on these NDs is shown in Figures 39 and 40. Early in September the study area received heavy intermittent rain. However, the colony emigrated and raided normally until a heavy rain in the afternoon of 9/5 left their nest area covered with 15 mm of water. By 17:30 the water had drained off and at 18:10 the first ants left the nest hole (nest 1 of Figure 39). By 18:30 the ants had reached point 2 of the figure; by 18:45 the fronts of the advancing column had extended about 15m SE of the nest. At this time workers and callow adults left the nest carrying larvae: the emigration had begun. By 19:00 the column SE of point 2 had disappeared and a column had reached an Ephedra bush at point 3. Larvae were being carried into a small hole under the bush. At 19:30 larvae were taken past the Ephedra and into another hole (point 4), but by 19:55 the larvae were carried in both directions between points 3 and 4, while a column had swung NW of point 4. By 20:05 the column had regained the old nest and larvae were soon being carried into a hole on its South side--the emigration was now moving fully and vigorously in a circle!

This circular emigration continued until a cloudburst broke it up at 22:00. Following this a scout column left point 2 and encountered a hole under an Ephedra bush (nest 2). By 24:00 the traffic was converging on point 2 from points 1 and 4 and was moving coherently on the new nest. At 03:00 the colony emigrated again under another Ephedra (nest 3) 3m east of nest 2. They raided from this nest until morning.

The colony raided and emigrated normally until ND 6, when another storm disrupted its activity. The ants were nesting in a rodent mound when the storm hit. The next afternoon (9/9) the colony was found 20m SW of the mound in the early evening. (Subsequent observations, including brood measurement, indicated that it was the same colony.) Throughout ND 7 there was heavy raiding from 3 distinct holes several meters apart, but no emigration. It appeared that the colony had emigrated (below ground) during the storm of ND 6 and was now scattered diffusely under the surface.

On ND 8 (9/10-9/11) the weather cleared and we attempted to begin the feeding experiments, so long delayed by the rain. The ants emerged from the three holes at 18:30 (Insert of Figure 40). The feeding box was centered between these holes and booty was placed in and around it in an attempt to lure the ants inside (see protocol for Feeding Experiments in Methods). However, the ants did not take any of our food. Much later in the evening they did accept the food, so their failure to do so at this time was not because the food was unpalatable. It seemed that the ants were simply unreceptive to food at this time.

Meanwhile, workers carrying brood were pouring out of all three holes. By 19:15 the situation was completely chaotic: workers were moving with food in both directions along several intersecting columns and the colony as a whole was moving nowhere. The queen was spotted within 3 m of the front of one of the east going columns (Insert in Figure 40).

At 19:30 a column slowly pushed eastward in a wide front. Workers carried brood in the very front of the column while the queen was kept in a larval cache. By 20:30 the column reached the rodent mound from which they had emigrated on ND 6 (nest 2 in Figure 40). Traffic moved rapidly into the mound once the first ants had reached it, but this emigration was not complete until 23:00. At this time two columns left the mound to the SE and NE. Some booty returned from the SE column, but by 23:45 an emigration had begun along the NE column. The emigration continued through 03:00 hours into nest 3, which was under several grass clumps.

A similar situation occurred with colony 77N-5. In this case no weather problems were associated with the abnormal emigration but nest inadequacy may still have been a factor. On ND 9 the colony emigrated under a small clump of grass. Workers entered and exited from the nest hole and piled up brood in caches outside the hole for several hours before finally settling there for the night, a sign that the nest may have been too small.

That impression was confirmed by observations on the following evening. The workers became active from nest 1 in Figure 41 at 18:00 and established a short column to the north which ended under another small clump of grass. By 18:15 larvae had left nest 1 and were moving under the clump of grass (nest 2). But by 18:30 the brood-laden traffic was bidirectional between these two nests. Some raiding to the north of nest 2 occurred between 18:25 and 19:15 at sites marked 1-4 in the figure. By 18:55 the workers had established another column which led under an Acacia bush to the SE of nest 1. In 20 minutes from the discovery of this site the emigration was moving there (nest 3 in Figure 40). From this nest the colony sent out a column and at 23:30 emigrated again (nest 4). Some raiding finally occurred from nest 4 but at 01:30 the emigration backtracked a few meters to nest 5, which was a small hole in the ground.

Another instance of an emigration starting without any prior raiding occurred with colony 77N-1A on ND 12. Apparently, no unusual environmental circumstances were involved. The ants left the old nest at 18:10 and ran along one of the previous night's raiding columns under an Ephedra bush from which a colony of Pheidole desertorum had been driven the night before. No Pheidole were in the vicinity at that time nor was any booty brought back along the column, but an emigration began at 18:45 and proceeded directly there. Following the emigration the colony raided normally and then went through a SP.

All 9 of the instances of emigrations that occurred with no prior raiding fall under one of the three categories illustrated above: they occurred on nights following heavy storms (3 cases), following signs of an inadequate nest (4 cases), or on the last day of a NP (2 cases). Special problems or requirements associated with the colony's nest situation are the common denominator of all nine cases.

N. nigrescens invariably nests in the ground, which precludes any description of nest characteristics and colony organization there. However, we recorded the surface features immediately around the hole or holes which the ants used as entry- and exit-points to their nests. A summary of the surface characteristics above 95 nests is presented in Figure 42. Most frequently (n = 50) the colony enters the ground directly under some vegetation. Usually this is an Ephedra bush or a clump of grass, only occasionally under an Acacia or a Mesquite bush. Next frequently (n = 18) the ants left the surface via a burrow or small hole in the mound of the banner-tailed kangaroo rat, Dipodomys spectabilis. A total of 17 nests were established in the abandoned nests of other ant species, chiefly those of Novomessor cockerelli and Pogonomyrmex sp. The remaining 10 nests in this sample were entered through crevices or holes in the dirt.

This information simply shows that the army ants use some preformed cavities in the soil for their nests, and that these are usually found under vegetation or in excavations made by animals.

B. Effects of Raiding on Emigration Characteristics

To determine the effects of the intra-colony food supply on nomadic behavior, correlations between the amount of food gathered (mg/larva) on one ND and some characteristics of the next ND's emigration were computed for colonies 76N-3 and 76N-8. The point-biserial correlation (McNemar, 1955) between food gathered on one ND and the occurrence or non-occurrence of the emigration on the next ND is 0.27 ($n = 21$; $t = 1.90$, $p > .05$); between booty intake and emigration distance was only .01 ($n = 15$; $p > .05$). There was also no discernible relationship between amount of booty captured and emigration direction or duration on the following ND.

The food supply in the immediate area around the nest may have exerted some effect on the direction of emigration. Some booty was brought back to the nest before about 84% of the emigrations (47/56), and the emigration moved towards one or a group of raiding sites 78% of the time (40/51). However, due to the early onset of most emigrations, more booty was captured during the emigrations, or after they had ended, before the emigration started (Figures 7, 9, 10, 11, 13, 22). When emigration started later a greater proportion of the booty was captured before the emigration started (Figures 8, 12).

Figure 43 is a frequency distribution of the number of raid columns that were active prior to the onset of the emigration. A low number of pre-emigration raid columns is the rule. Only 18 of 33 emigrations (54.5%) were preceded by two or more raid columns.

The raiding success of each column was determined prior to 14 of these emigrations. The assessment of raiding success is based on some combination of the following measures: 1) counts of booty brought back to the nest; 2) number of raid sites on the column; 3) total time the column was active. Table 12 presents these data and shows which column the emigration proceeded over on these 14 occasions. All the measures are in agreement on most NDs. Furthermore there are two or more measures available for each column in 12 of these emigrations, while the assessment for the columns before the other 2 emigrations is based on the most direct measure, the booty counts.

Table 12 shows that the colonies emigrated over the most successful raid column 9 times; they took a less successful column 4 times. On one ND (77N-1A: ND 7) the difference in raid success between the two columns was too close to call (in part because of conflicting evidence between the measures); this ND has been left out of the analysis. The observed difference is not significant ($\chi^2 = 1.92$ df = 1, $p > .10$), but this may be due to the small sample size.

In Figure 44 a map of the raiding and emigration activities of colony 77N-5 on ND 12, 7/16-7/17, is presented. The events surrounding this migration are illustrative of the points we have been trying to make in this section and they will be described to serve as a summary.

The colony became active from its nest at 18:05 and sent a heavy column (column 1 in Figure 44) to the NE of the nest. Prey was discovered and engaged at nine sites. Traffic in both directions was heavy and much booty returned over this column in its nearly 3 hours of activity. At 18:25 a second column started but never got farther than 10 m from the old nest. Only one raid site (which brought in only a few pieces of booty) was established on this column, which died at 19:35.

At 19:10 a third column began to form to the SW of the nest. It was a very weak column as outgoing traffic never exceeded 20 ants/minute for the first half-hour, despite some termites discovered at site 1 in the figure. By

19:40 additional prey had been discovered and recruitment from the nest increased somewhat, but neither the outbound nor the booty-laden returning traffic ever reached one-half of that on column 1. By 20:35 column 3 had reached the base of a rodent mound about 25 m from the nest: at 20:40 the ants were exploring a small hole on the surface of the mound. No booty was taken from this hole or from anywhere else on the mound. By 20:50 an emigration had started from the old nest and was moving along column 3. At 21:00 the emigration had reached the small hole in the rodent mound, which had become the new nest.

The following important features of the raiding-emigration relationship are illustrated in this night's activity: 1) raiding goes on for about 2.5 hours prior to the onset of the emigration; 2) the emigration proceeds over one of the raiding columns, but not necessarily over the most successful column; 3) workers find and explore a site on the raid column into which the colony eventually emigrates, though this site need not be a raid site; 4) the emigration begins within a few minutes after this site has been discovered.

C. Effects of Emigration on Raiding

It is clear from the observations reported above that raiding can exercise a strong influence on the emigration, though the two systems operate independently in certain circumstances. The emigration represents a considerable expenditure of energy and time and, in turn, affects the course of raiding.

Table 13 summarizes the data in Figures 7-22. It shows the total number of pieces of booty brought into the nest during each period for all NDs from each colony. Booty comes in at a higher rate whenever an emigration is not in progress (for the most part). The differences between the observed food intake in each time period and the intake expected if there were no difference in the intake rate is highly significant for 76N-3 ($\chi^2 = 13800$, df = 1, $p < .001$) and for 76N-8 ($\chi^2 = 36065$, df = 1, $p < .001$).

On nearly every ND that an emigration occurs the amount of booty coming into the nest drops sharply around the time of emigration onset. Booty flow remains low for a variable period afterwards. On five of these NDs (Figures 9, 11, 17, 18, 22) booty flow to the nest ceased for periods of 2 hours or more. Overall there were 13 such gaps in raiding which totalled 21 hours on 10 of the 13 NDs when there was an emigration.

Colony 76N-8 had more gaps than 76N-3 (compare Figures 7-14 with Figures 15-22) possibly because it had a less favorable adult:brood ration (.54 vs .70). There were simply fewer adults available to move the brood when the emigration began; hence emigrations were more disruptive of raiding.

These gaps were not an artifact of counting booty close to the nest. The colonies had no raiding columns active during these periods; they were, however, emigrating vigorously at these times. Booty flow waxed and waned on most NDs (Figures 7-22), but there is no comparable gap in booty flow raiding at any other time the colony is active. Small gaps at the very beginning of activity in the evening occurred because it took some time for the columns to form, find food, capture it and return it to the nest.

The absence of raid columns (or a marked diminution of their activity) during emigrations was seen on most NDs of all the colonies we observed, but was not quantified with those colonies. After the emigration had been in progress for some time the raiding columns formed from the new nest and the flow of booty resumed.

D. Feeding Experiments

Table 14 is a compilation of the food administered and the food gathered by normal raiding on each day during the experimental period. The table also indicates the NDs on which no emigration occurred. First I will describe the course of the experiments with each colony separately.

The experiments with 76N-3 began on ND 9 and continued through ND 13, during which an average of .48 mg/larva/night was administered. The colony took all food offered in the feeding box back to its nest. The colony emigrated on the first two nights along columns that did not bring much food back to the nest (i.e. they emigrated away from the direction and area of greatest raiding success--that of the food box). The colony's normal raiding decreased on this and all subsequent nights. The colony did not emigrate on the last three nights of the experiment (NDs 11, 12, 13).

In 1977 the experiment was performed on two colonies. We started with 77N-8 on ND 3 and continued to feed them an average of 1.04 mg/larva/night through ND 12, except for ND 7 when the experiment was suspended due to heavy rain. Like 76N-3 this colony emigrated on the first two nights of the experiment over columns that did not gather any booty. The activity on these nights is shown in Figures 45 and 46. The colony also emigrated on the fourth experimental night (ND 6). However, there was no emigration on four of the last five experimental NDs. The lone emigration in this period occurred on ND 9. It began at 18:00 with no prior raiding, and before we could set up the feeding box to start the experiment.

The colony's normal booty gathering fell off almost immediately and stayed low except on ND 9 when the ants gathered about 10 g on their own. All of this booty was gathered after the emigration and our feeding experiment was completed.

Later in the same summer the experiment was performed on colony 77N-1A, starting on ND 2 and continuing through ND 5. The colony took all food offered in the box on each day, but did not show any other signs of surface activity on those days, aside from that of several workers who milled around the nest holes. I became concerned about the colony's health and suspended the experiment. On ND 6 the colony still showed no activity on the surface. On ND 7 the colony emigrated but no raiding occurred before, during, or after the emigration. On NDs 8 and 9 the colony emigrated while raiding gradually picked up in intensity. The experiment was resumed on ND 10 and the colony did not emigrate on this or on the following night. The colony gathered some food on its own in addition to that which it was fed artificially on those NDs.

In Table 15 the effects of the experiment on emigration frequency are summarized and compared with the emigration frequency during control NPs from the same colonies. The control samples do not contain any first or last NDs, for reasons discussed earlier. The experimental samples include only the 20 days on which the experiment was performed, not including days on which the experiment could not be conducted because of bad weather or other reasons (given above). The differences in emigration frequency between the control and experimental samples of NDs were consistent from colony to colony, and the data from all colonies are summed and presented at the bottom of Table 8. The overall differences in emigration frequency are significant ($\chi^2 = 14.7$, df = 3, $p < .01$).

Variation in the amount of food given during the experimental NPs was not related to the occurrence of an emigration. The point-biserial correlation between amount of food administered on each of the 24 NDs during the experimental period (all days in Table 12 except ND 7 of colony 77N-8) and the occurrence of an emigration on that ND is only .23, which is not significant ($t = 1.48$, df = 22, $p > .05$).

The low number of emigrations during the experimental NPs preclude any meaningful comparison of other emigration characteristics (distance, onset, direction). Nevertheless, there is some useful information to be gained from the few emigrations that occurred: 1) an emigration can occur even when abundant booty is found close to the old bivouac (76N-3: NDs 9, 10; 77N-8: NDs 3, 4, 6); 2) an emigration can move far away from an area of great booty capture (76N-3: 14.3 m on ND 9, 50.8 m on ND 10; 77N-8: 18.1 m on ND 3, 35.4 m on ND 4, 37.5 m on ND 6); 3) an emigration occurs with no prior raiding when the colony's booty supply is high (77N-1A: NDs 7, 8, 9; 77N-8: ND 9).

The effects of the artificial feeding on normal raiding were even more dramatic and immediate than those on emigration frequency. The food offered in those experiments practically eliminated normal foraging. The effects on colony 77N-1A were the most pronounced: the colony did not gather one piece of booty on its own for six consecutive NDs, including the last two days of this period when the colony was fed nothing. It is puzzling to interpret this effect since colony 77N-1A was fed the least amount overall and the least mg/larva/ND. Furthermore, the most heavily fed colony (77N-8) gathered just as much food on its own as the other colonies (Table 14).

DISCUSSION

Brood-Stimulative Theory and Nomadic Behavior in *N. nigrescens* and other Ecitonines

The results of this study are in complete agreement with those of Schneirla (1958, 1961, 1963) regarding the existence of discrete and alternating nomadic and statary phases. However there is a large difference between the length of the NSC of *N. nigrescens* in this study and that reported by Schneirla. The NPs of the colonies in this study averaged only 13 days in length, while Schneirla (1971) reported an average NP length of 19 days. There is a smaller discrepancy in SP length: Schneirla reports an average of 19 dyas while my colonies averaged close to 17 days. However, the median test indicates that both differences are significant (NP difference: $\chi^2 = 19.8$, df = 1, $p < .01$; SP difference: $\chi^2 = 9.7$, df = 1, $p < .01$).

Figure 44 shows the growth of larvae from this study and from that of Schneirla (1958). In this study the larvae were fully grown by ND 13; in Schneirla's study the larvae were not fully grown until ND 17-18. The larvae are approximately the same size on ND 1; therefore the difference is mainly due to a faster growth rate in the larvae I studied. The difference in growth rate might be due to the difference in temperature in the two habitats (Table 1).

The significance of this finding is that the NP ends in both habitats when the larvae are fully grown. Brood-stimulative theory is thus supported as the basis for cyclic behavior because a large variation in brood development has now been correlated with similar variations in NP length within a species. Differences in phase lengths between species have already been related to larval growth (Schneirla, 1971 and references cited).

Brood-stimulative theory is also supported by the decreased raiding and emigration activity during the feeding experiments. In two of the colonies emigrations occurred at the beginning of the experiment (first 2 nights for 76N-3; 3 of the first 4 nights for 77N-8). After this there was only one emigration in the combined total of 9 NDs from the two colonies. This pattern of response suggests that the failure to emigrate resulted from the cumulative effects of consistent overfeeding, in accord with hypothesis 6. It is also consistent with the hypothesis that well-fed larvae stimulate the adults less than hungry larvae (Rettenmeyer, 1963). Perhaps overfeeding of adults also contributed to this result, but it is not known how much the adults feed during the NP.

However, the other colony on which the experiment was performed did not emigrate on each of the six experimental nights, a pattern of response which suggests that emigrations fail to occur because abundant food is found close to the bivouac. This colony also did not raid on its own on any of the experimental nights; furthermore, the course of the colony's recovery to normal raiding and emigrating while the experiments were suspended suggests that it, too, had been overfed. Thus overfeeding seems the most plausible explanation for the colonies' failures to emigrate during the feeding experiments.

I am also in agreement with Schneirla (1971) and Rettenmeyer (1963) about the difference between the phases in the extent of raiding and the increase in raiding activity as the SP draws to a close. Brood stimulation is probably responsible for these changes. However, characteristics of behavior within the normal NP do not change as brood-stimulative theory predicts.

First, *N. nigrescens* does fail to emigrate on a small proportion of its NDs. The pattern of these failures is shown in Table 16. Data from this study and from Schneirla (1958) show that failures to emigrate occur at all points in the NP, and are not necessarily more likely between ND 2 and 6. A lull in brood stimulation in the early part of the NP (Schneirla and Brown, 1950) cannot account for these results. However, failures to emigrate are not strongly related to the previous ND's raiding success, either. These findings suggest that the level of brood stimulation does not fluctuate through the NP either as a result of intrinsic developmental changes, or from the normal variation in food intake.

Other factors must be examined to account for the failure to emigrate within the NP.

Comparisons of emigration frequency in _E_. _burchelli_ in Brazil and Panama, in dry and rainy seasons, are also presented in Table 16. (Even the data from Panama shows that the failure to emigrate is only slightly more frequent in the early part of the NP.) The data of Teles da Silva (1977) shows that emigration frequency in _E_. _burchelli_ is strongly related to environmental factors: there is a marked increase in the failure to emigrate in the rainy season, which she has attributed to bad weather.

Brood-stimulative theory also fails to account for emigration distance. All the available evidence shows that emigrations in the middle of the NP are the longest (Figure 7; Schneirla and Brown, 1950; Schneirla, 1958; Rettenmeyer, 1963). Finally, neither emigration onset time, duration, nor raiding intensity vary systematically with ND.

Emigration Mechanism

I suggested earlier that recruitment to food might account better than brood stimulation for the frequency, direction and distance of emigrations, and that the emigration basically resulted from a massive recruitment to the food gathered in prior raiding. This theory also has a mixed record in accounting for the evidence.

On most NDs raiding precedes the emigration and the transition from one type of activity to another appears smooth and gradual. In addition, the emigration usually follows the course of a raiding column and ends up in or near a group of raiding sites. Furthermore, when two or more raiding columns are active prior to the emigration, the colony usually follows the course of a raiding column and ends up in or near a group of raiding sites. Furthermore, when two or more raiding columns are active prior to the emigration, the colony usually moves over the column with the greatest raiding success. Unfortunately, several observations suggest that the link between emigration and raiding is more coincidental than causal.

1. Emigrations can occur with no prior raiding. These emigrations occur at times when there are special problems associated with the nest site and/or when food gathering is a low priority activity. When one nest has been disturbed or is inadequate, the workers locate and recruit to another nest independently of food. It may be that during severe nest disturbances like that described on pp. 55-56, the workers are relatively unresponsive to food.

2. Raiding can go on all night with no emigration following from it. Some of these NDs without emigrations were preceded by NDs with unusually high amounts of booty capture. It is possible that the failure to emigrate on these NDs resulted from a lull in brood stimulation with well-fed larvae.

In general, however, the success of any one ND's raiding did not influence the likelihood of the emigration on the next ND. Furthermore, prey sites were always diffusely distributed; thus, failures to emigrate cannot be attributed to "windfall" booty finds close to the old nest.

3. The emigration usually occurs early in the colony's surface activity period, and more booty is captured during or after the emigration than before it. Emigration onset time is not related to the amount of booty captured on the previous ND.

4. The emigration sometimes moves away from the area of greatest raiding success. Some colonies emigrated into areas completely removed from their previous raiding activity. Emigration distance is not related to the amount of booty captured on the previous ND.

5. The emigration does not result from gradual recruitment to a huge booty cache formed by the ants in potential nest sites. Caches are usually not formed by the ants in or near the new nest before the emigration begins. Recruitment from the nest is sporadic and closely tied to the discovery of raid and nest sites.

6. The emigrations begin within a few minutes after the next nest has been found by ants on the exploratory column. The nest is usually formed under some shrub or in a rodent mound--there must be some crucial requirements that these

sites provide--and is not usually in a raid site. In fact, the presence of prey that has to be captured in a potential nest site seems to delay the onset of emigration to that site.

Further evidence that raiding and emigration are dissociable behaviors comes from the feeding experiments. From the first day of the experiments with each of the three colonies normal raiding was much curtailed. It took longer to prevent a colony from emigrating. Those emigrations that occurred during the experimental period moved far away from the area of greatest raiding success (which was our feeding box) and they occurred with no additional raiding in the area to which the colony emigrated.

Changing of nest sites is common and widespread among ants, and in the few intensive studies made of this problem it has been found that the mechanisms employed for recruitment on emigrations differ somewhat from those used to recruit to food. For instance, in _Camponotus sericeus_, workers recruiting to food regurgitate to nestmates and make "fast runs" inside the nest; workers recruiting to new nests grasp nestmates by the mandibles and pull them forward (Holldobler, Maschwitz & Moglich, 1974). While tandem running is employed in both types of recruitment, reluctant recruitees are carried to nests but never to food. In related species (_Camponotus socius_, _Formica fusca_ and _F. sanguinea_) the cues for emigrations are different than those for recruitment to food; furthermore, emigrations are organized by a relatively few nest-changing "specialists" among the workers (Holldobler, 1971; Moglich and Holldobler, 1974, 1975). Similarly, in Oecophylla longinoda recruitment to food involves different tactile cues than those used to recruit to new nests (Holldobler and Wilson, 1977a, b), but rectal gland secretions guide workers outside the nest in both contexts.

The behavior of newly-eclosed Ecitonine adults also indicates that different mechanisms underly recruitment to food and new nest sites. Callows emigrate proficiently with the colony within 48 hours of their eclosion but to do participate in raids until 3 to 7 days later (Schneirla, 1971). Studies of N. nigrescens in the laboratory show that the callows remain tightly clustered inside the nest during raiding until the emigration begins. Callows are recruited out of the nest by adults who break up the clusters with tactile cues (Topoff and Mirenda, 1978). Once out of the nest callows use deposited trail pheromones (Topoff, Boshes and Trakimas, 1972) and probably also tactile cues from nestmates on the column to get from one bivouac to the next. The possibility that workers deposit a unique trail substance when they emigrate is not ruled out by these experiments, but it seems unlikely that such chemical cues would be sufficient to induce emigrations. It is also possible that the recruitment-to-food substance hypothesized by Chadab and Rettenmeyer (1975) may be used with tactile cues inside the nest to recruit on emigrations.

A recruitment-to-nest mechanism helps to maintain colony organization by ensuring that another nest is available before the colony leaves the old one. Nest sites serve as a base of operations for the colony, as a shelter from environmental stresses, and as a place within which optimal physical conditions can be created for the queen and brood (Schneirla et. al., 1954; Jackson, 1957; Schneirla, 1971: 61-66). An emigration also diverts much time and energy away from raiding and exposes the colony to dangers on the surface. Any mechanism that could minimize the time spent in emigration and make the transfer of bivouac site more efficient should be of considerable adaptive value. If recruitment-to-food were the mechanism underlying emigrations, abortive emigrations and disorganized emigrations would be more common than they are, since raiding success does not guarantee an adequate nest site. Without such a system it is hard to see how the timing of the emigration (in relation to the discovery of the new nest site) could be so precise, or how the ants could emigrate so swiftly and directly to the new nest.

There must be at least one common factor that underlies both raiding and emigration behavior, however, since they vary together in several ways (phase differences, feeding experiments). The most likely candidate for this common factor is brood stimulation. I suggest that this stimulus, whatever its exact nature, acts as a non-specific, generalized arousal factor that increases the responsiveness of workers to other classes of stimuli (food, nest sites) that provide the occasions for the specific recruitment systems to come into play. A brood-stimulative effect on worker foraging behavior has been demonstrated experimentally for *Myrmica rubra*: food collection is related to larval size (Brian and Hibble, 1963) and larval number (Brian, 1973). *M. rubra* workers are stimulated to forage by the shape of the larval head and by larval food ingestion (Brian and Abbott, 1977).

Emigration and the Foraging Strategy

In considering the foraging strategy of *N. nigrescens* and the role that emigrations play in fulfilling it, I must emphasize the normally close association of raiding and emigration. Despite the fact that these two behaviors are dissociable under-certain circumstances, and may result from the operation of different recruitment systems, they are for the most part so closely linked as to seem inseparable. Virtually all emigrations are preceded by raids, proceed over one of the raiding columns (usually the column of greatest raiding success), and terminate in or near a group of raid sites.

How does a recruitment-to-nest mechanism facilitate an emigrate-to-food strategy? The answer is that workers in exploratory columns that leave the bivouac are responsive to both food and potential nest sites; they recruit to either when found. In the normal case a nest site is found near the raid sites and so a colony in the nomadic "condition" emigrates near the raid sites, or even in a raid site. There is a longer latency to emigrate into a raid site because it takes some time to make such a site secure from the dangerous defensive manuevers of prey. When two or more raiding columns are available to choose from, the colony usually emigrates over the column of the greatest raid success because the concomitants of that success (number of foragers, number of raid sites discovered, area of field covered) also make the discovery of a suitable nest site along that column more likely.

The strategy is unfortunately not manifested as clearly in this study as expected. The major discrepancies between our expectations and observations are considered below with possible explanations for those discrepancies.

1. The colony sends out only one or two exploratory columns that make a rather narrow sweep of the available area prior to the emigration. The emigration occurs early in the surface activity period. It does not seem that the colonies are sampling the relative availability of food in the area around the bivouac before arriving at a "decision" about which di-

rection to emigrate in. The factor that limits the extent of raiding within the NP seems to be the size of the worker force. Larger colonies average more columns and area covered per ND than smaller colonies. It may be that some of our colonies were atypically small and that larger colonies would show more extensive raids.

2. A colony's movements during the course of a NP are very irregular in direction and distance. It is not uncommon for colonies to stay within a few meters of one another for several nights, for one colony to move into an area recently vacated by another, or for a series of emigrations to bring a colony back into an area it recently emigrated from. In addition, emigrations are generally shorter than the maximum distance of raids and a colony may raid over the same general area from different nest sites following its emigrations. In general, the colonies did not change their foraging areas as completely or efficiently as an optimal strategy might predict. The most efficient way to change the foraging area would be to emigrate in a consistent direction. For nomadic animals whose foraging area is essentially unbounded, the optimal directionality is 1.0 (Pyke, 1978). Our colonies clearly were not behaving in accord with a strategy that optimized the changing of their foraging grounds.

Perhaps a colony can afford to be less than optimal in this respect when prey is abundant and/or diffusely distributed, as was the case in the present study. Almost every raiding column active for a few minutes found some booty; it literally seemed as though booty was every where. It is evidently sufficient for colonies in such a habitat to move unpredictably through the continuous zone of prey, since they only exploit a small portion of it on any given night's raiding. I would predict more directionality in habitats where food is not so abundant. In addition, emigrations should be longer and/or more frequent when food is less available.

Variation in the spacing, timing, and also frequency of emigrations must also be related to the availability of nesting sites. On the hard-packed, desert pavement substrate of my study site, where there were no trees, few rocks, or even woody shrubs, suitable nest sites may have been in short supply. Since the nomadic pattern depends on the availability of temporary nests, any reduction in the number of those sites is bound to complecate and perhaps even eradicate a coherent movement pattern.

3. The nest factor may account for the few instances when the colonies emigrated away from the area of greatest raid success. When nests are available in any direction, the colony should move in the direction of the greatest raid success. But raid success and nest availability need not always go together, particularly when colonies of small ants are the preferred prey and when other nest sites are in short

supply. On NDs when no nest is found in the direction of the greatest raiding, but in another direction, the recruitment-to-food and recruitment-to-nest mechanisms work at cross purposes.

4. The most confusing aspect of the emigration-raiding relationship concerns the disruption of raiding that occurs during the emigration. The disruption can become severe, particularly when the adult:brood ratio is low and the colony is having difficulty making the transfer of bivouacs. Conversely, a colony is more successful in raiding before or after emigrations, or on NDs when no emigration occurs. I have no idea if the high rate of booty intake could be kept up for a long period of time without emigrations. Instances of longer periods without emigrations have not been reported. It is difficult to demonstrate the adaptive value of a trait when there is little variation in it to correlate with measures of fitness, and when the variation that does exist yields information contrary to what might be expected at the first level of analysis.

Perhaps the key to understanding this particular puzzle is in the principle of stringency (Wilson, 1975: 42):

> ...time-energy budgets evolve so as to fit
> the time of greatest stringency.

When food is scarce, those army ant colonies most adept at changing their foraging ground (and at moving into areas of great raiding success as well) are selected for.

When food is abundant the colonies are for the most part unable to take advantage of the situation by suspending their emigrations because of constraints imposed by the mechanisms suited to more severe conditions.

TABLES

Table 1

Characteristics of Two Habitats in which *Neivamyrmex nigrescens* has been studied

Investigator		Schneirla	Mirenda
Weather Station		SWRS	Rodeo
Vegetational Associations		Evergreen-deciduous woodlands	Woody shrubs, grasses
Elevation (M)		1650	1250
Annual Rainfall (mm) 15-year average		509	287
Average temp. (^{o}C) in August, 1977	Max	29.2	33.3
	Min	13.4	18.1

Table 2

Designations, Dates of Study, Sizes, and Phase Lengths of Six Colonies

Colony	Dates	Size[a]	Adults / Larvae	Days Nomadic	Days Statary	Days in Cycle
76N-3	7/18-8/5				18	
	8/5-8/18	23320 A	0.70	13		31
		33160 L				
	8/18-9/3				16	
	9/3-9/17[b]	43400 A	1.49	14		30
		29060 L				
76N-8	7/27-8/8	12000 A	0.54	(13)[c]		
		22300 L				
	8/8-8/24				16	
	8/24-9/7	32200 A	1.29	15		31
		(25000 L)				
77N-1A	7/6-7/23				17	
	7/23-8/4	9500 A	2.02	12		29
		4710 L				
	8/4-8/22				18	
	8/22-9/4[b]	12815 A	0.60	13		31
		21240 L				
77N-5	7/5-7/19	(25000 A)	1.25	(14)[c]		
		(20000 L)				
	7/19-8/3				15	
77N-7	7/29-8/14				16	
	8/14-8/28	(30000 A)	2.67	14		30
		(20000 L)				
	8/28-9/14				17	
	9/14-9/27	(90000 A)		13		30
77N-8	8/5-8/18[b]	15000 A	0.47	13		
		31740 L				
	8/18-9/6				19	
	9/6-9/17	41380 A	1.40	11		30
		(30000 L)				
	MEAN	35010 A	1.42	13.2	16.9	30.3
		24721 L				
	S.D.	27356 A		1.1	1.2	0.2
		8405 L				

[a] All sizes are estimates, but those sizes in parentheses were not based on counts. A = Adults. L = Larvae.

[b] NP in which a feeding experiment was conducted.

[c] Maximal length based on brood size when discovered (see text).

Table 3

Approximate Starting and Ending Times of Raids During Nomadic and Statary Phases of Two Colonies

	Colony 76N-3				Colony 76N-8			
	Nomadic		Statary		Nomadic		Statary	
Day	Start	End	Start	End	Start	End	Start	End
1	19:30	05:00	20:30	23:40			20:00	00:50
2	19:15	04:45	20:00	01:15			22:50	01:10
3	20:00	03:00	NO RAID				NO RAID	
4	19:00	00:30	NO RAID		20:00	05:00	01:30	05:00
5	19:00	05:30	NO RAID		19:45	04:45	NO RAID	
6	19:00	05:30	NO RAID		19:15	05:00	NO RAID	
7	19:30	03:00	21:00	22:00	19:00	05:00	22:00	03:00
8	20:30	05:15	NO RAID		23:00	05:45	22:00	00:30
9	19:00	05:15	00:10	02:00	20:15	01:00	NO RAID	
10	19:30	05:00	NO RAID		19:00	05:45	NO RAID	
11	20:00	02:00	22:00	03:00	19:30	01:00	23:05	01:30
12	NO RAID		20:30	21:40	19:15	05:00	24:00	04:00
13			22:10	23:00	20:00	03:00	20:30	21:00
14			21:30	04:00			22:00	02:00
15			24:00	01:30			22:50	03:30
16			20:30	03:30			20:00	03:30
17			21:30	04:00				
18			20:30	04:30				

Table 4

Indices of Raiding Activity in Three Colonies During Nomadic Phase

Colony	ND	Raid Columns	Area (M^2)	Raid Sites	Hours Observed	$\frac{M^2}{Hour}$	$\frac{Raid\ Sites}{Hour}$
77N-1A	2	2	64	7	4.5	14	1.56
	6	2	118	9	4.0	30	2.25
	7	2	173	6	4.0	43	1.50
	8	1	77	6	4.0	19	1.50
	9	2	25	6	8.5	3	0.70
	10	2	71	6	8.5	8	0.70
	11	2	338	15	11.0	31	1.40
	12	1	149	2	2.0	75	1.00
TOTALS	8	14	1015	56	46.5	22	1.20
77N-5	5	2	113	4	4.5	25	0.89
	6	4	241	15	8.5	28	1.76
	7	1	314	8	4.5	70	1.77
	8	1	102	4	0.5	203	8.00
	9	9	498	23	6.0	83	3.83
	10	2	238	9	5.0	48	1.80
	11	4	587	23	8.5	69	2.70
	12	2	191	15	2.8	68	5.40
	14	1	228	17	6.0	38	2.80
TOTALS	9	26	2542	118	46.3	54	2.54
77N-7	?	2	554	25	8.0	69	3.13

Table 5

Grams*, Hours and Rates of Booty Intake by Colony 76N-3 during Nomadic Phase

	Counted			Estimated			Total		
ND	Grams	Hours	Rate	Grams	Hours	Rate	Grams	Hours	Rate
1	25.59	9.50	2.69				25.59	9.50	2.69
2	12.73	9.50	1.34				12.73	9.50	1.34
3	5.62	7.00	0.80	2.60	2.00	1.30	8.22	9.00	0.91
4				16.20	10.00	1.62	16.20	10.00	1.62
5	3.77	3.50	1.08	8.96	5.50	1.62	12.73	9.00	1.41
6	24.95	10.50	2.38				24.95	10.50	2.38
7				16.20	10.00	1.62	16.20	10.00	1.62
8	6.11	10.50	0.68				6.11	10.50	0.68
9	21.07	10.25	2.06				21.07	10.25	2.06
10	13.79	9.50	1.45				13.79	9.50	1.45
11	10.60	6.00	1.77	5.31	3.00	1.77	15.91	9.00	1.77
12	0.00	0.00	----				0.00	0.00	----
13				16.20	10.00	1.62	16.20	10.00	1.62
TOT	124.23	76.25	1.62	65.47	40.50	1.62	189.70	116.75	1.62

*Wet weight

Table 6

Grams*, Hours and Rates of Booty Intake by Colony 76N-3 during Statary Phase

	Counted			Estimated			Total		
SD	Grams	Hours	Rate	Grams	Hours	Rate	Grams	Hours	Rate
1				2.77	3.00	0.93	2.77	3.00	0.93
2	0.00	5.00	0.00				0.00	5.00	0.00
3	0.01	1.00	0.01				0.01	1.00	0.01
4	0.00	0.00	----				0.00	0.00	----
5	0.00	0.00	----				0.00	0.00	----
6	0.00	0.00	----				0.00	0.00	----
7	0.00	1.00	0.00				0.00	1.00	0.00
8	0.00	0.00	----				0.00	0.00	----
9	0.41	2.00	0.20				0.41	2.00	0.20
10	0.00	0.00	----				0.00	0.00	----
11	1.41	2.00	0.71	2.77	3.00	0.93	4.18	5.00	0.84
12	0.63	1.00	0.63				0.63	1.00	0.63
13	0.68	1.00	0.68				0.68	1.00	0.68
14	4.29	6.00	0.71				4.29	6.00	0.71
15				0.93	1.00	0.93	0.93	1.00	0.93
16	11.72	7.00	1.67				11.72	7.00	1.67
17	7.92	6.00	1.32				7.92	6.00	1.32
18	9.71	7.75	1.25				9.71	7.75	1.25
TOT	36.78	39.75	0.93	6.47	7.00	0.93	43.26	46.75	0.93

*Wet weight

Table 7

Grams*, Hours and Rates of Booty Intake by Colony 76N-8 during Nomadic Phase

	Counted			Estimated			Total		
ND	Grams	Hours	Rate	Grams	Hours	Rate	Grams	Hours	Rate
1				8.70	10.00	0.87	8.70	10.00	0.87
2				8.70	10.00	0.87	8.70	10.00	0.87
3				8.70	10.00	0.87	8.70	10.00	0.87
4	7.44	9.00	0.83	0.49	0.50	0.87	7.93	9.50	0.84
5	2.01	9.00	0.22				2.01	9.00	0.22
6	1.82	9.75	0.19				1.82	9.75	0.19
7	1.83	10.00	0.18				1.83	10.00	0.18
8	9.79	6.75	1.45	0.66	3.00	0.33	10.45	9.75	1.07
9				8.70	10.00	0.87	8.70	10.00	0.87
10	21.08	9.75	2.16				21.08	9.75	2.16
11				18.20	9.50	1.92	18.20	9.50	1.92
12	12.46	9.75	1.28				12.46	9.75	1.28
13	5.49	7.00	0.78	4.10	2.50	1.64	9.59	9.50	1.04
TOT	61.92	71.00	0.87	58.25	55.50	1.06	120.17	126.50	0.95

*Wet weight

Table 8

Grams*, Hours and Rates of Booty Intake by Colony 76N-8 during Statary Phase

	Counted			Estimated			Total		
SD	Grams	Hours	Rate	Grams	Hours	Rate	Grams	Hours	Rate
1				6.26	4.50	1.39	6.26	4.50	1.39
2	2.61	2.50	1.04				2.61	2.50	1.04
3	0.00	0.00	----				0.00	0.00	----
4				4.86	3.50	1.39	4.86	3.50	1.39
5	0.00	0.00	----				0.00	0.00	----
6	0.00	0.00	----				0.00	0.00	----
7	1.79	2.25	0.80	3.48	2.50	1.39	5.27	4.75	1.11
8	0.79	2.50	0.32				0.79	2.50	0.32
9	0.00	0.00	----				0.00	0.00	----
10	0.00	0.00	----				0.00	0.00	----
11	1.93	2.50	0.77				1.93	2.50	0.77
12				5.56	4.00	1.39	5.56	4.00	1.39
13	0.17	0.50	0.34				0.17	0.50	0.34
14				6.95	5.00	1.39	6.95	5.00	1.39
15	4.88	4.50	1.08				4.88	4.50	1.08
16	17.77	6.75	2.63				17.77	6.75	2.63
TOT	29.94	21.50	1.39	27.11	19.50	1.39	57.05	41.00	1.39

*Wet weight

Table 9

Summary of Grams, Hours, and Rates of Intake of Booty During the Nomadic and Statary Phases of Two Colonies

Colony		NP	SP
	Grams	189.7	43.2
76N-3	Hours	116.7	46.7
	Rate	1.6	0.9
	Grams	120.2	57.1
76N-8	Hours	126.5	41.0
	Rate	0.9	1.4

Table 10

Characteristics of 8 Nomadic Phases of Six Colonies

Colony	Dates	NDs Observed	# NDs Emig. Occurred	# NDs no Emig. Occurred	# Emig.	Total Meters	M/ND	M/Emig.	ϑ[a]	r[b]
76N-3	8/5-8/18	13	11	2	14	420.3	32.3	30.0	8	.18
76N-8	7/29-8/8	10	7	3	10	228.0	22.8	22.8	11	.29
	8/24-9/1	9	9	0	10	190.3	21.1	19.0	85	.32
77N-1A	7/23-8/4	12	10	2	13	270.0	22.5	20.8	102	.34
77N-5	7/6-7/19	12	9	3	19	280.8	23.4	14.8	7	.07
77N-7	8/14-8/28	14	14	0	20	426.7	30.5	21.3	228	.33
	9/14-9/27	13	13	0	14	280.0	21.5	20.0	338	.59*
77N-8	9/6-9/17	11	10	1	17	427.2	38.8	25.1	52	.42*
	TOTALS	94	83	11	117	2523.3	26.8	21.5		

[a] The mean direction of all emigrations in the nomadic phase.

[b] The strength of movement around the mean direction.

*$p < .05$

Table 11

Number of Emigrations and Failures to Emigrate through NP

ND	# Cases	# Emigrations	Emig/ND	# Failures to Emigrate	% of Failure
1	6	8	1.3	---[a]	
2	6	7	1.2	1	16.6
3	6	8	1.3	1	16.6
4	7	11	1.6	0	0.0
5	6	9	1.5	2	33.3
6	7	10	1.6	1	14.3
7	8	10	1.3	0	0.0
8	8	10	1.3	0	0.0
9	7	11	1.6	1	14.3
10	6	9	1.5	1	16.6
11	5	9	1.8	2	40.0
12	4	5	1.3	2	50.0
13	5	6	1.2	---[a]	
14	2	3	1.5	---[a]	

[a] Emigrations cannot fail to occur on first or last NDs.

Table 12

Comparisons of Raiding Success on Column Used for Emigration and Columns Not Used for Emigration on 13 Nomadic Days

Colony	Date	ND	Column	Pieces of Booty	Raid Sites	Hours Raided	Emigrated Over?
76N-3	8/5	1	1	36	---	1.0	NO
			2	1260	---	1.4	YES
	8/6	2	1	3534	---	4.5	YES
			2	5360	---	4.8	NO
	8/13	9	1	3084	---	2.3	NO
			2	5360	---	5.5	YES
76N-8	7/30	5	1	90	---	1.5	NO
			2-4	0	---	1.3	NO
			5	150	---	1.0	YES
	7/31	6	1	50	---	0.5	NO
			2	0	---	0.3	NO
			3	43	---	1.0	NO
			4	147	---	1.3	YES
77N-1A	7/28	6	1	1000	6	4.0	YES
			2	250	3	2.5	NO
	7/29	7	1	1300	2	2.2	NO
			2	1100	4	2.3	YES
	7/30	8	1	0	0	0.3	NO
			2	4175	5	4.0	NO
			3	950	2	3.5	YES
	8/1	10	1	0	0	0.3	NO
			2	15	1	1.5	NO
			3	1315	4	6.0	YES
			4	0	0	1.5	NO
			5	310	1	3.0	NO
	8/2	11	1	3120	14	5.5	YES
			2	255	1	7.0	NO
77N-5	7/14	10	1	---	4	0.9	NO
			2	---	0	0.5	YES
	7/15	11a*	1	---	5	3.5	YES
			2	---	4	2.0	NO
			3	---	2	1.5	NO
		11b*	4	---	10	4.5	YES
			5	---	1	0.5	NO
	7/16	12	1	---	9	2.5	NO
			2	---	0	1.1	NO
			3	---	4	1.4	YES

*Raid success was determined prior to each of the two emigrations on ND 11.

Table 13

Pieces of Booty Gathered by 2 Nomadic Colonies During Different Observation Periods

Colony		Emigration			No Emigration
		Before	During	After	
	Pieces	23178	30790	31863	8472
76N-3	Hours	18.0	37.5	14.7	6.0
	Rate	1288	821	2160	1412
	Pieces	1509	7400	11316	28131
76N-8	Hours	8.0	34.3	8.7	20.0
	Rate	180	216	1293	1407

Table 14

Booty Intake During the Feeding Experiments and Emigration

Colony & Size	Date	ND	Food Given mg/larva	Food Gathered mg/larva	Total mg/larva
76N-3	9/10-9/11	9	.52	.07	.59
	9/11-9/12	10	.69	.00	.69
43,000A	9/12-9/13	11*	.45	.17	.62
29,070L	9/13-9/14	12*	.39	.00	.39
	9/14-9/15	13*	.36	.07	.43
77N-8	8/7-8/8	3	.45	.02	.47
	8/8-8/9	4	.61	.01	.62
15,000A	8/9-8/10	5*	1.19	.16	1.35
31,740L	8/10-8/11	6	1.25	.00	1.25
	8/11-8/12	7*	.00	.00	.00
	8/12-8/13	8*	1.26	.00	1.26
	8/13-8/14	9	.82	.31	1.13
	8/14-8/15	10*	1.49	.00	1.49
	8/15-8/16	11*	.92	.00	.92
	8/16-8/17	12*	1.45	.00	1.45
77N-1A	8/23-8/24	2*	.56	.00	.56
	8/24-8/25	3*	.78	.00	.78
12,815A	8/25-8/26	4*	.42	.00	.42
21,240L	8/26-8/27	5*	.24	.00	.24
	8/27-8/28	6*	.00	.00	.00
	8/28-8/29	7	.00	.00	.00
	8/29-8/30	8	.00	.01	.01
	8/30-8/31	9	.00	.16	.16
	8/31-9/1	10*	.45	.14	.59
	9/1-9/2	11*	.42	.19	.61

*NDs on which there was no emigration.

Table 15

Emigration Frequency during the Experimental and Control Nomadic Phases

Colony		Experimental Phase	Control Phase
76N-3	Emigration	2	15
	No Emigration	3	3
77N-1A	Emigration	0	12
	No Emigration	6	3
77N-8	Emigration	4	8
	No Emigration	5	3
TOTAL	Emigration	6	35
	No Emigration	14	9

Table 16

Comparison of Emigration Frequency in *Eciton burchelli* and *Neivamyrmex nigrescens*: Species and Habitat Differences

Species (season)	Number of Colonies	Aggregate[a] of NDs	Number of Failures to Emigrate	ND of Failure	Source
E. burchelli (dry)	7	96	16	2,2,3,3,3, 3,4,5,6,6, 7,8,9,10, 12,13	Schneirla & Brown, 1950
E. burchelli (rainy)	3	43	5[b]	3,4,6,9,10	Schneirla & Brown, 1950
E. burchelli (dry)	1	207	44	not reported	Teles da Silva, 1977
E. burchelli (rainy)	1	120	51	not reported	Teles da Sivla, 1977
N. nigrescens	9	69	18	2,2,3,3,5, 7,7,8,9,10, 11,11,13,15, 16,20,20,20	Schneirla, 1958
N. nigrescens	6	94	11	2,3,5,5,6, 9,10,11,11, 12,12	present study

[a] These samples include first and last NDs.

[b] Four of these failures occurred in a single colony subjected to an experimental reduction of the larval brood.

FIGURES

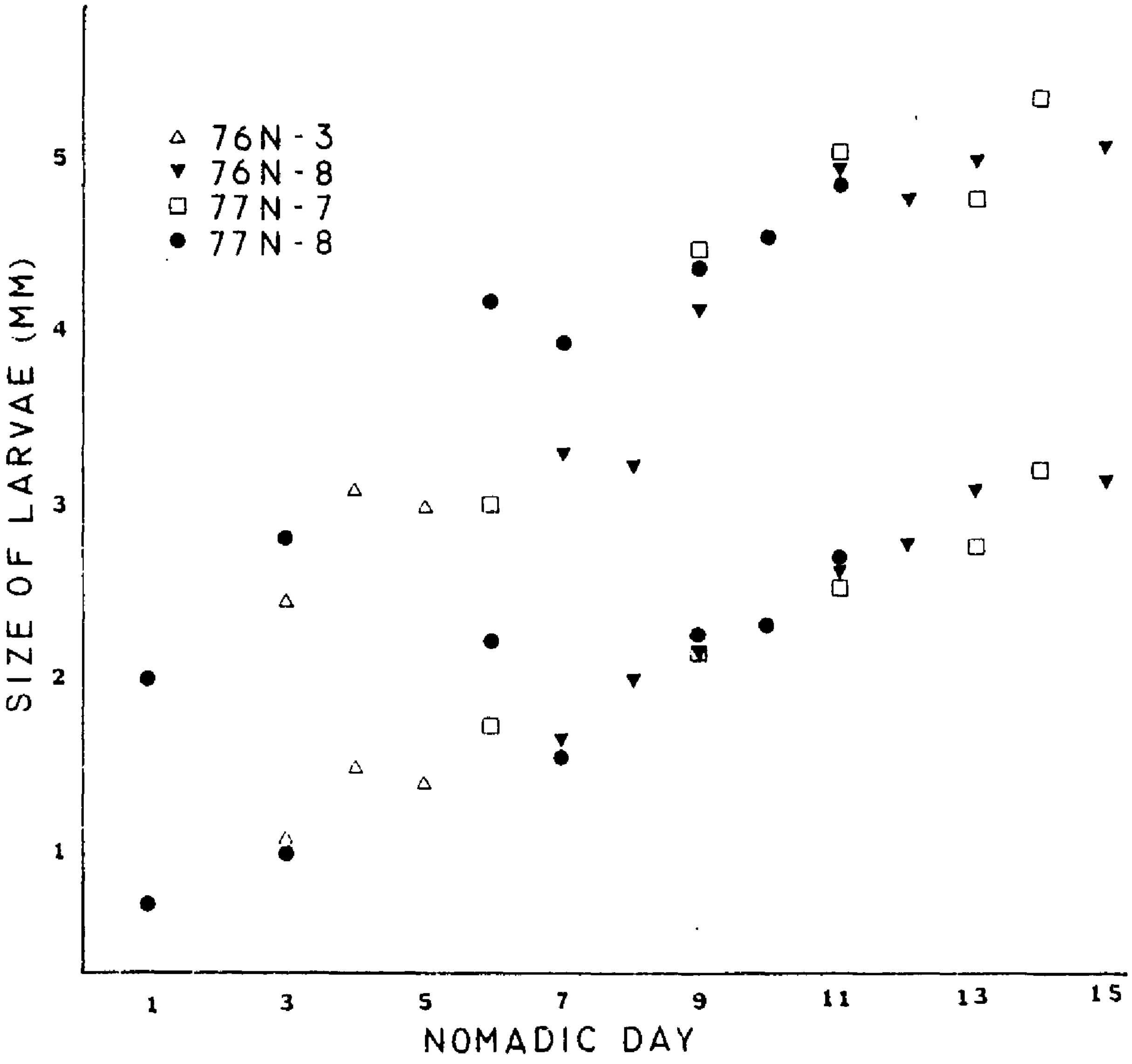

Figure 1. Growth of larvae from four colonies through the nomadic phase. Upper points: mean size of the 10 largest larvae in the sample. Lower points: mean size of the 10 smallest larvae in the sample. Sample sizes ranged from 100-200 larvae.

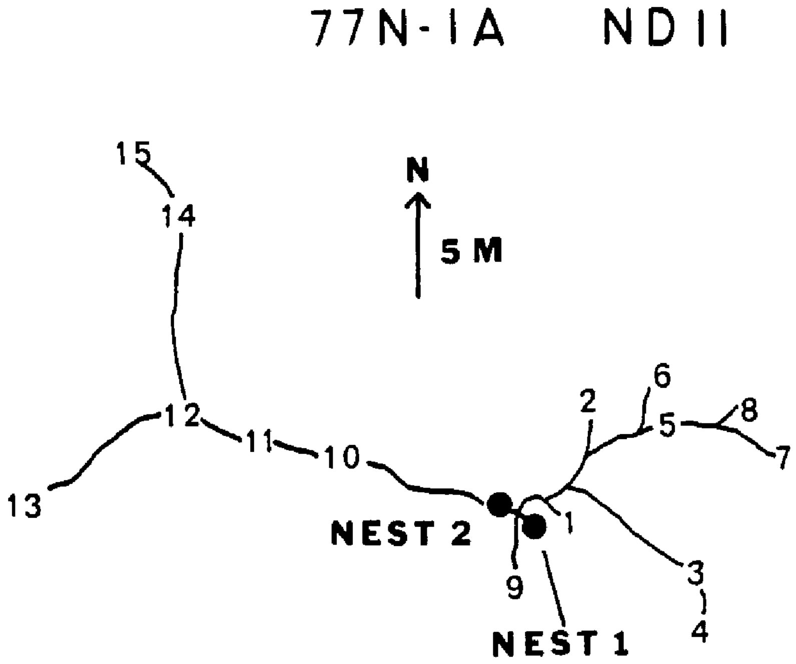

Figure 2. Raiding and emigration activity of colony 77N-1A on ND 11 (8/2-8/3) from 18:00-05:00 hours. Numbers indicate sites where prey was found and the order in which sites were discovered. All the raid sites were discovered before the emigration began at 04:30 (from nest 1 to nest 2).

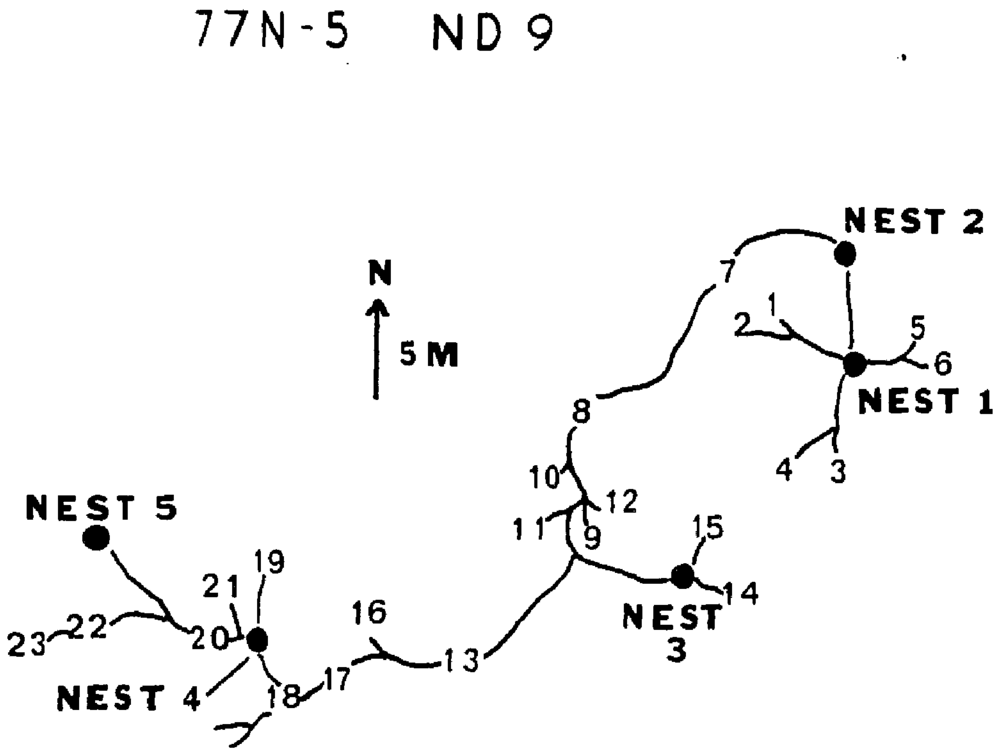

Figure 3. Raiding and emigration acitivity of colony 77N-5 on ND 9 (7/13-7/14) between 18:00-01:00 hours. The colony made four separate emigrations (from nest 1 to nest 2, etc.) beginning at 18:00, 20:00, 22:10, and 01:00. Raiding at the numbered sites took place during the almost continuous emigration activity.

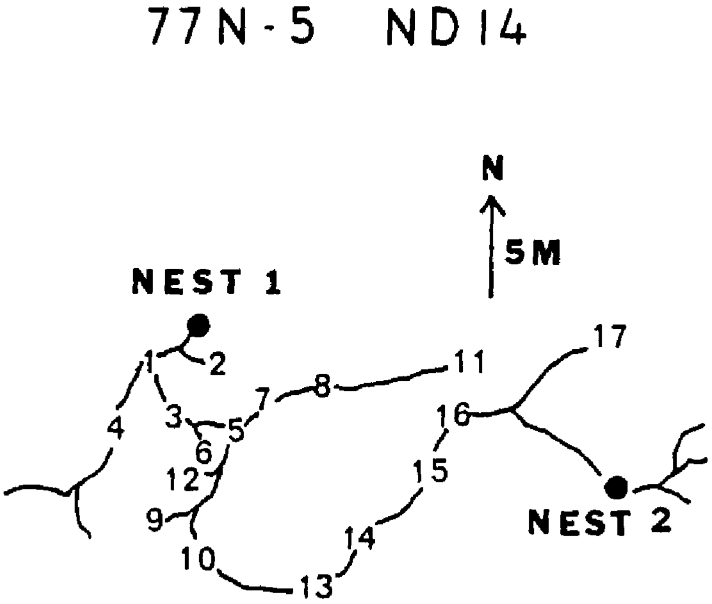

Figure 4. Raiding and emigration activity of colony 77N-5 on ND 14 (7/18-7/19) from 18:00-01:00 hours. Raiding occurred at the numbered sites before the emigration started at 24:00 hours.

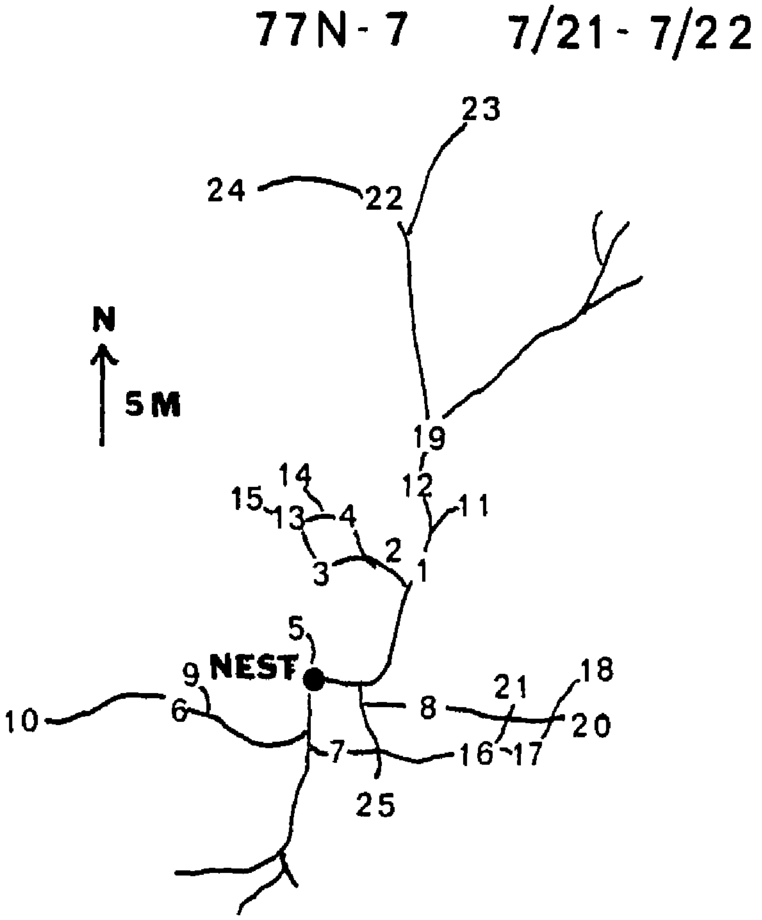

Figure 5. Raiding activity of colony 77N-7 on 7/21-7/22 (late in NP) between 18:30-00:30. The colony raided extensively in all directions from its nest but did not emigrate.

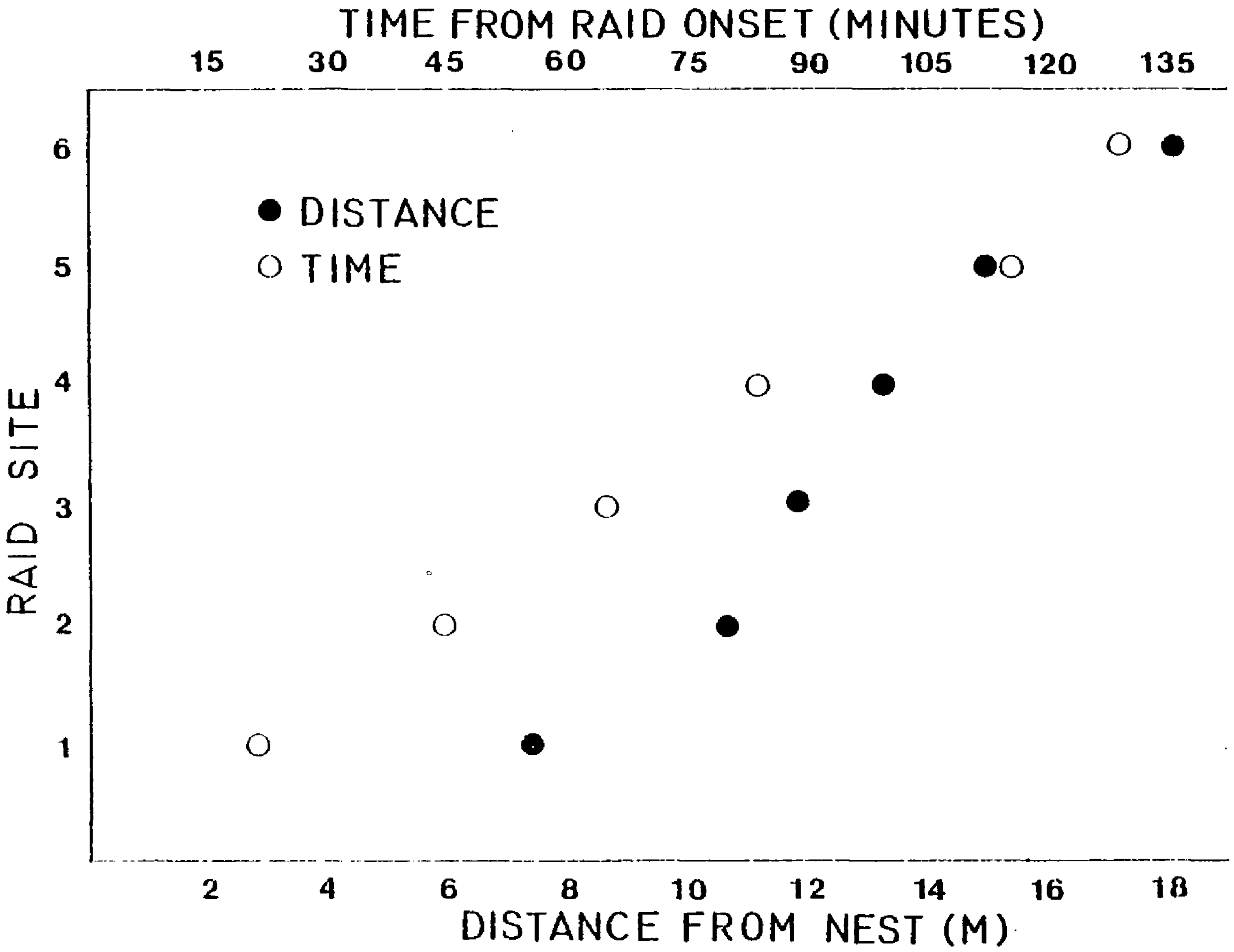

Figure 6. The discovery of raid sites as a function of time active and distance travelled from the nest. The data points are average values for each column listed in Table 4.

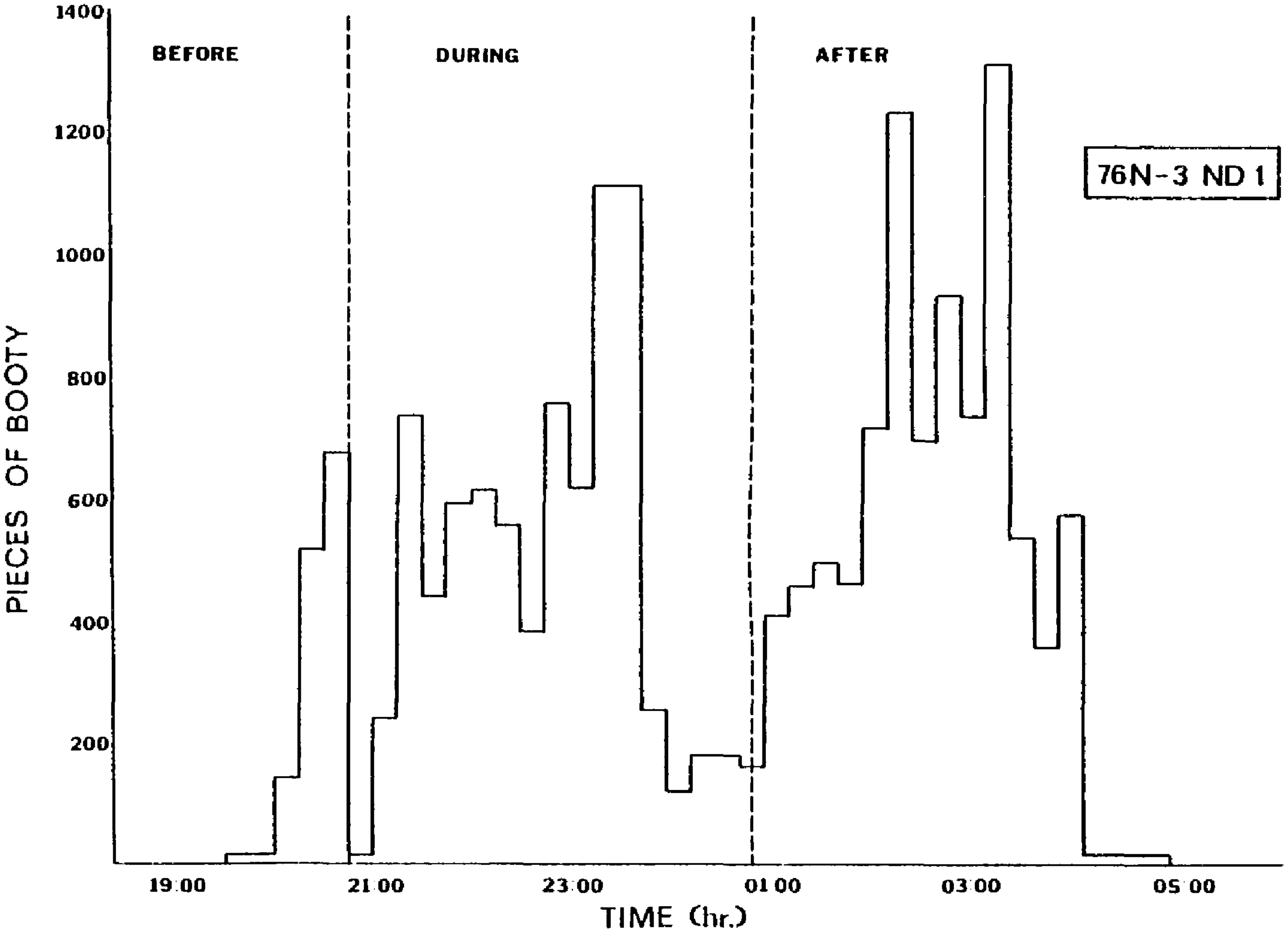

Figure 7. Booty intake of colony 76N-3 before, during and after the emigration on ND 1(8/5-8/6). The intake is shown as pieces of booty carried into the nest in blocks of 15 minutes. Counts were started at 19:30 when the colony became active and continued to 05:00 when the colony ceased its surface activity.

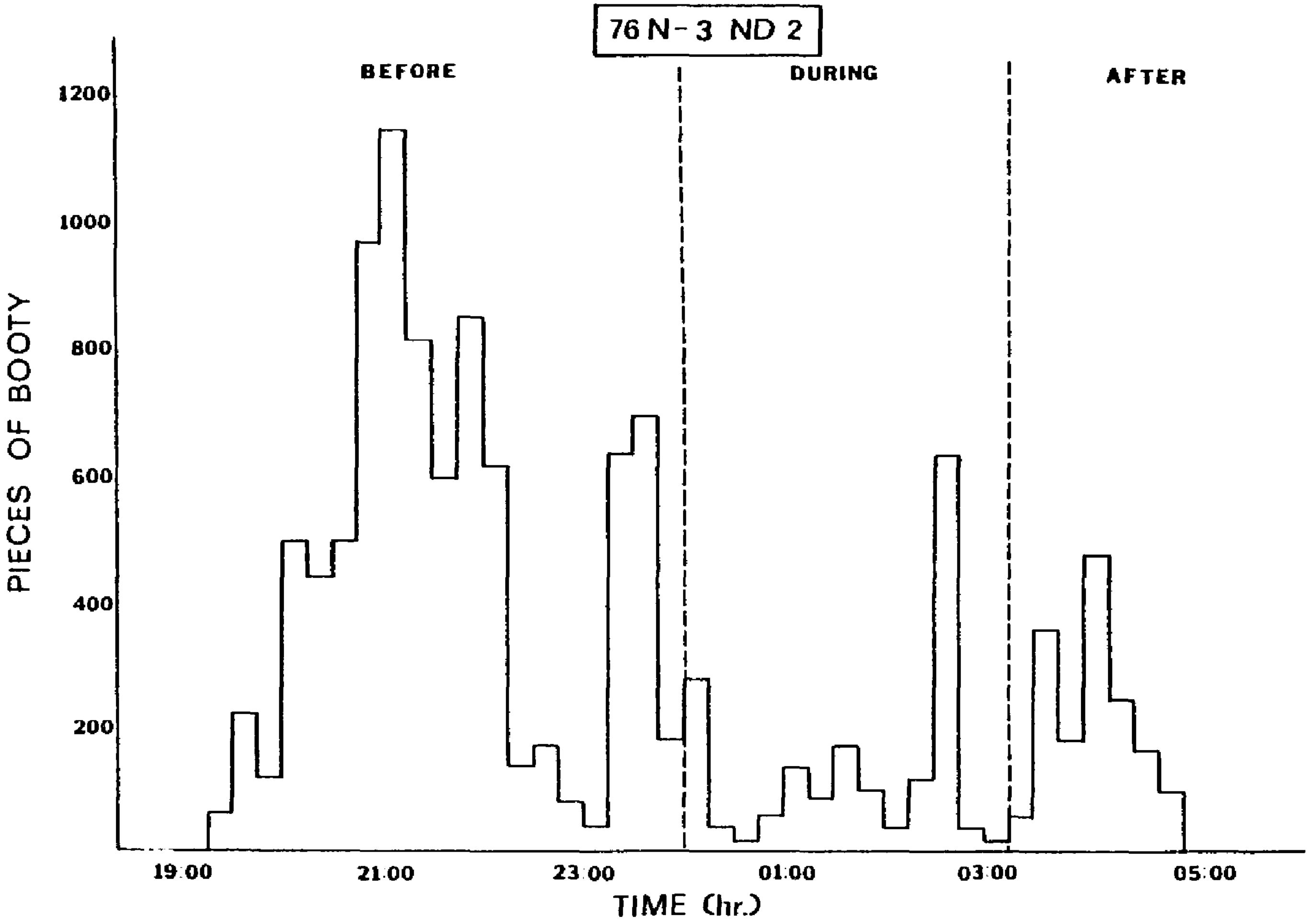

Figure 8. Booty intake of colony 76N-3 before, during and after the emigration on ND 2 (8/6-8/7), shown as in Figure 7. Counts were made between 19:15 and 04:45 hours, covering all raiding activity.

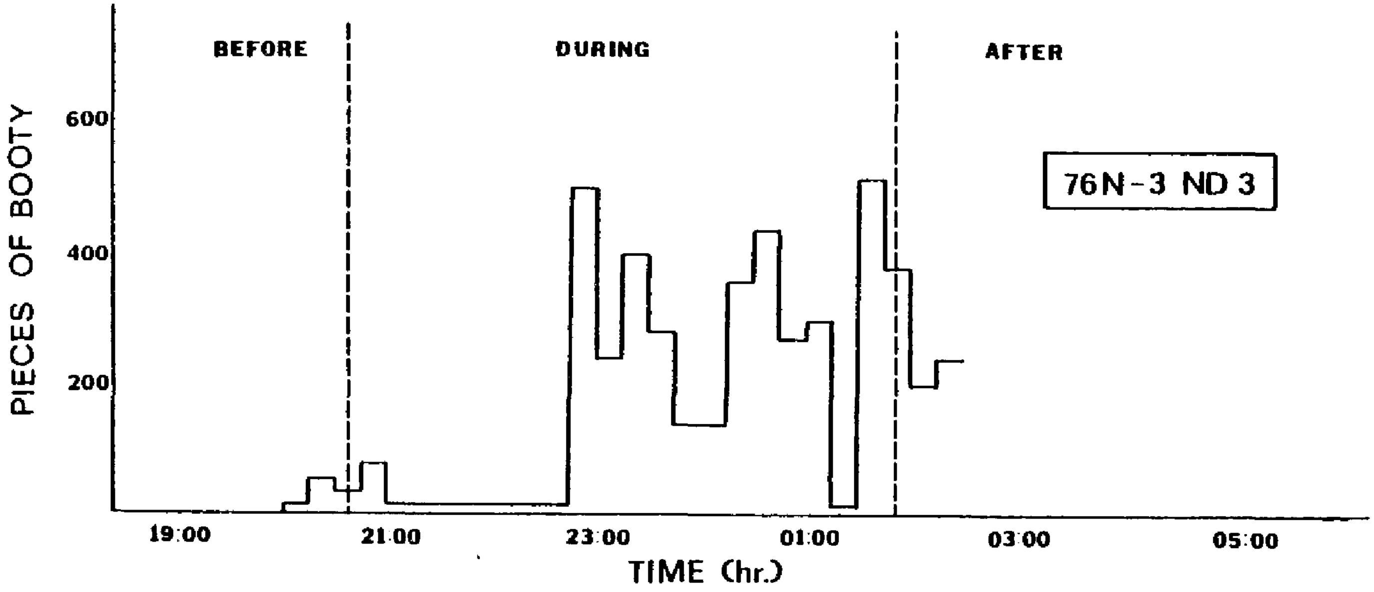

Figure 9. Booty intake of colony 76N-3 before, during and after the emigration on ND 3(8/7-8/8), shown as in Figure 7. Counts were made between 20:00 and 02:45, but the colony continued raiding after this time.

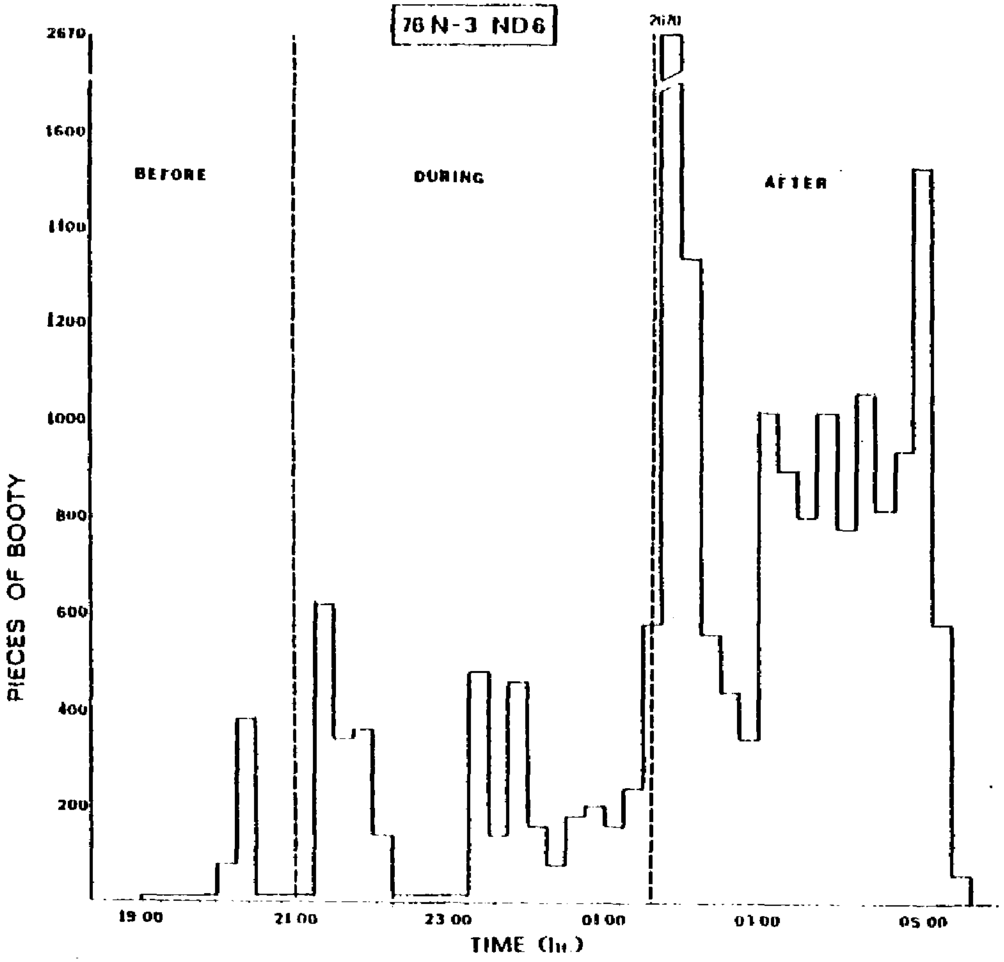

Figure 10. Booty intake of colony 76N-3 before, during and after the emigration on ND 6 (8/10-8/11), shown as in Figure 7. Counts were made between 19:00 and 05:30 hours, covering all raiding activity.

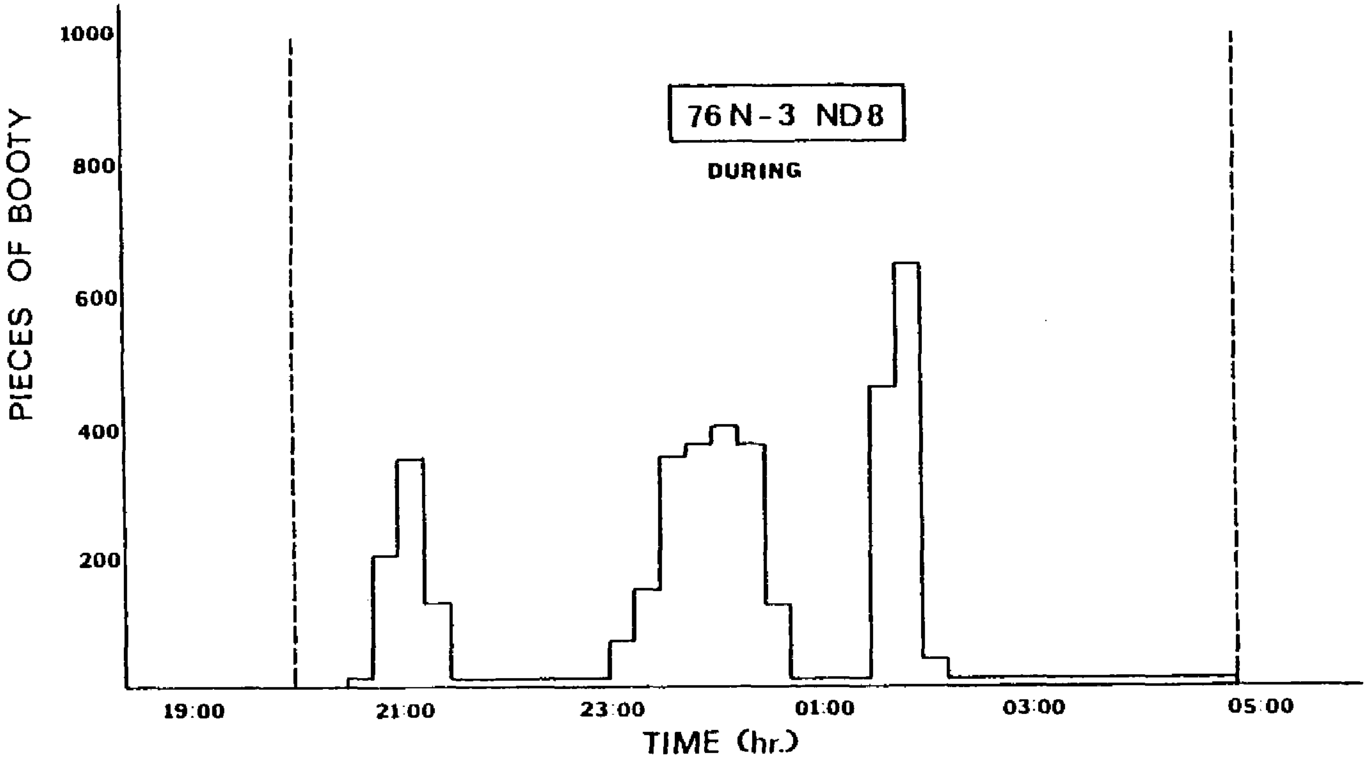

Figure 11. Booty intake of colony 76N-3 during the emigration on ND 8 (8/12-8/13), shown as in Figure 7. Counts were made between 20:30 and 05:00 hours, covering all raiding activity during this prolonged emigration.

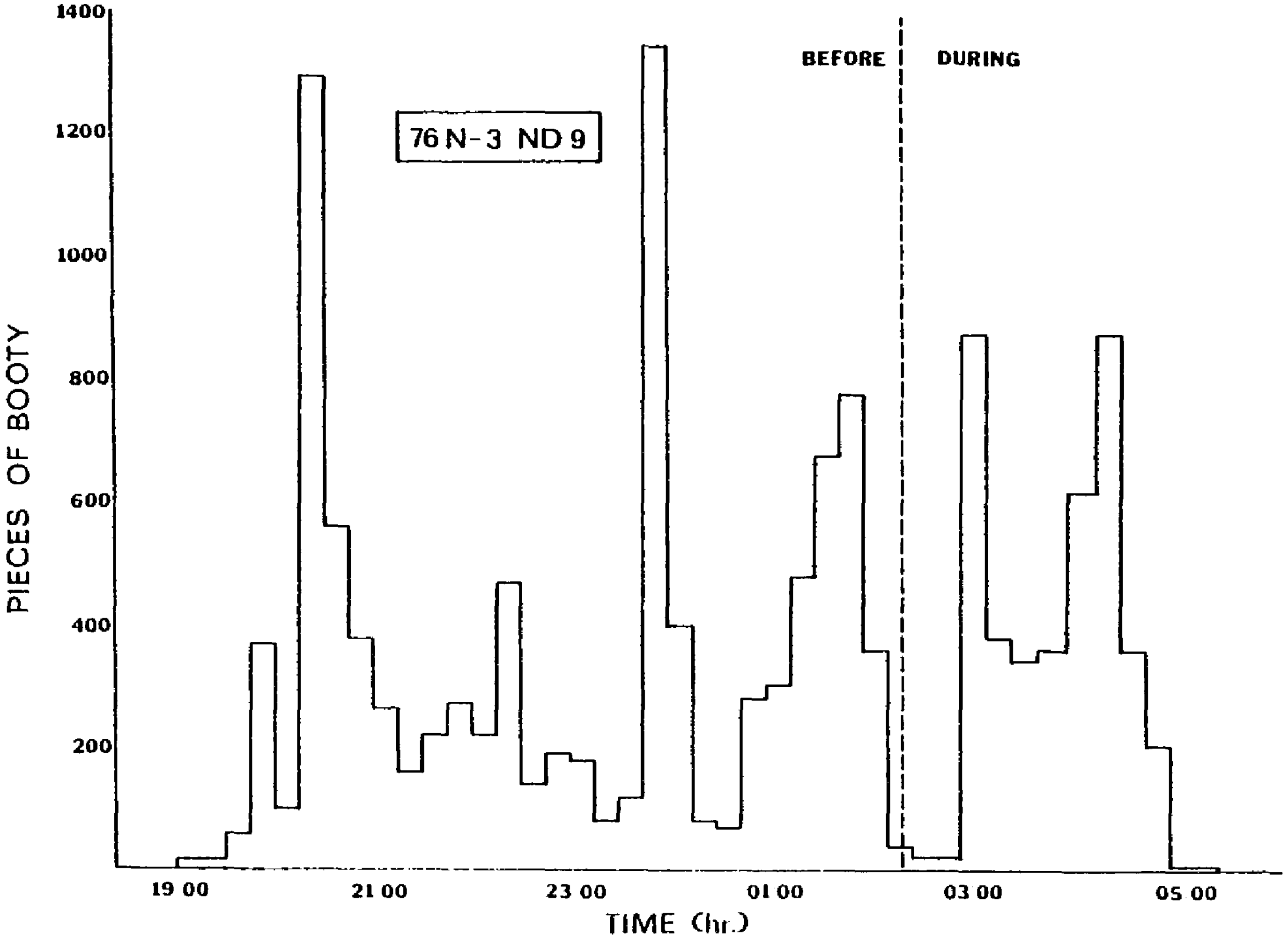

Figure 12. Booty intake of colony 76N-3 before and during the emigration on ND 9 (8/13-8/14), shown as in Figure 7. Counts were made between 19:00 and 05:15 hours, covering all raiding activity.

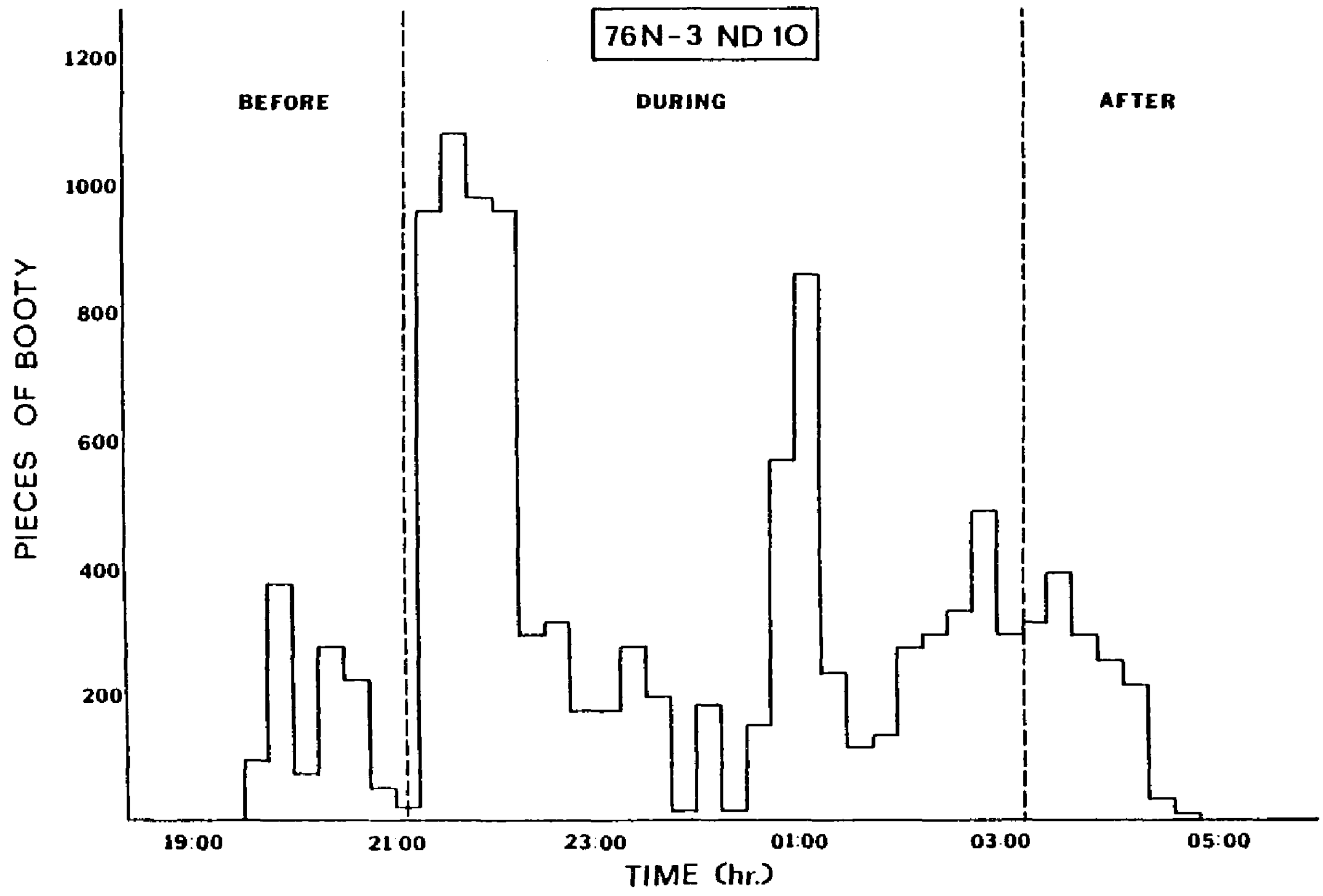

Figure 13. Booty intake of colony 76N-3 before, during and after the emigration on ND 10 (8/14-8/15), shown as in Figure 7. Counts were made between 19:30 and 05:00 hours, covering all raiding activity.

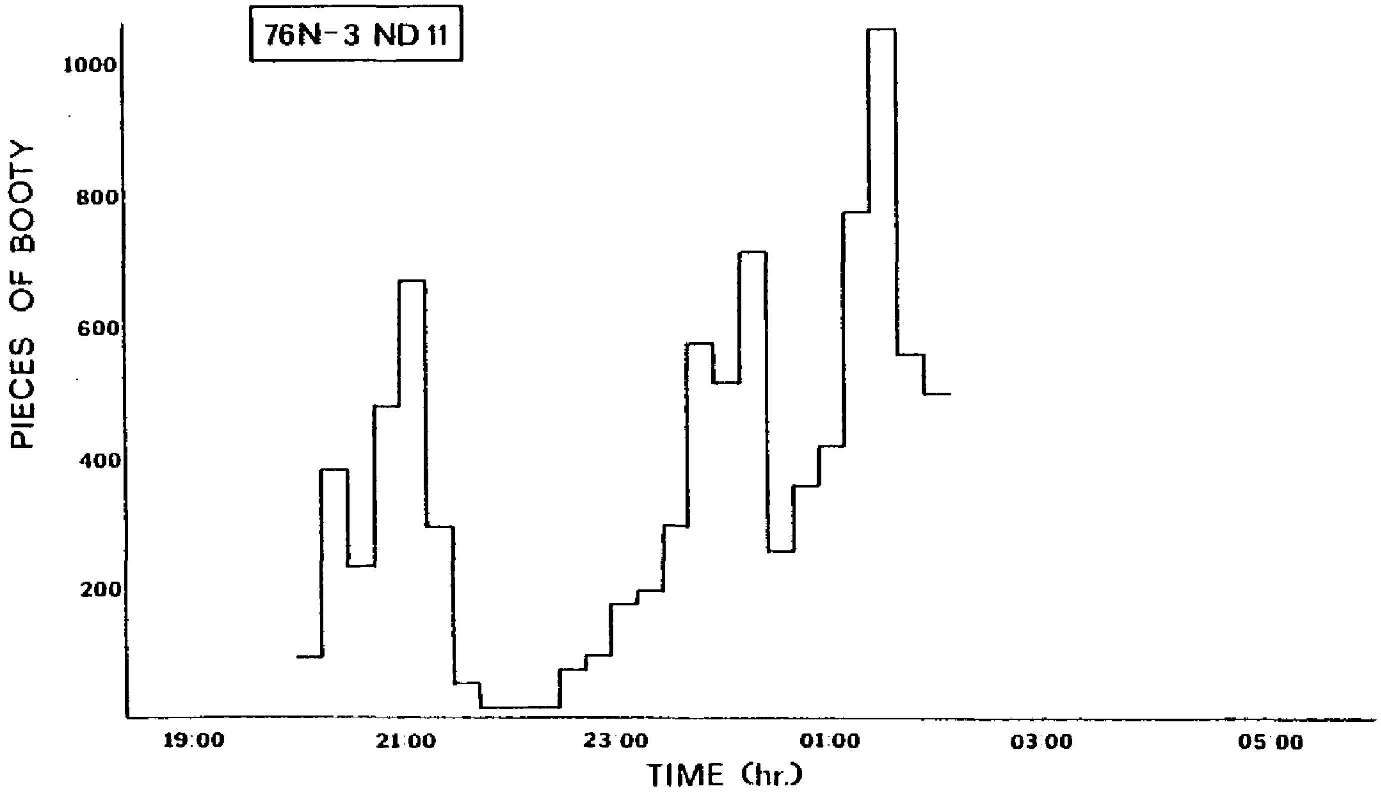

Figure 14. Booty intake of colony 76N-3 on ND 11 (8/15-8/16). There was no emigration. Counts were made between 20:00 and 02:15 hours, but raiding occurred before and after this period.

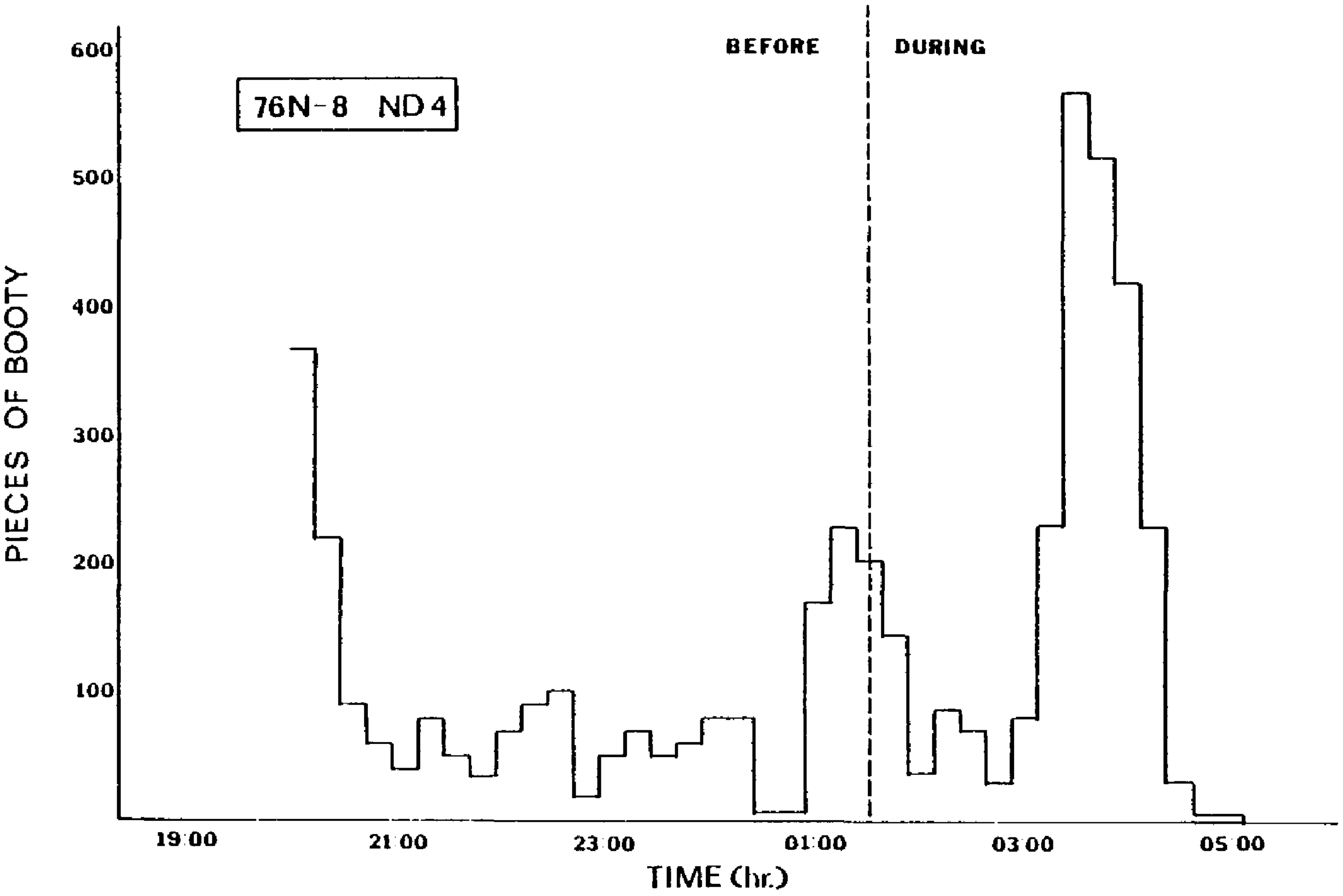

Figure 15. Booty intake of colony 76N-8 before and during the emigration on ND 4 (7/30-7/31), shown as in Figure 7. Counts were made between 20:00 (a few minutes after the colony became active) and 05:15 (when the colony ceased raiding).

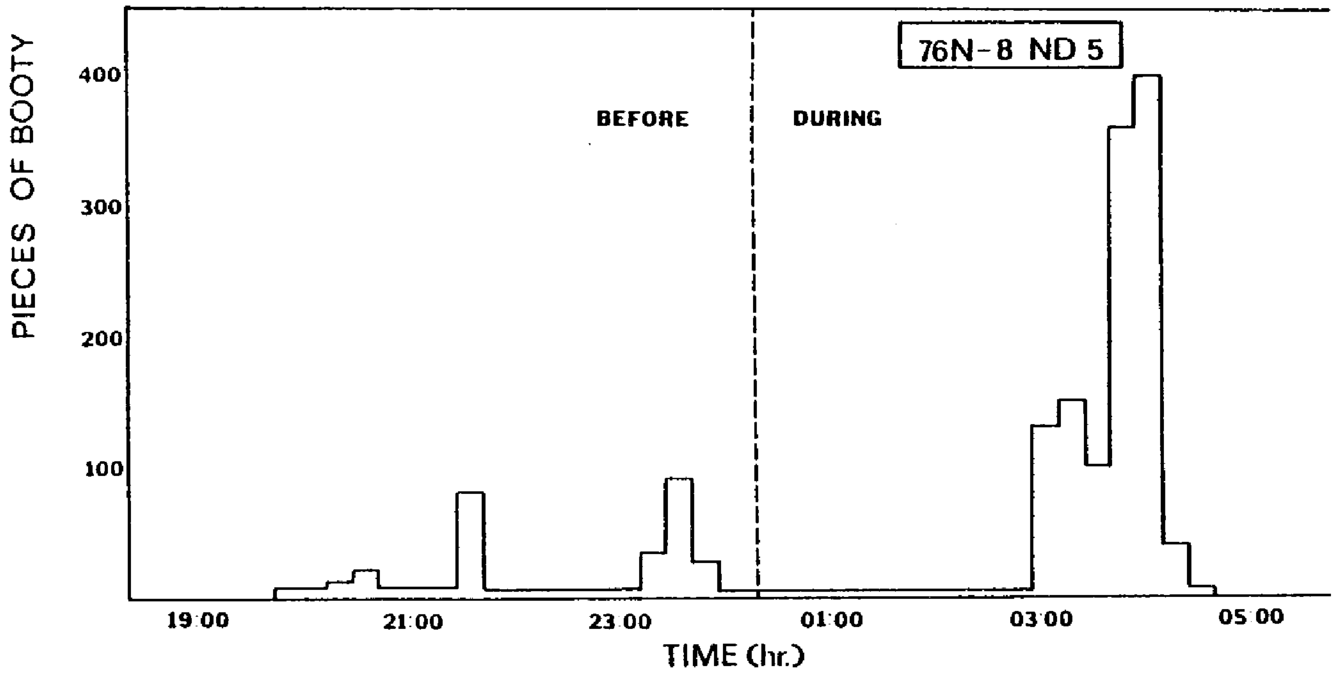

Figure 16. Booty intake of colony 76N-8 before and during the emigration on ND 5 (7/31-8/1), shown as in Figure 7. Counts were made between 19:45 and 04:45 hours, covering all raiding activity.

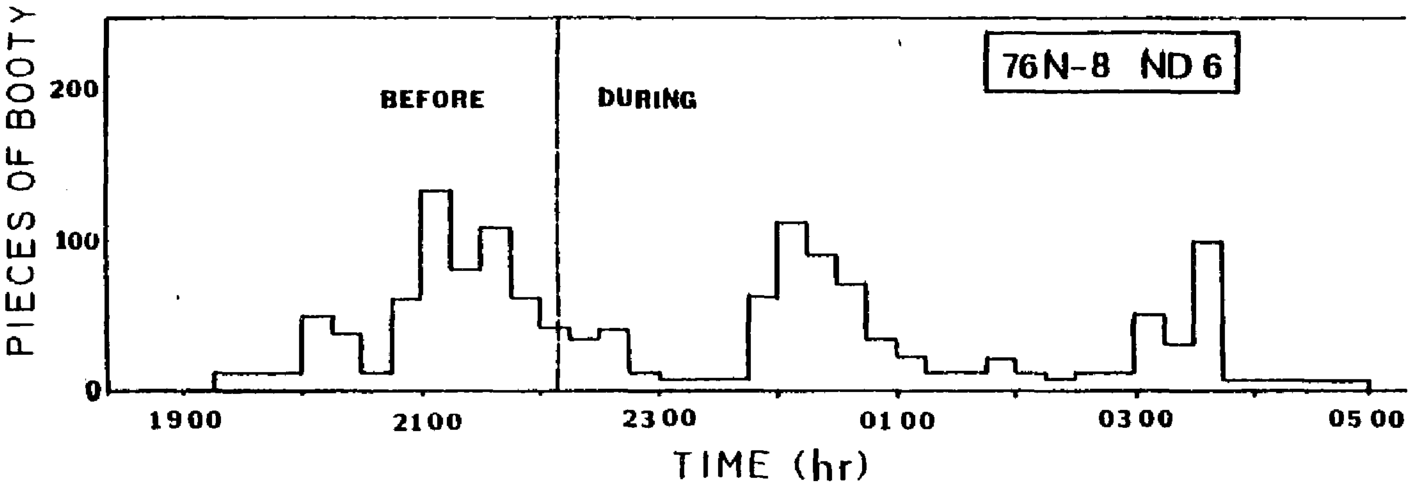

Figure 17. Booty intake of colony 76N-8 before and during the emigration on ND 6 (8/1-8/2), shown as in Figure 7. Counts were made between 19:15 and 05:00 hours, covering all raiding activity.

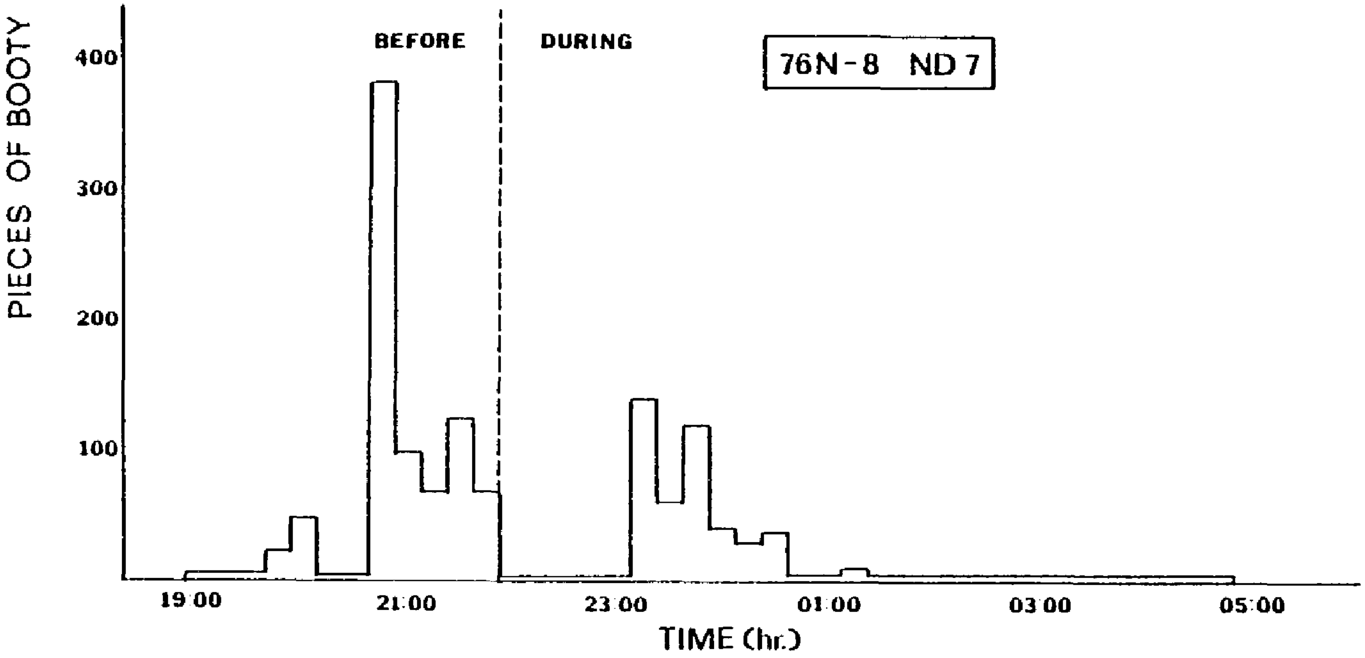

Figure 18. Booty intake of colony 76N-8 before and during the emigration on ND 7 (8/2-8/3), shown as in Figure 7. Counts were made between 19:00 and 05:00 hours, covering all raiding activity.

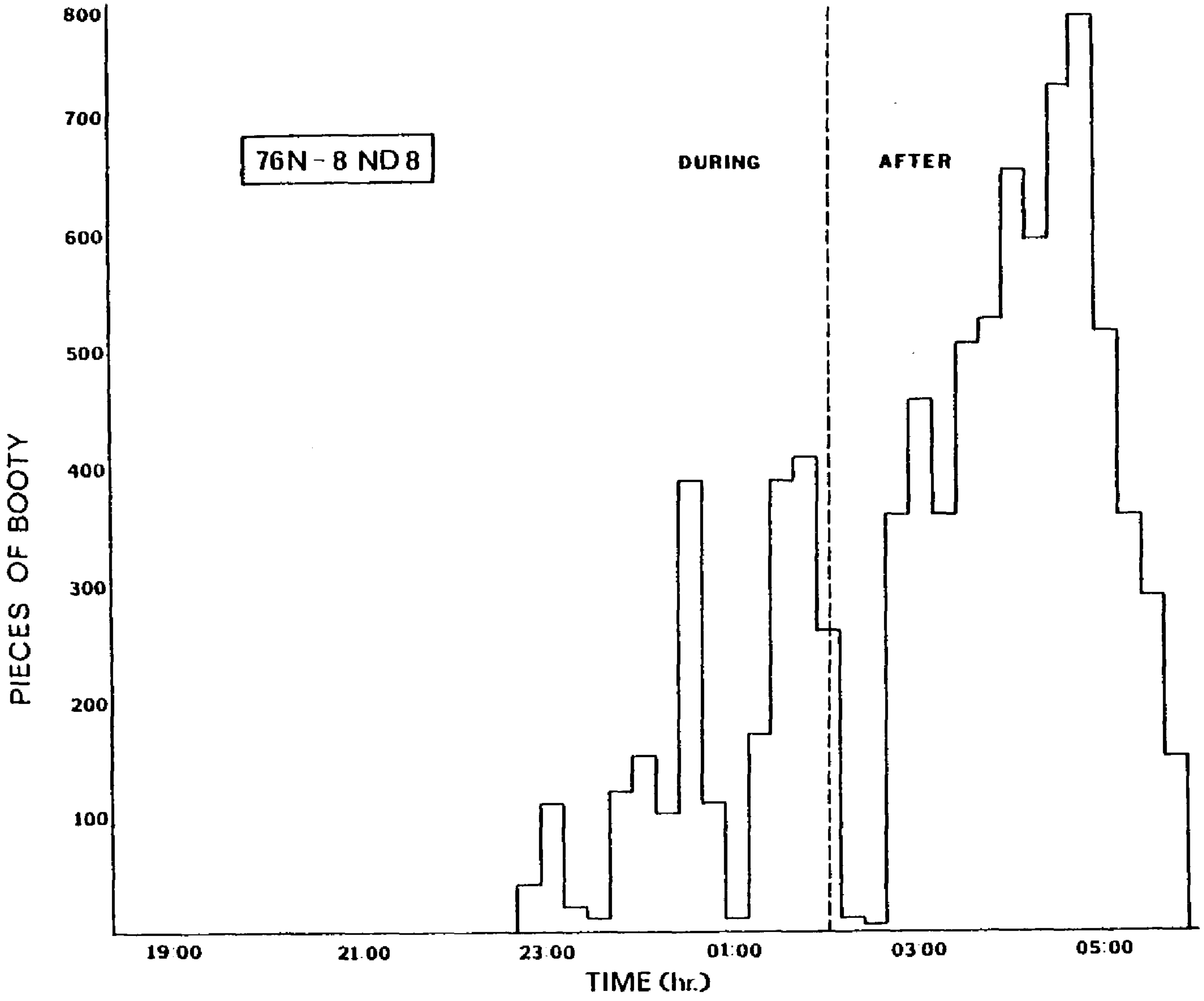

Figure 19. Booty intake of colony 76N-8 during and after the emigration on ND 8 (8/3-8/4), shown as in Figure 7. Counts began at 22:45 and continued until the colony ceased raiding at 05:45.

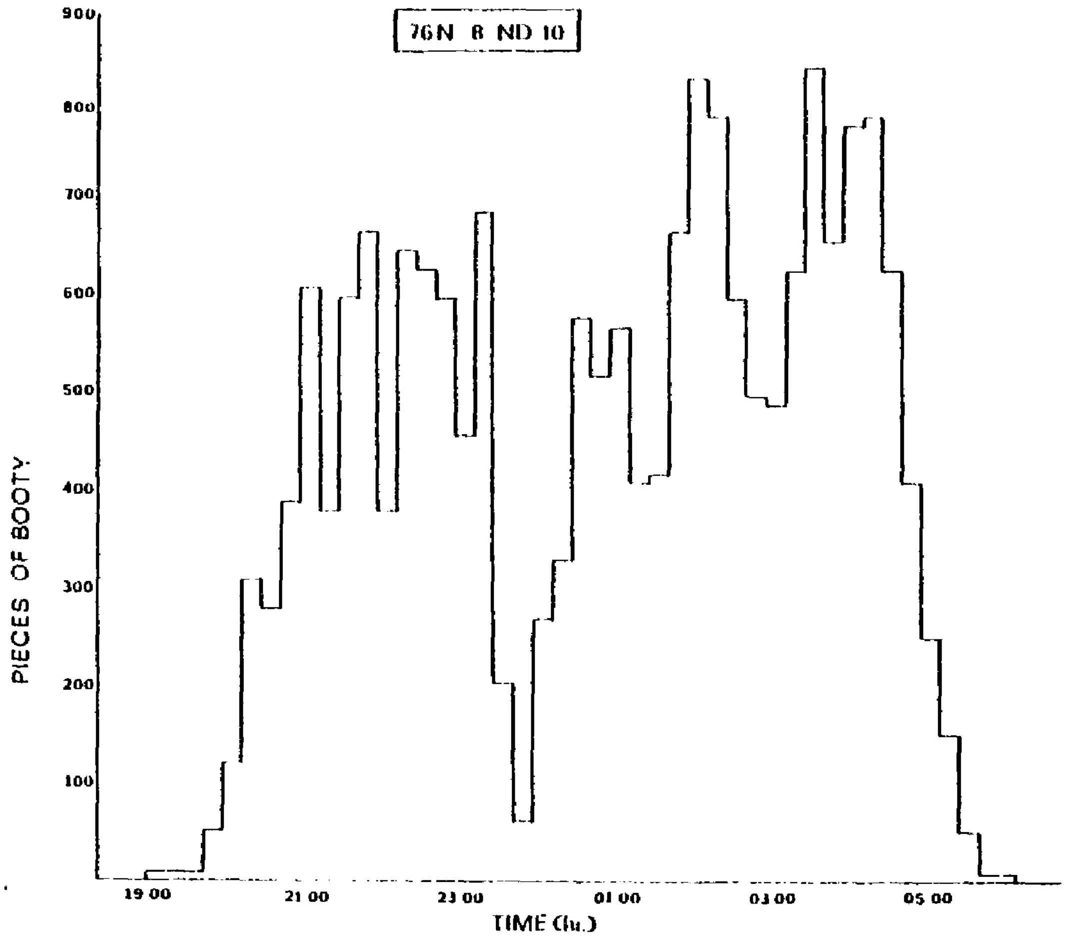

Figure 20. Booty intake of colony 76N-8 on ND 10 (8/5-8/6), shown as in Figure 7. There was no emigration. Counts were made between 19:00 and 06:00 hours, covering all raiding activity.

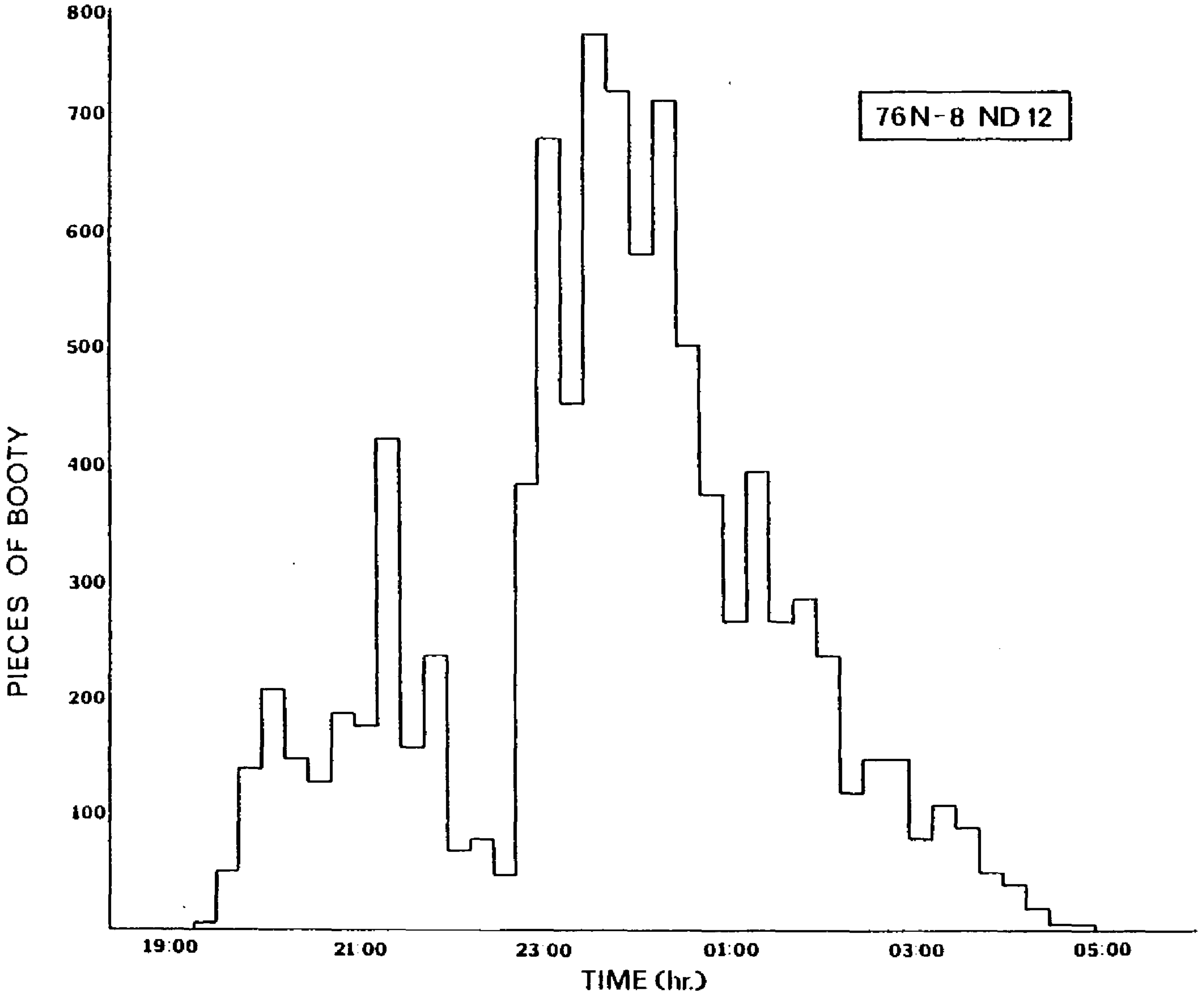

Figure 21. Booty intake of colony 76N-8 on ND 12 (8/7-8/8), shown as in Figure 7. There was no emigration. Counts were made between 19:15 and 05:00 hours, covering all raiding activity.

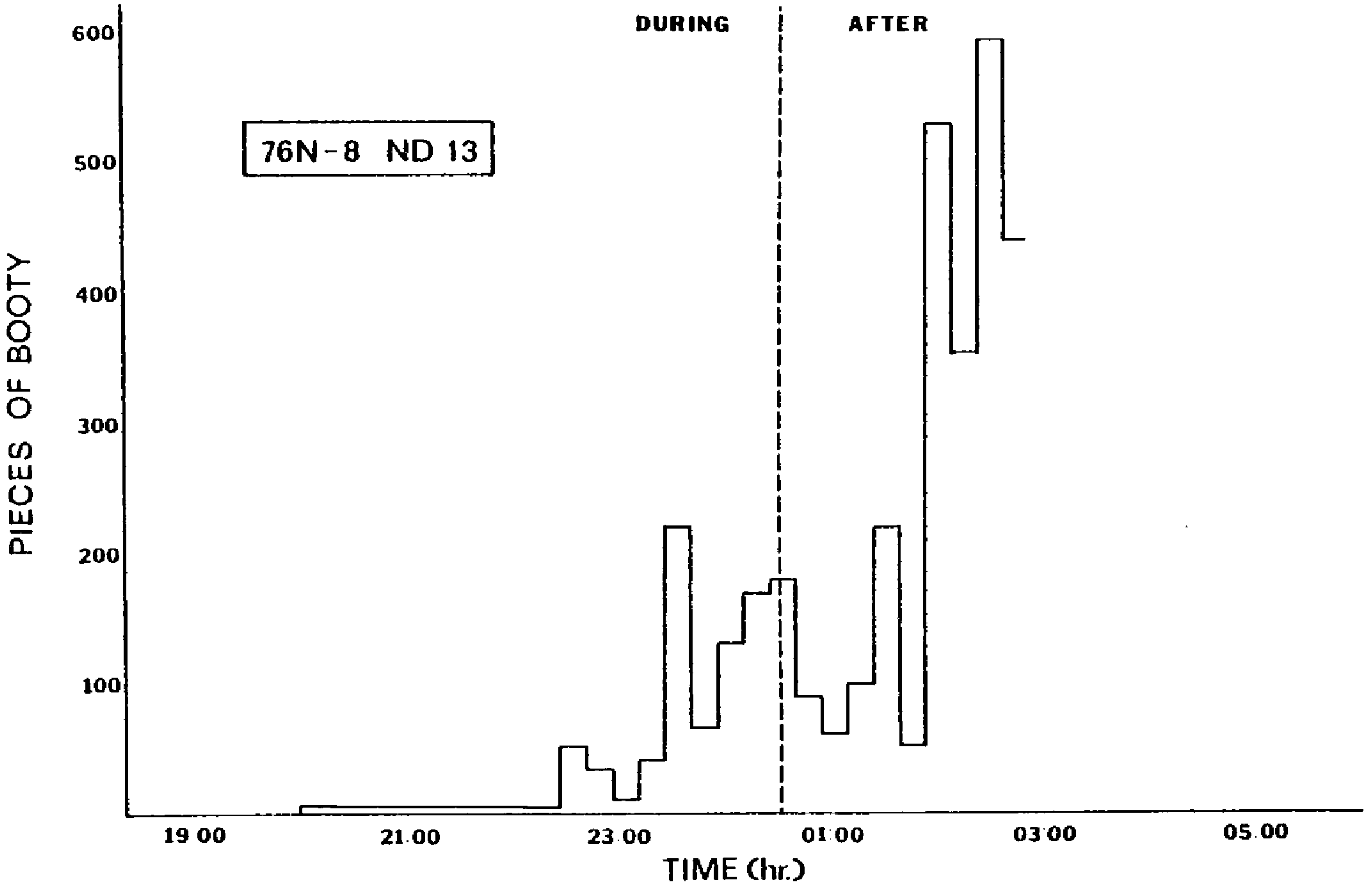

Figure 22. Booty intake of colony 76N-8 during and after the emigration on ND 13 (8/8-8/9), shown as in Figure 7. Counts began at 20:00 (the emigration was already in progress) and continued to 03:00, but raiding continued after this time.

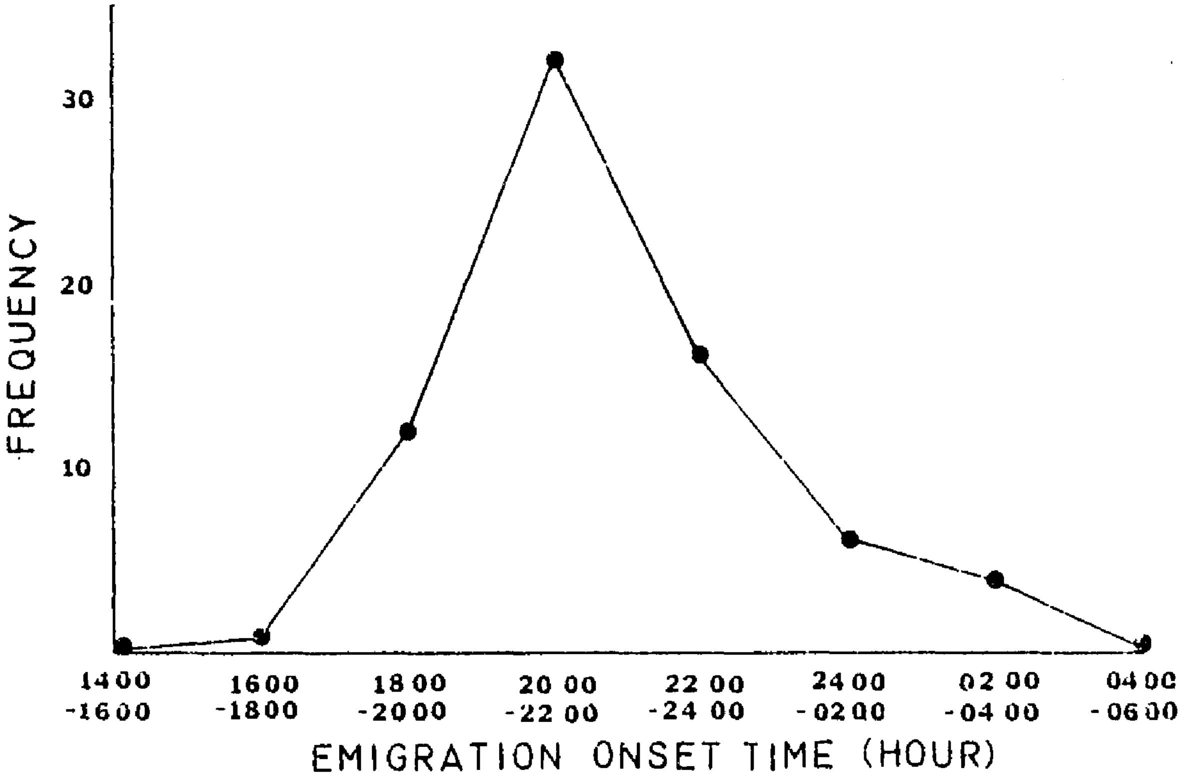

Figure 23. Frequency distribution of emigration onset times.

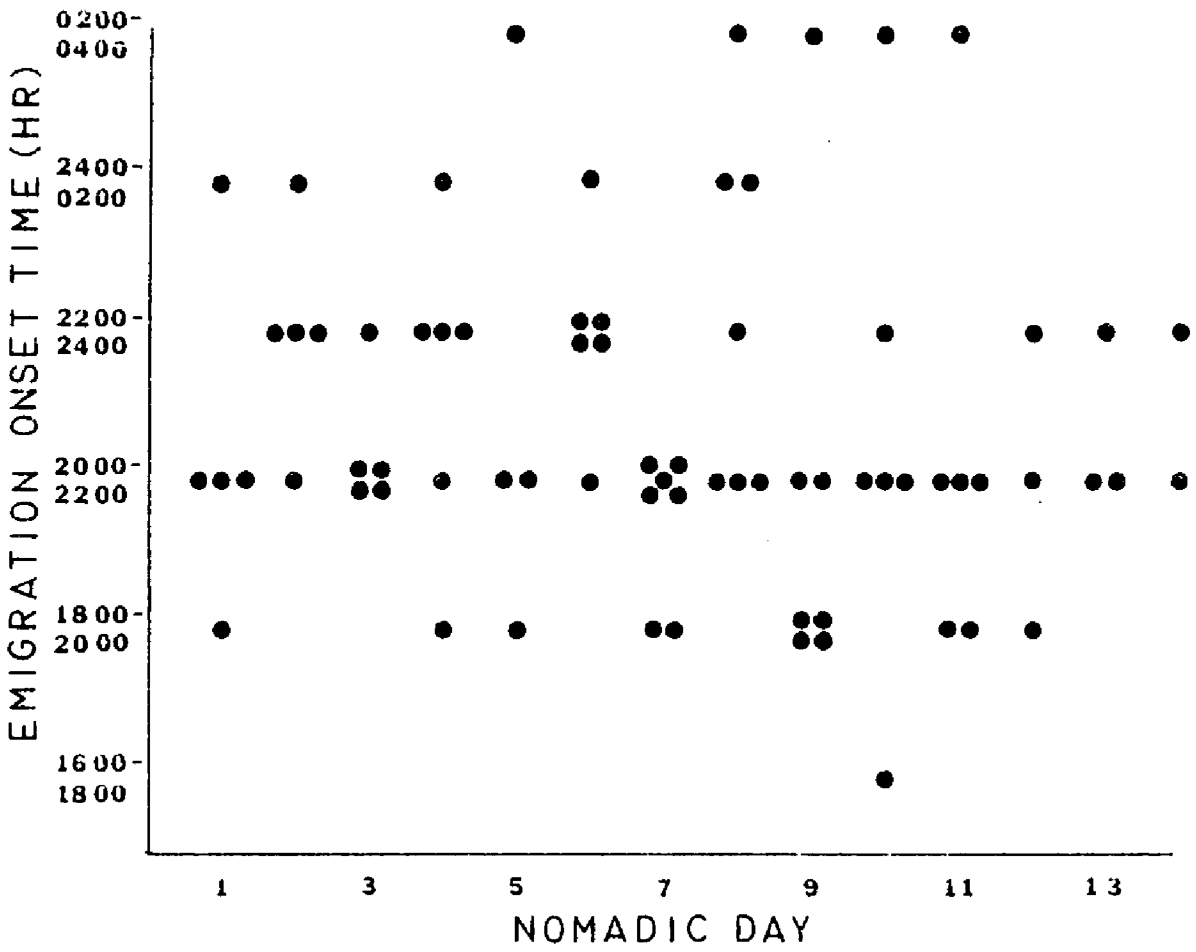

Figure 24. Emigration onset time as a function of ND.

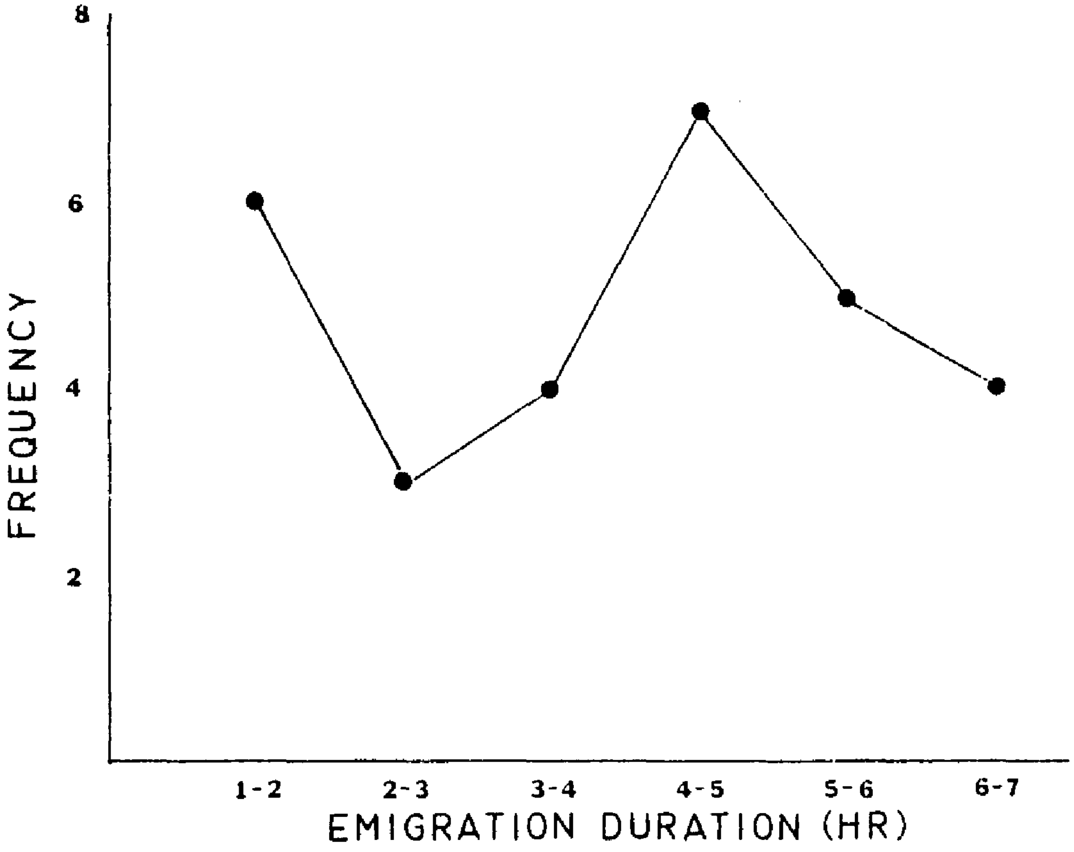

Figure 25. Frequency distribution of emigration durations.

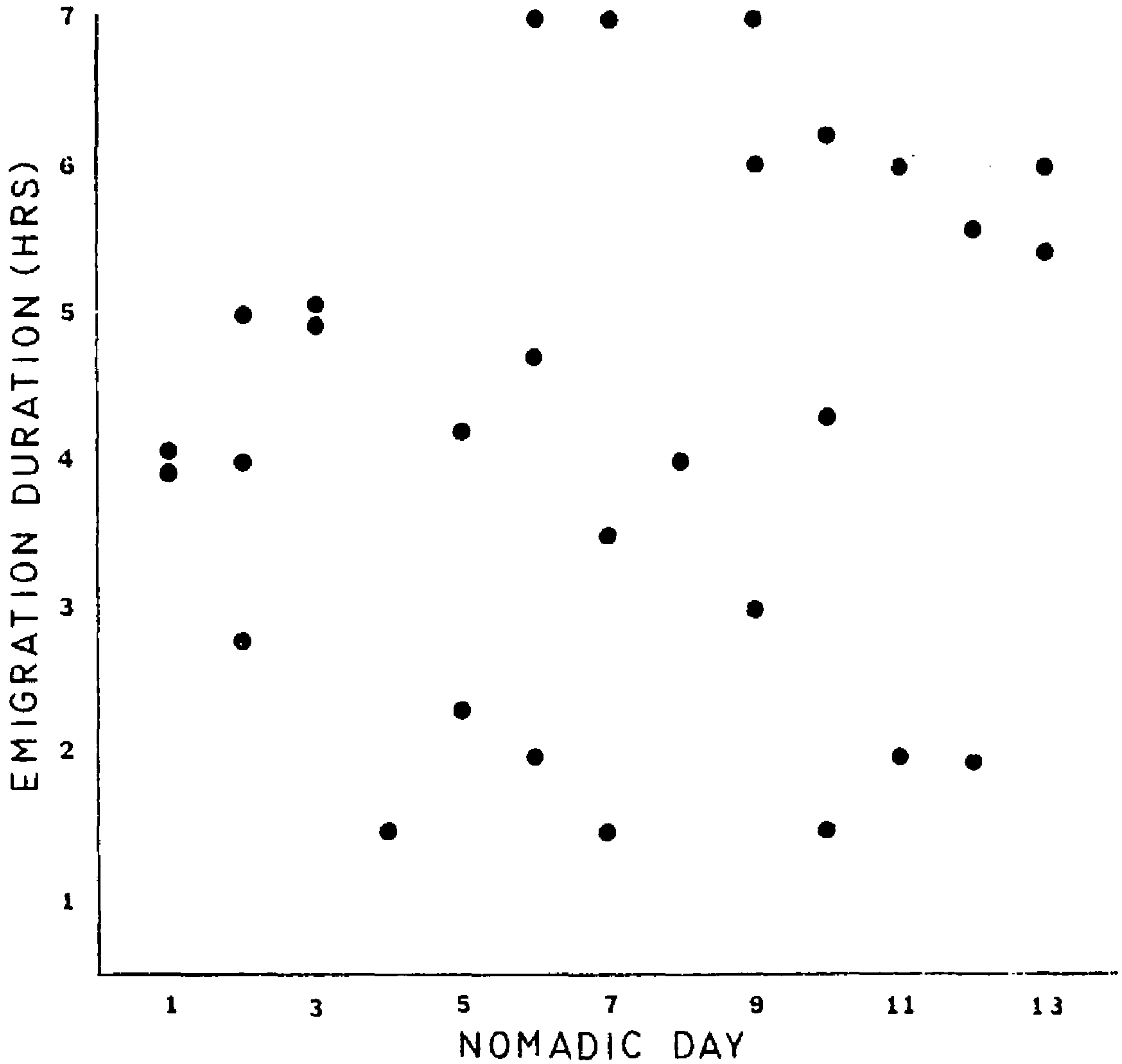

Figure 26. Emigration duration as a function of ND.

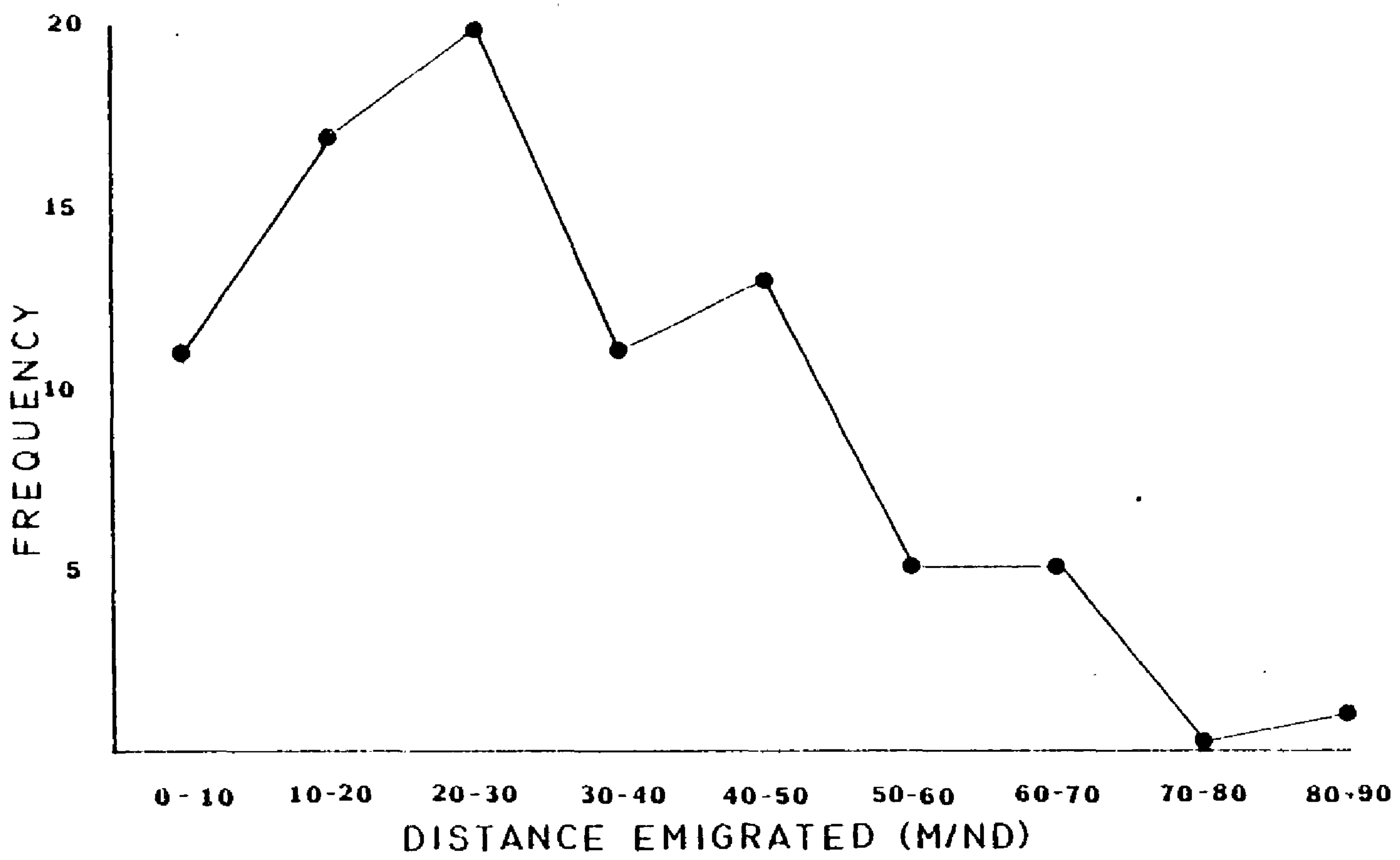

Figure 27. Frequency distribution of emigration distances.

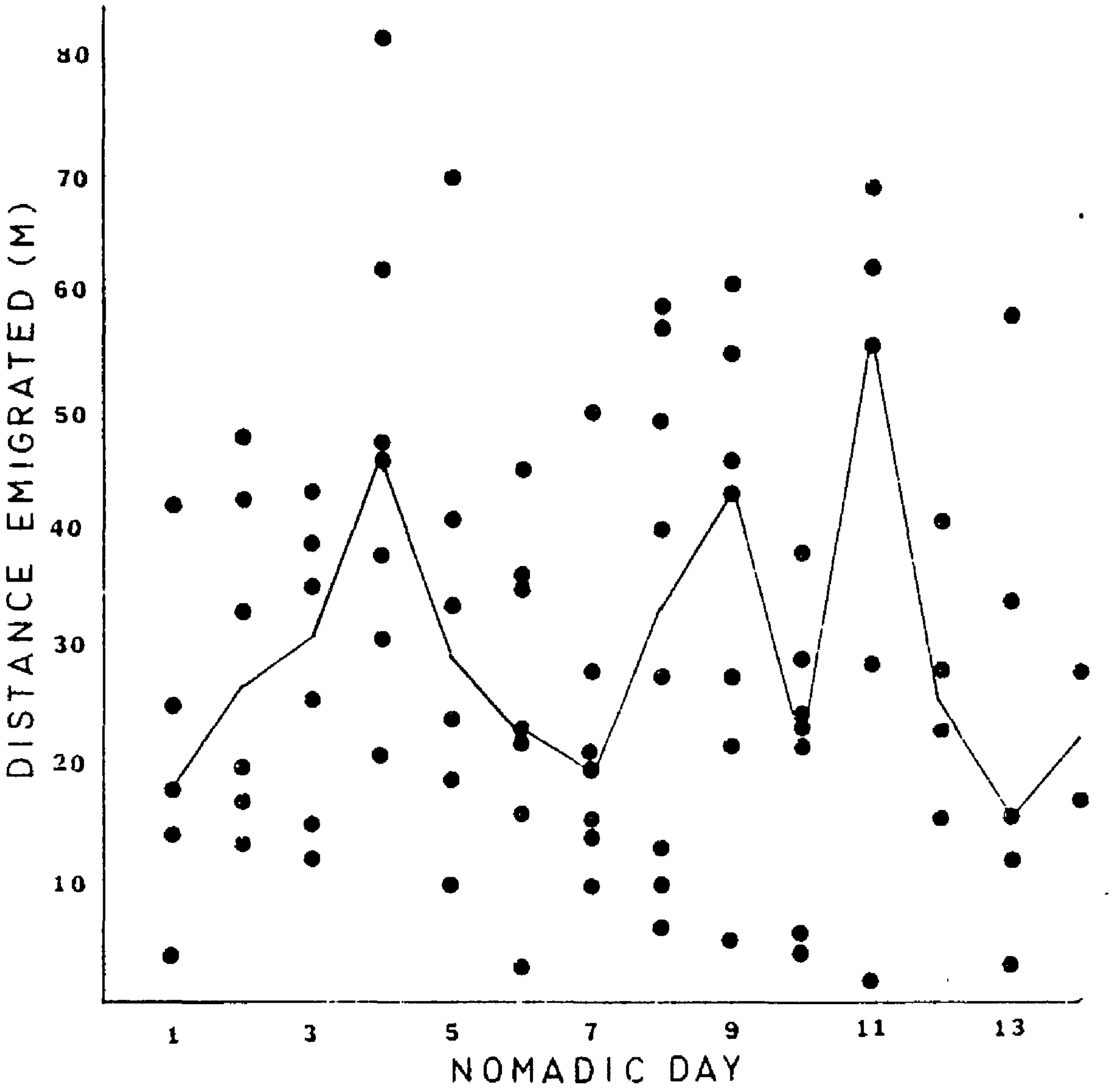

Figure 28. Emigration distance as a function of ND. The line connects the median distances of each ND.

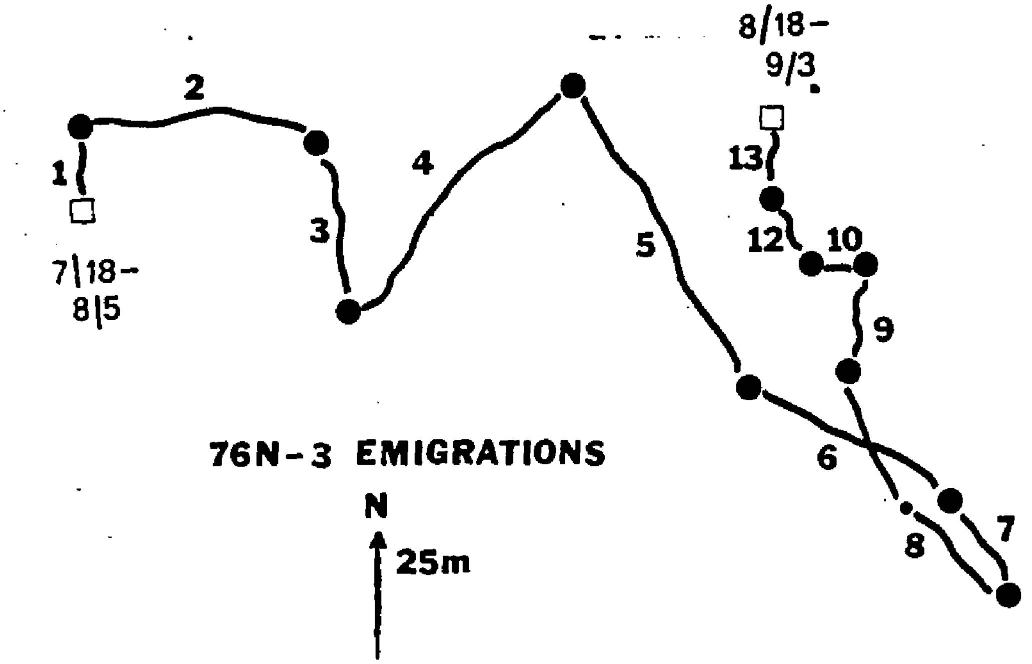

Figure 29. Movements of colony 76N-3. The colony was statary from 7/18-8/5, then became nomadic and changed its nest on 12 of the next 13 days. There were 2 emigrations on ND 8 and no emigration on ND 11. After ND 13 the colony became statary (8/18-9/3). The numbers alongside the emigration routes indicate the ND on which that movement occurred. • --interim bivouac; ● --nomadic bivouac; □--statary bivouac.

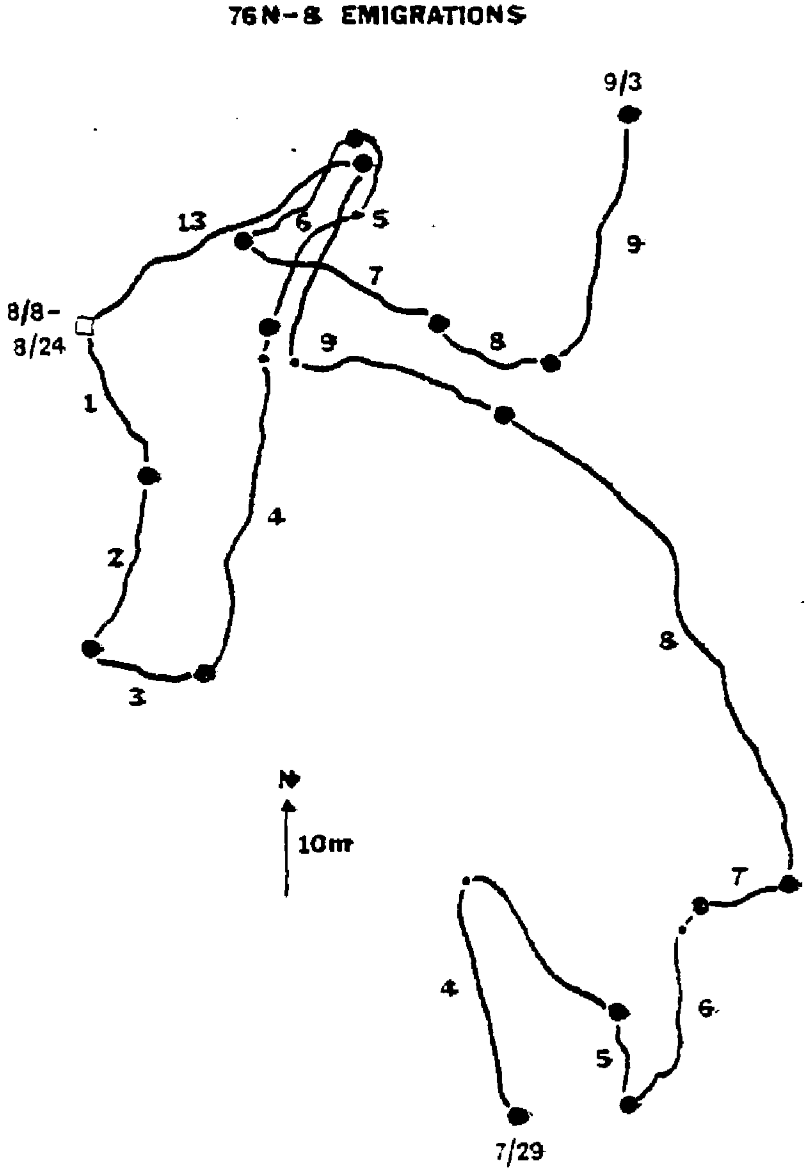

Figure 30. Movements of colony 76N-8. The colony was emigrating when encountered on 7/29, and changed its nest of 6 of the next 9 days. There were two emigrations on ND 4, 6, and 9 and no emigration on ND 10, 11, 12. After ND 13 the colonywas statary (8/8-8/24), then changed its nest on the next 9 days. There were two emigrations on ND 4 and 5. Numbers and symbols as in Figure 29.

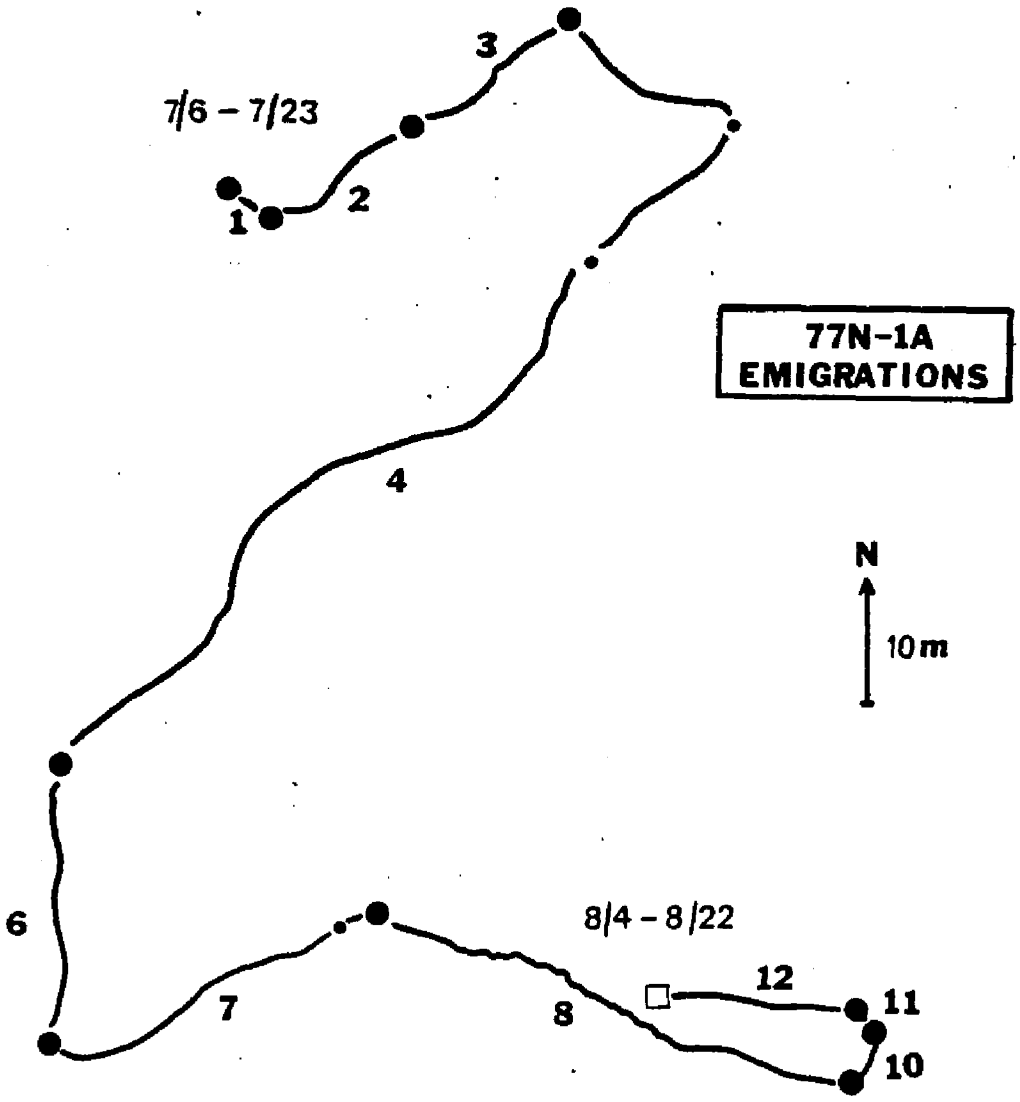

Figure 31. Movements of colony 77N-1A. The colony was statary from 7/6-7/23, then changed its nest on 10 of the next 12 days. There were 3 emigrations on ND 4, 2 emigrations on ND 7, and no emigration on ND 5 and 9. After ND 12 the colony became statary (8/4-8/22). Numbers and symbols as in Figure 29.

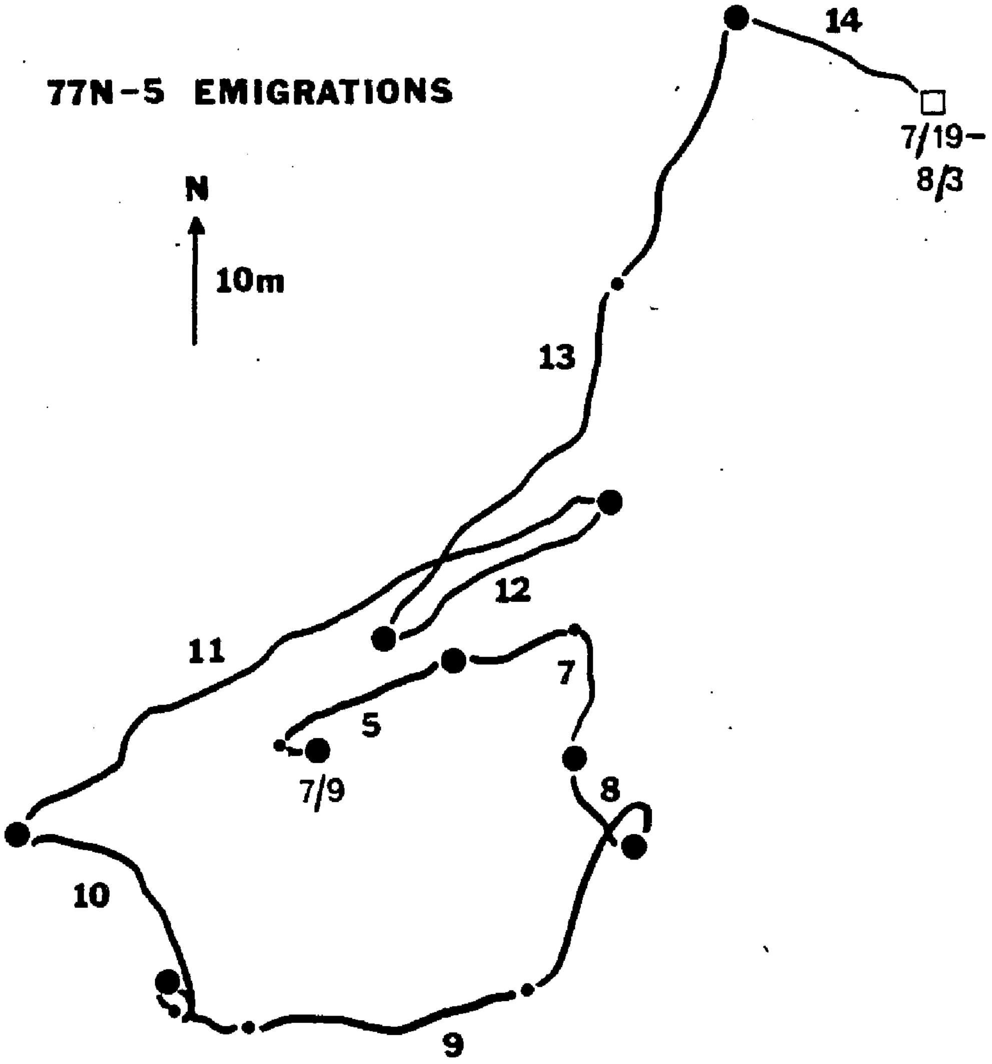

Figure 32. Movements of colony 77N-5. The colony was emigrating when encountered on 7/9, then changed its nest on 7 of the next 9 days. There were 4 emigrations on ND 9, 2 emigrations on ND 5, 7 and 13, and no emigration on ND 6. After ND 14 the colony became statary (7/19-8/3). Numbers and symbols as in Figure 29.

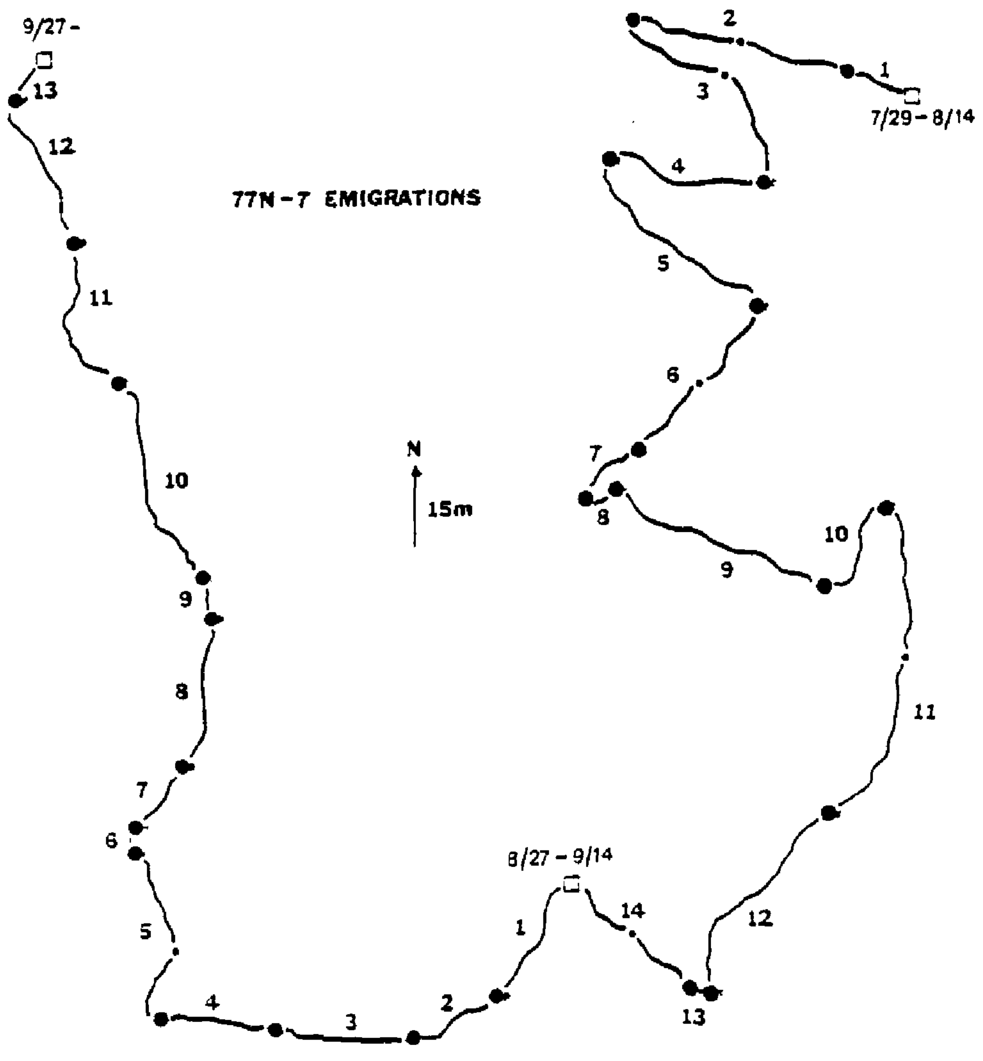

Figure 33. Movements of colony 77N-7. The colony was statary from 7/29-8/14, then changed its nest on the next 14 days. There were 2 emigrations on NDs 2, 3, 6, 11 and 14. The colony was statary from 8/27-9/14, then changed its nest on the next 13 days. There were 2 emigrations on ND 5. Numbers and symbols as in Figure 29.

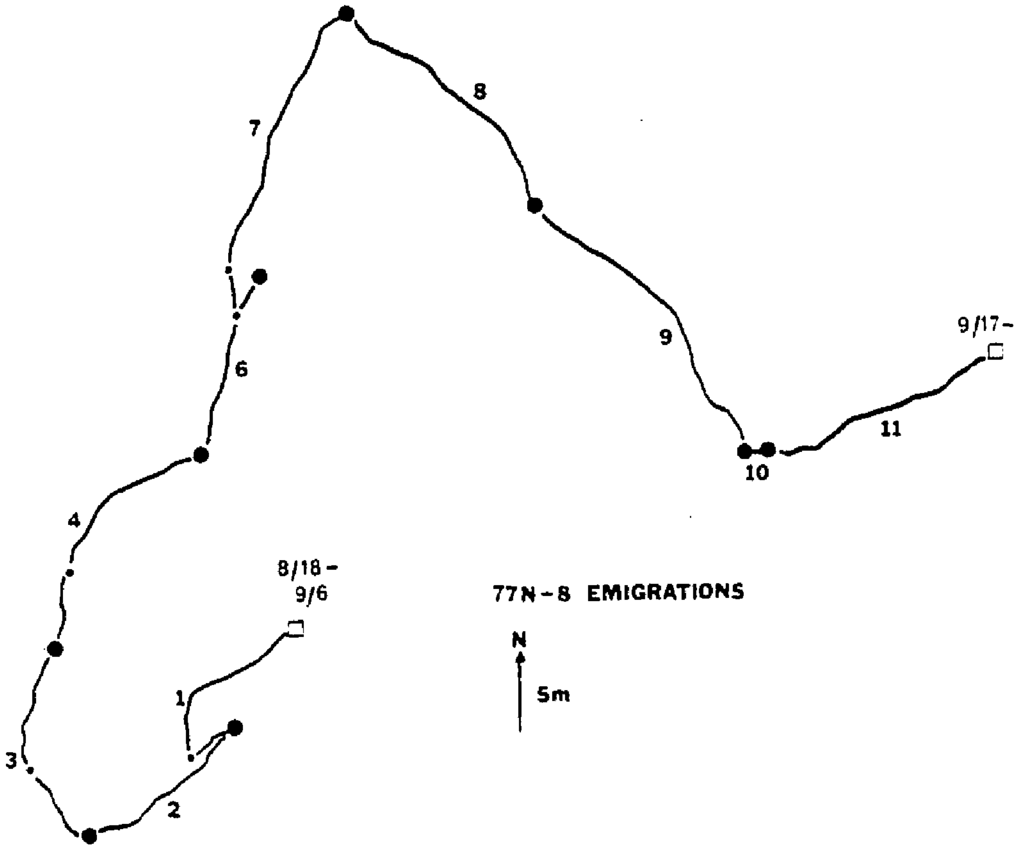

Figure 34. Movements of colony 77N-8. The colony was statary from 8/18-9/6, then changed its nest on 10 of the next 11 days. There were 2 emigrations on NDs 1, 3, 4, 6 and 7 and no emigration on ND 5. After ND 11 the colony became statary (9/17-) and was no longer followed. Numbers and symbols as in Figure 29.

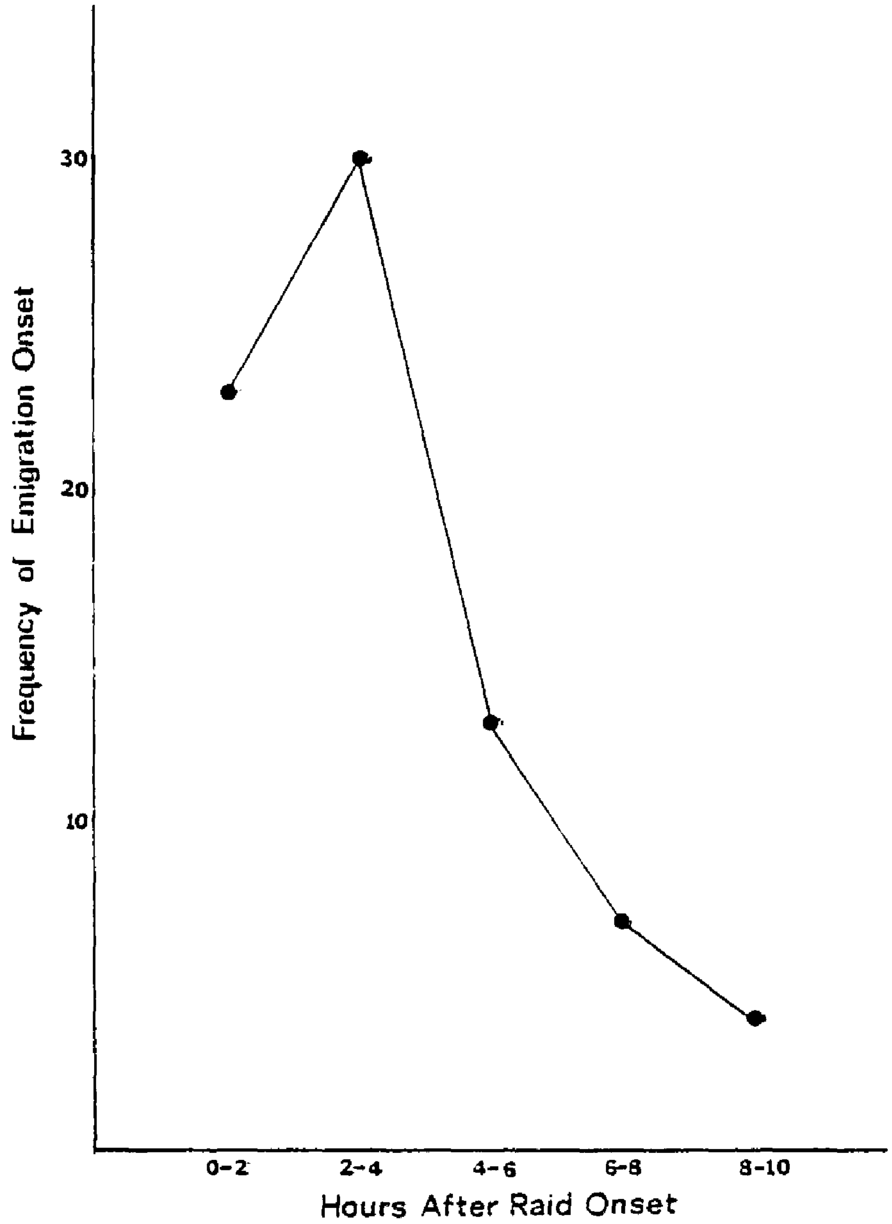

Figure 35. Frequency distribution of latencies from the onset of raiding to the onset of the emigration.

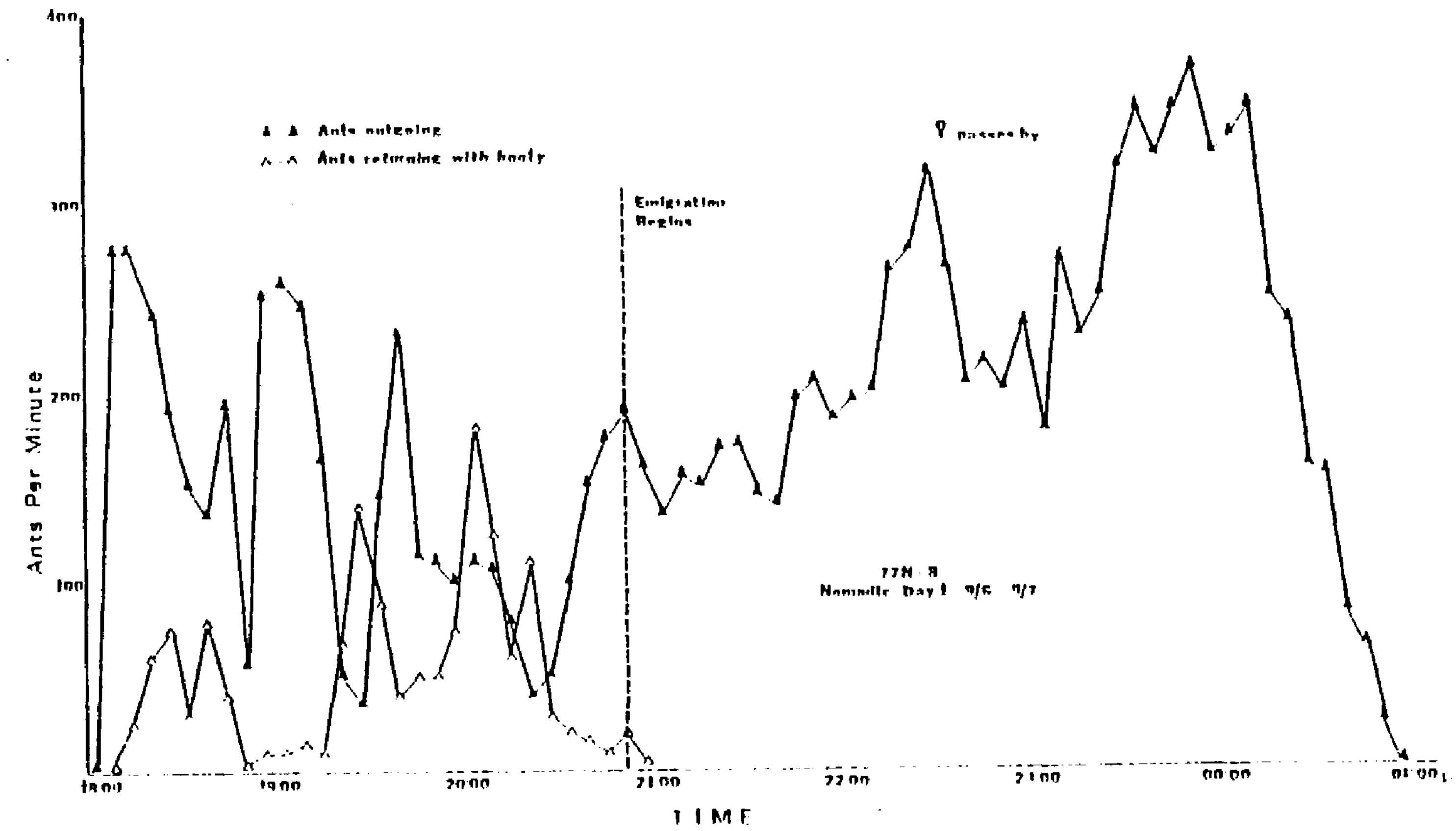

Figure 36. The transition from raiding to emigration in colony 77N-8 on ND 1 (9/6-9/7). See text for further details.

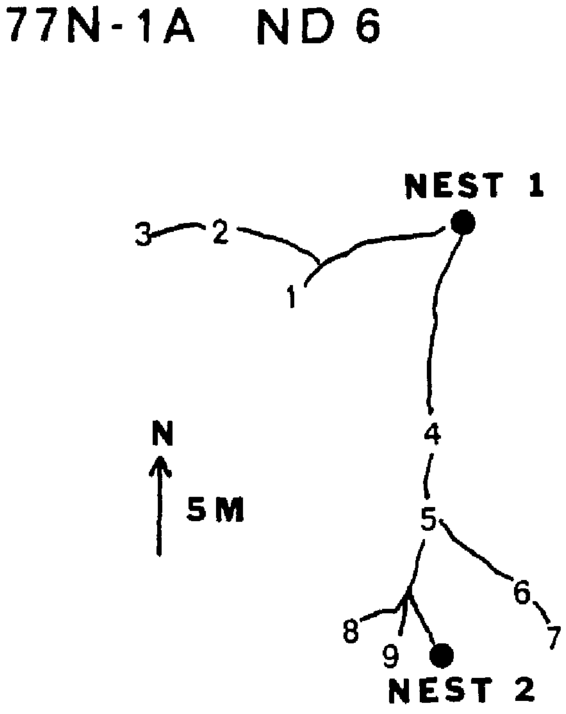

Figure 37. Raiding and emigration activity of colony 77N-1A on ND 6 (7/28-7/29) from 19:10 to 23:40 hours. Raiding took place at the numbered sites before the emigration began at 23:40. See text for further details.

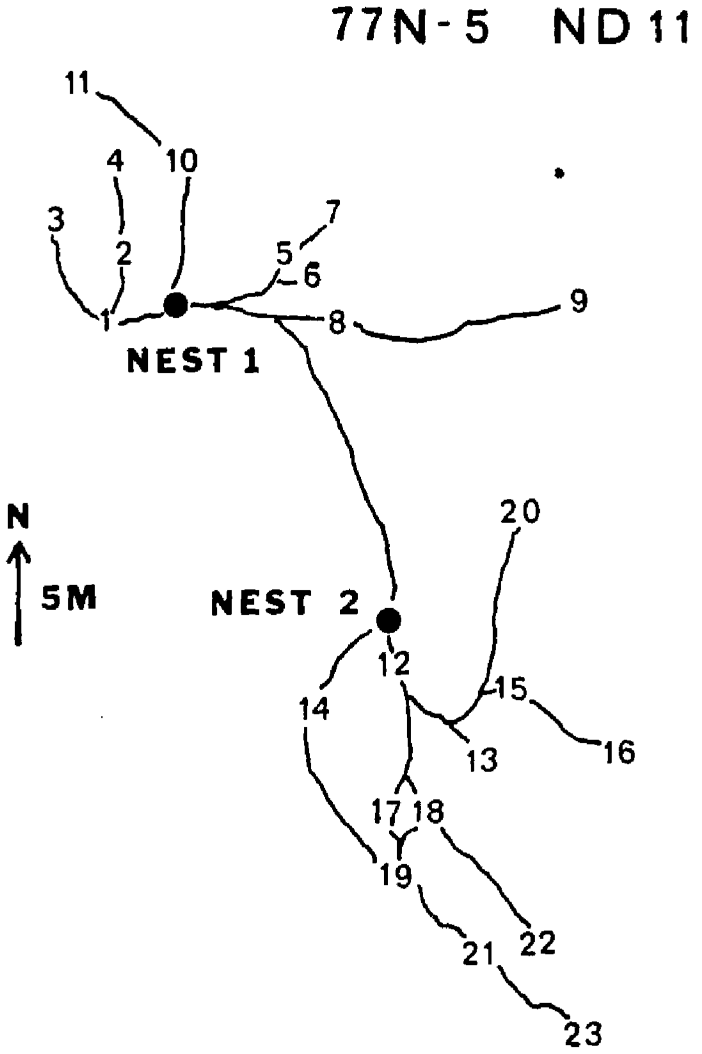

Figure 38. Raiding and emigration activity of colony 77N-5 on ND 11 (7/15-7/16) from 19:00 to 23:00 hours. Raiding took place at sites 1-11 before the emigration, which began at 21:00 and moved away from the areas of previous raiding. Raiding from nest 2 (sites 12-23) began after the emigration had been in progress for an hour. See text for further details.

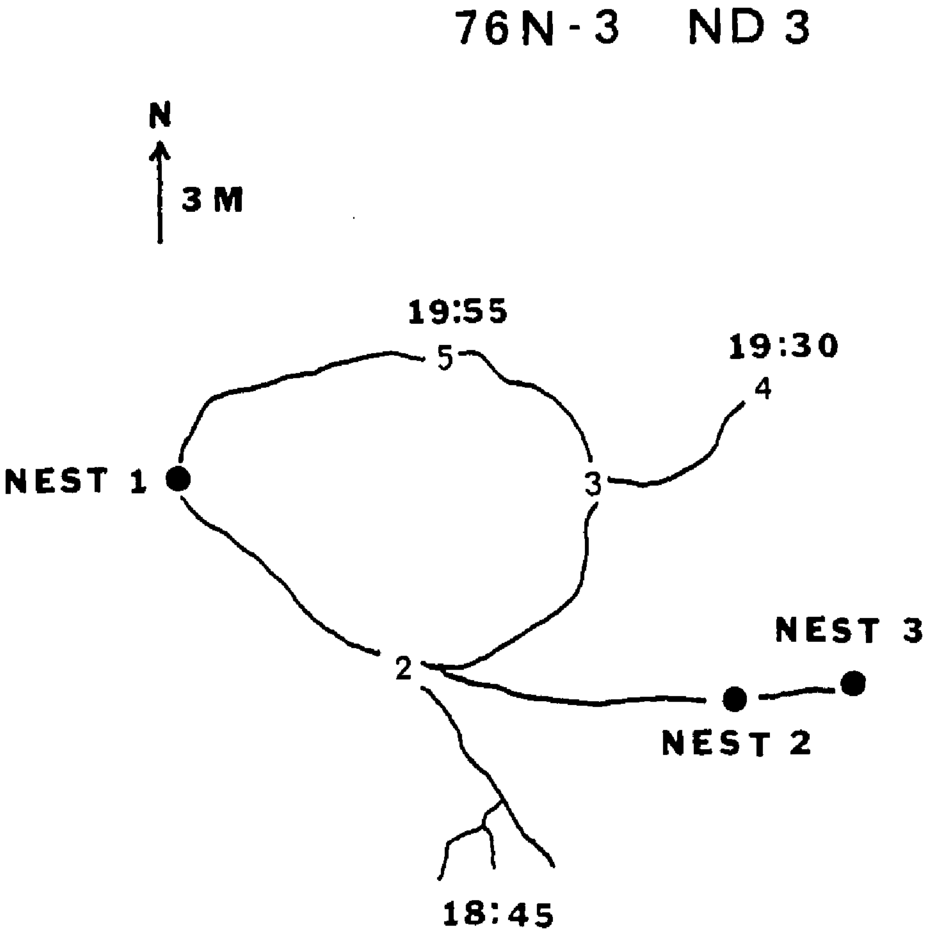

Figure 39. Emigration of colony 76N-3 on ND 3 (9/5-9/6) between 18:00 and 03:00. The colony emigrated in a circle following a nest disturbance. See text for further details.

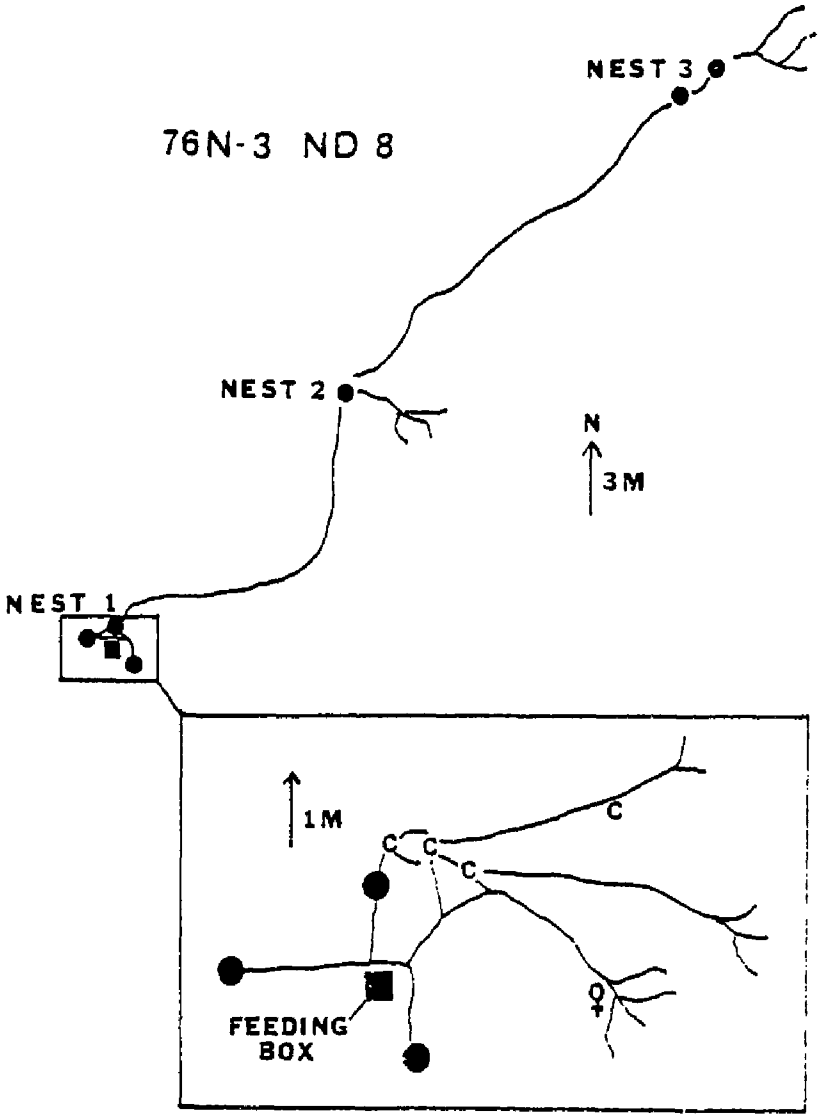

Figure 40. Emigration of colony 76N-3 on ND 8 (9/10-9/11) between 19:00 and 03:00 hours. The inset shows the confused pattern of movement when the colony became active at 19:00. **C**--brood cache formed at trail junction; ♀--location of queen at column front; ●--bivouac. See text for further details.

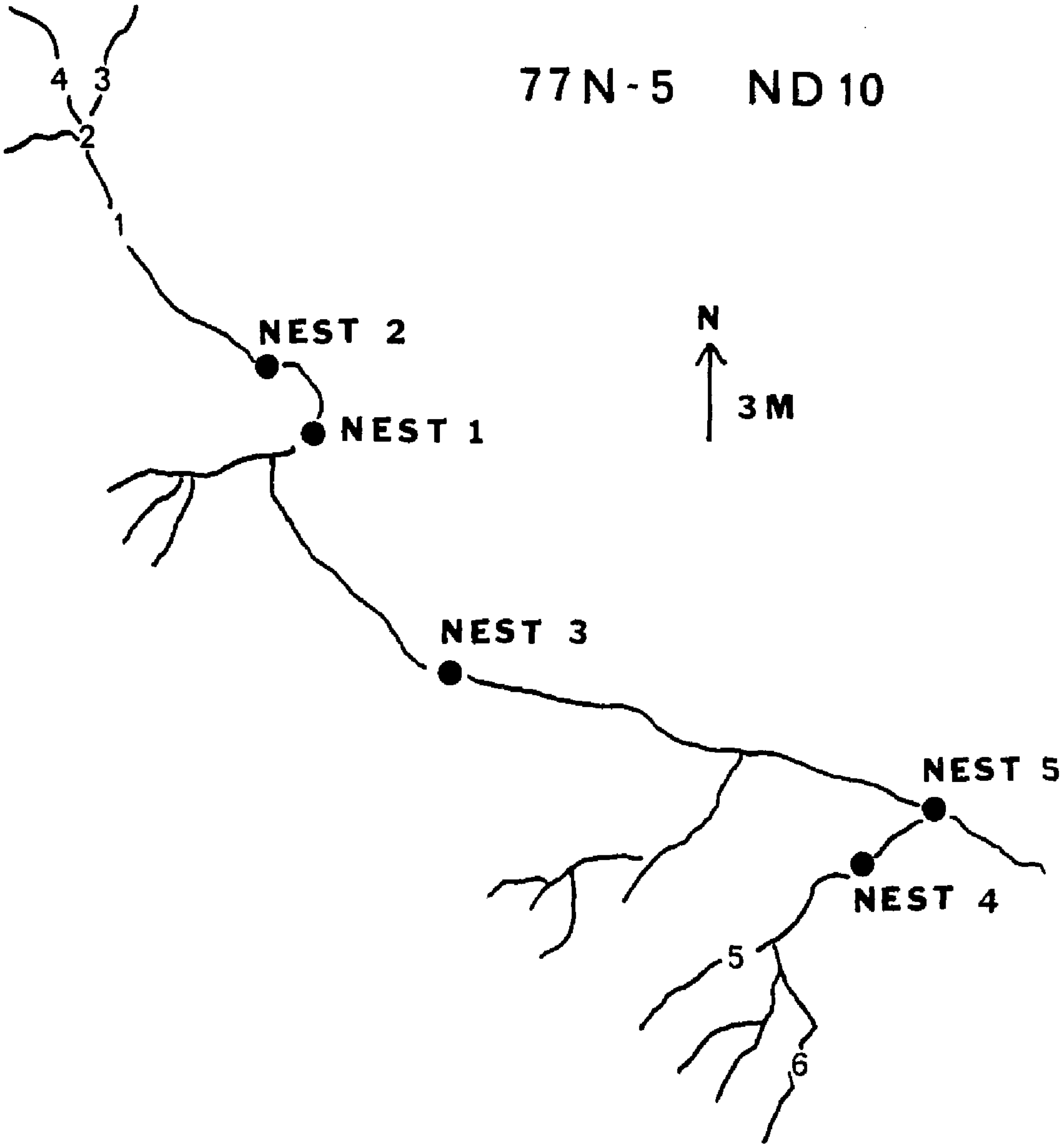

Figure 41. Raiding and emigration activity of colony 77N-5 on ND 10 (7/14-7/15) between 18:00 and 01:30. See text for details.

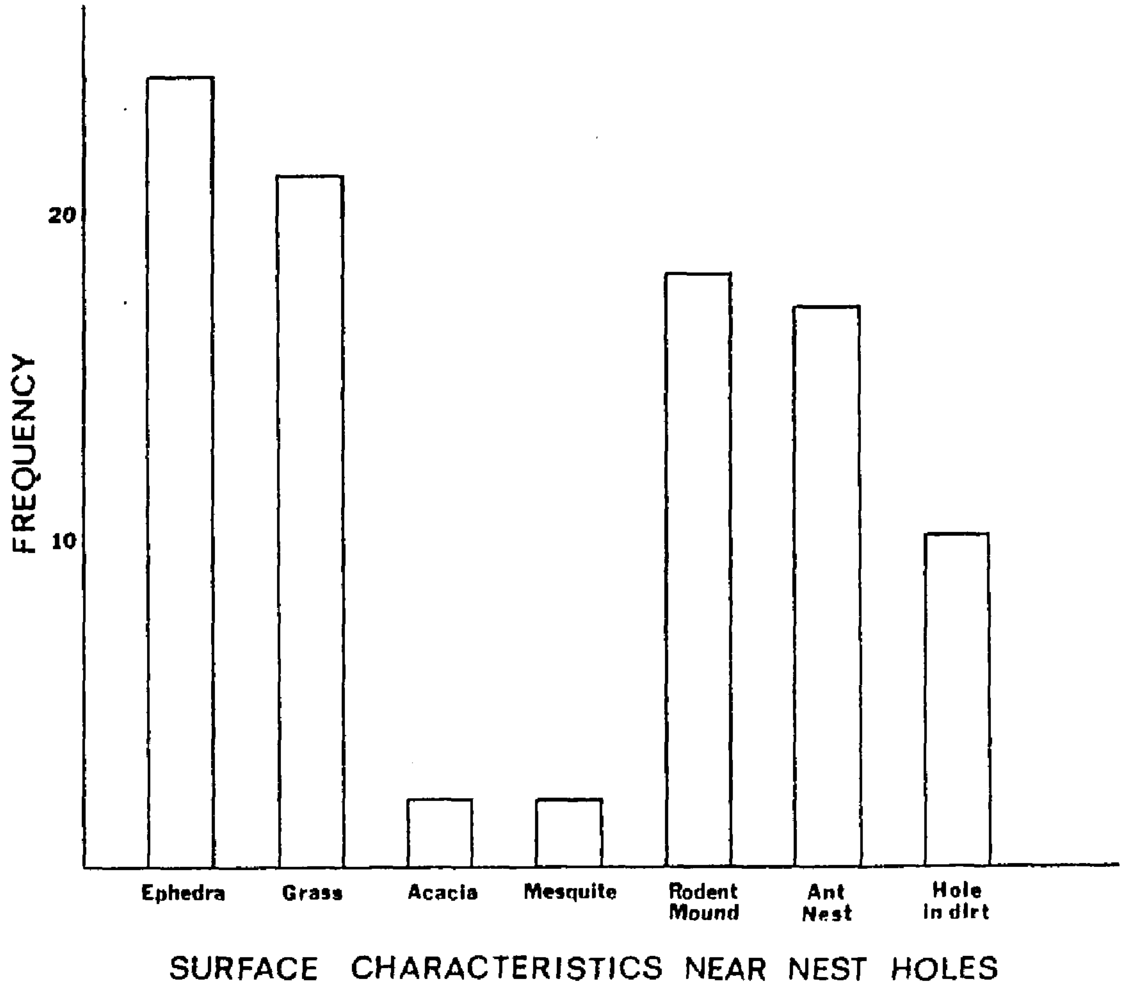

Figure 42. Surface characteristics near the nest holes of army-ant bivouacs.

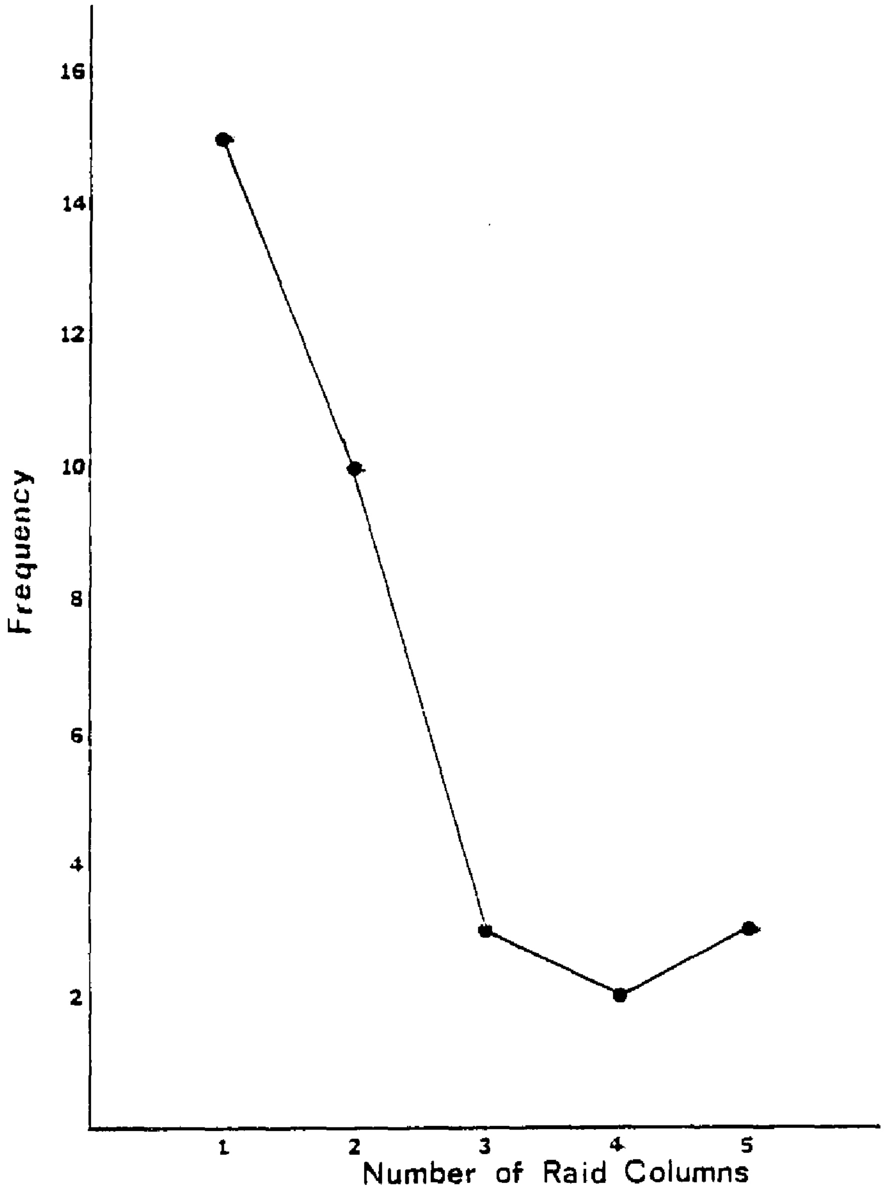

Figure 43. Frequency distribution of number of raid columns active before the onset of the emigration.

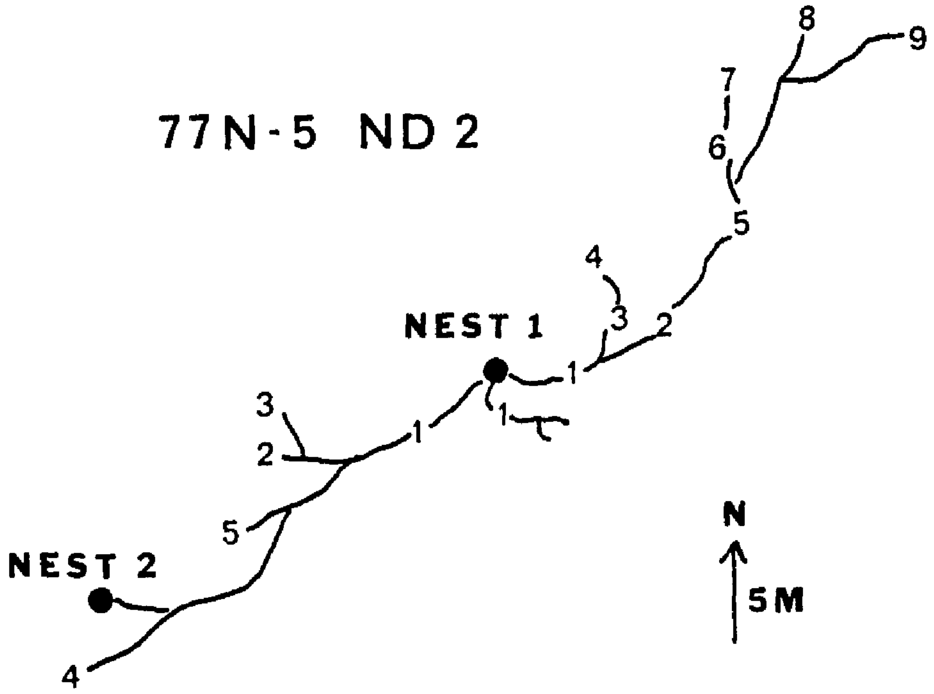

Figure 44. Raiding and emigration activity of colony 77N-5 on ND 2 (7/16-7/17) between 18:00 and 21:00 hours. See text for explanation.

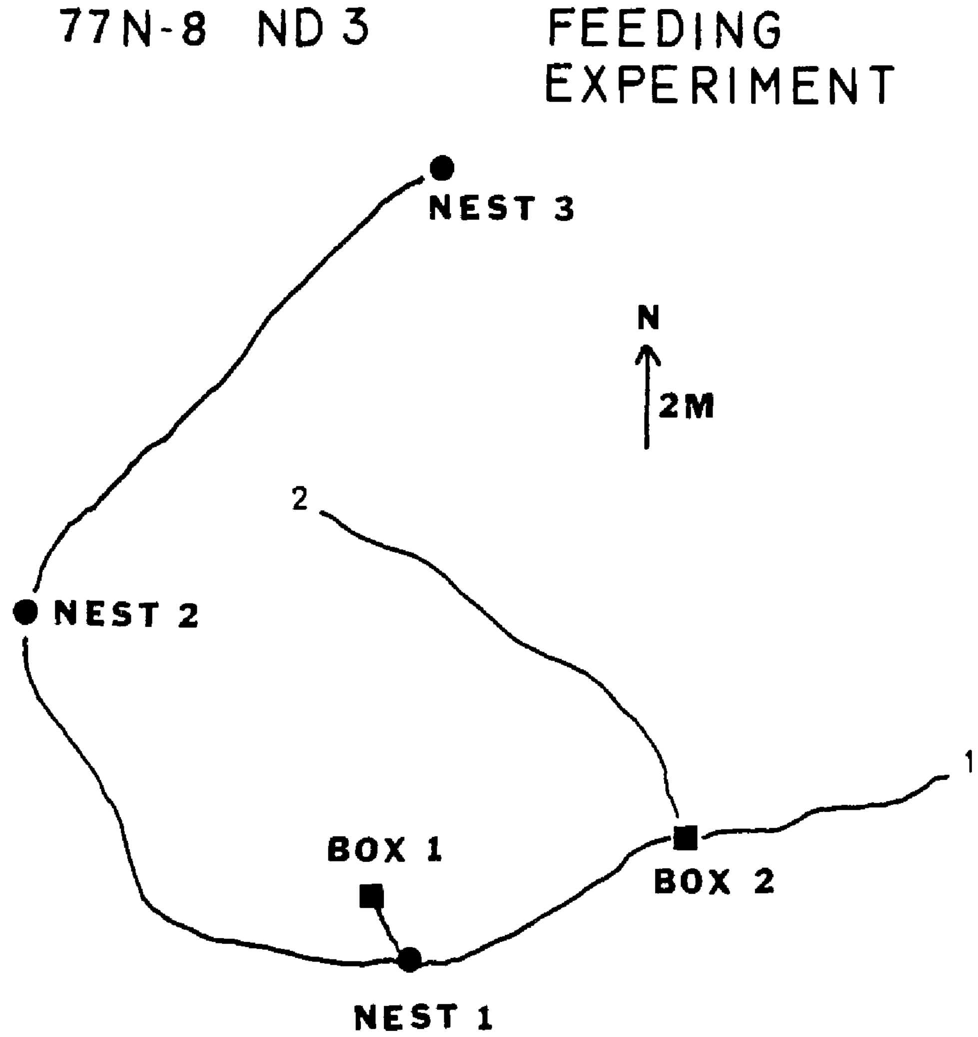

Figure 45. Emigration of colony 77N-8 after the feeding experiment on 8/7. The colony emigrated away from the area in which it was fed over a column that did not bring any booty back to the nest. ■--feeding box. Numbers indicate raid sites the colony found while taking food in the boxes. See text for further details.

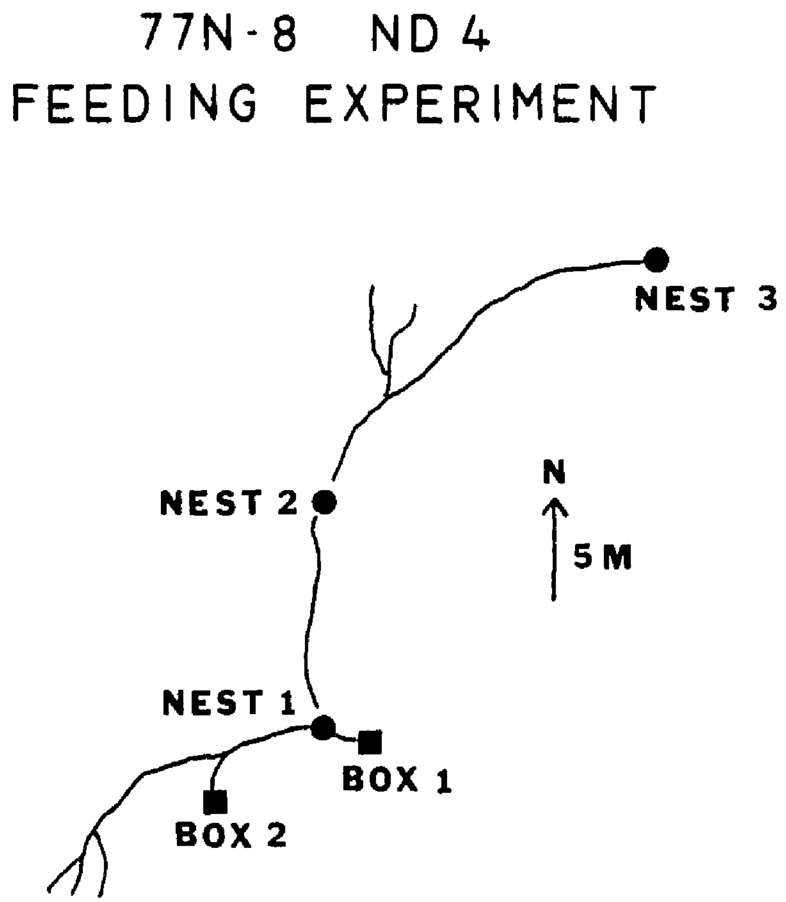

Figure 46. Emigration of colony 77N-8 after the feeding experiment on 8/8. The colony emigrated away from the area in which it was fed along a column that did not discover any raid sites. ■--feeding box. See text for further details.

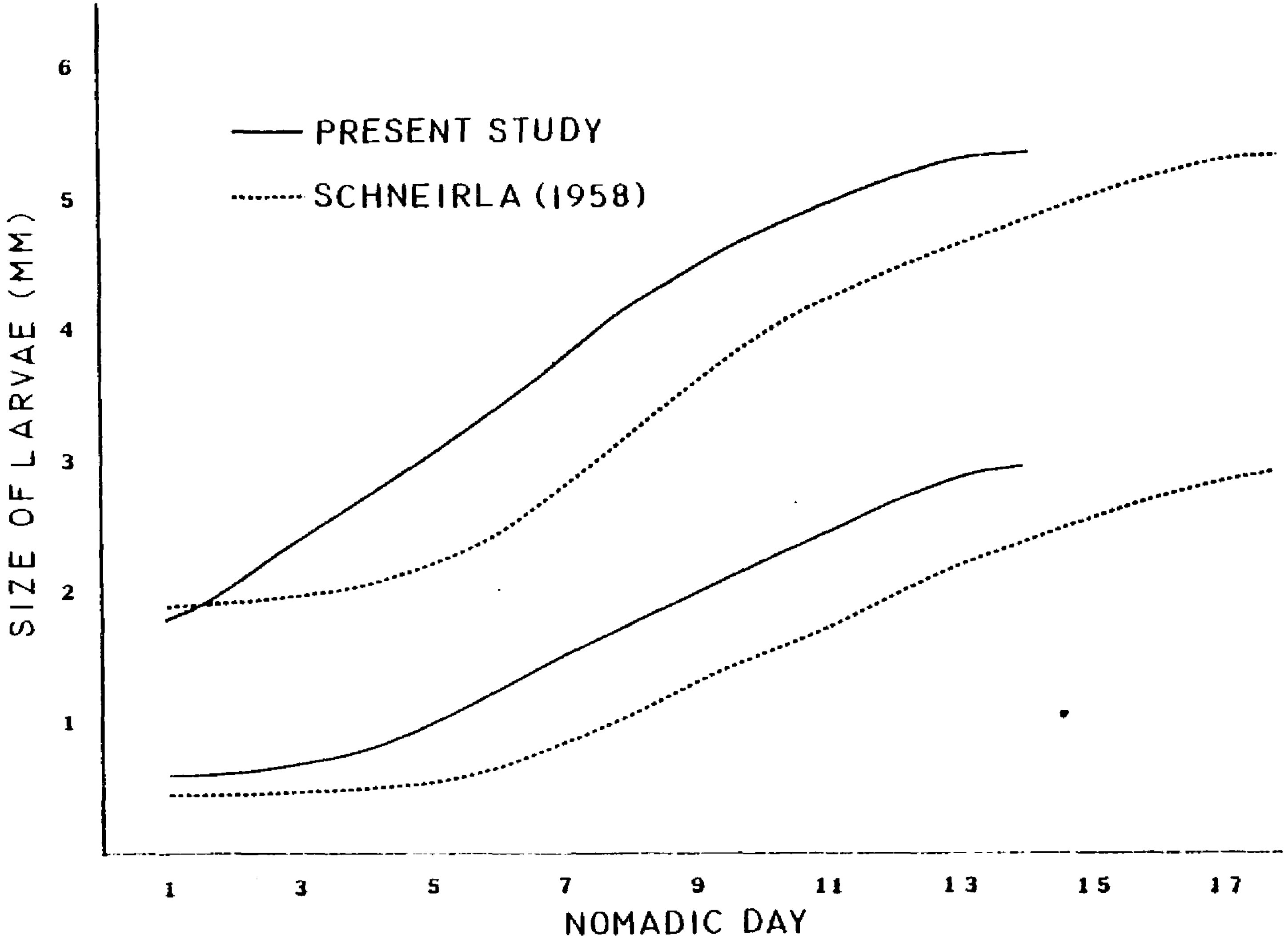

Figure 47. Comparison of larval growth in the present study with that in a different habitat (Schneirla, 1958).

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