THE BEHAVIOR AND BIOLOGY OF CERTAIN NEARCTIC ARMY ANTS
LAST PART OF THE FUNCTIONAL SEASON, SOUTHEASTERN ARIZONA *

T. C. SCHNEIRLA

(*The American Museum of Natural History*, Central Park West, New York 24.)

OUTLINE

* The field expenses of this investigation were supported through a grant from the Research Fund of the Council of the Scientific Staff of the American Museum of Natural History. Study of preserved material has been subsidized by a grant from the National Science Foundation.

Dr. Mont. A. Cazier, Director of the Southwestern Research Station of this Museum, aided the progress of the investigation in many ways, not the least of which was his invaluable help in finding new colonies. His interested cooperation is acknowledged appreciatively, as is that of Mr. John Gordon Anderson, Foreman, and Miss Ellen Ordway, then Scientific Assistant at the Southwestern Research Station. Mr. Robert Miller, of Rodeo, New Mexico, participated efficiently as field assistant.

Dr. Roy Whelden, Haskins Laboratory, Union College, kindly made available valuable information from his histological studies of the queens.

INTRODUCTION

Nomadism and a predatory, carnivorous life are characteristic of the known doryline ants. In tropical American species, emigration and related colony functions vary regularly in close relation to cyclic reproductive changes within the colony (22, 24, 27) rather than being irregular and dependent upon local food supply as was formerly thought (32, 16). There prevails in these species, throughout the year in both rainy and dry seasons, an unbroken succession of functional cycles, in which nomadic phases of high activity alternate regularly with statary phases of sessile life and low activity. This character of functional cyclicity depends upon massive stimulative effects exerted by the brood upon the worker population of the colony at specific recurrent stages.

Among doryline ants of the New World the genus *Eciton* in many respects contrasts strongly with the genus *Neivamyrmex*. Although *Eciton* is essentially tropical, ranging between 26° N and 26° S, *Neivamyrmex* extends widely into the North and South Temperate Zones from about 45° N in the upper Mississippi Valley to 45° S in Patagonia. Whereas *Eciton* has only 12 known species, *Neivamyrmex* has 113 (5) and possibly more. Numerous *Eciton* species are strongly epigaeic and even arboreal in raiding and nesting (29, 28); however, all *Neivamyrmex* species are hypogaeic in nesting and many in their raiding also. Workers, males and queens in *Eciton* are considerably larger than the corresponding castes in *Neivamyrmex*, the workers major in *Eciton* have large heads and huge hook-shaped mandibles unlike the smaller ones of *Neivamyrmex* workers, and other differences exist.

One striking difference between these doryline genera is that the essentially subterranean *Neivamyrmex* species range into the North and South Temperate Zones where their representatives have evolved under the conditions of an annual winter. The range of *Neivamyrmex* species is thus much wider than that of *Eciton*. The question thereby arises of what similarities and what differences may exist between *Eciton* and the Nearctic species of *Neivamyrmex* in their behavior patterns and related biological properties. This is the first of three studies designed to investigate representative *Neivamyrmex* species indigenous to the Northern Temperate Zone with respect to their adaptive patterns in comparison with that known for *Eciton*.

EARLIER RESULTS ON *NEIVAMYRMEX*

For an introduction to the biology of this ant genus, the publications of Wheeler (33, 35, 36), Emery (12), Bruch (9), Smith (30, 31) Borgmeier (5) and Creighton (11) may be consulted. It is clear from the literature that all *Neivamyrmex* species are essentially hypogaeic in contrast with species of *Eciton*. In the tropics their colonies are usually seen in or close to the forests or the gallery cover of rivers. However, Smith (31) notes for eastern areas in the United States that *Neiv. nigrescens* and *opacithorax* are not entirely subterranean, as their columns may be seen on the surface even in full sunlight. He states that in rugged country they are found in the valleys and on gentle slopes and plateaus but never on steep, exposed places.

Colonies of *Neivamyrmex* commonly nest in the soil, often beneath objects lying on the ground or partially buried. In the eastern U. S. their nests are often found in rotten logs and stumps and in the ground beneath these, and occasionally in or near the foundations of buildings (31). There is one report from Brazil of a colony of *Neiv. legionis* found nesting

7 m. up in a hollow tree (21), but even in the tropics nests of these ants entirely above ground may be rare. Observations of exposed *Neivamyrmex* bivouacs have not been reported, and in the tropics I have never found a colony of this genus whose nest was not very well sheltered.

In the central cavities of the nests of *Neivamyrmex*, clusters of workers are commonly found, as Wheeler (33) reported, " . . . in compact masses, often as large as a man's fist." Although this condition is confirmable for *Neiv. nigrescens* and *opacithorax*, other species may deviate. Under certain conditions, or perhaps typically, the occupied cavities may be enlarged by the digging operations of the *Neivamyrmex* themselves (8).

A seasonal adaptation of some kind would be expected in the *Neivamyrmex* of subtemperate and temperate areas, and this is indicated in Wheeler's (33) statement that in Texas,

" . . . during the winter and spring months, at least, the Ecitons (i.e., *Neivamyrmex* species) I have observed occupy the same nest. This they probably do until their young are raised."

Wheeler offered no evidence to support this statement clearly, and his suggestion of a time-limited raising of brood prior to a spring emigration is misleading. The possibility remains however that Nearctic *Neivamyrmex* species are characterized by an interruption of regular colony function under winter conditions, in contrast to species indigenous to the tropics and subtropics in which brood production and regular colony function may continue throughout the year.

The concept of long-continued nests ("Dauernester"), advanced by von Ihering (19) for *Labidus coecus* and accepted by others for *Neivamyrmex* species as well, suggests perhaps the maintenance of winter quarters. But the term as used by von Ihering and later by other writers seems to go beyond this. For example, Gallardo (14) reported a case discovered in the Sierra Ventana of Argentina, in which a colony of *Neiv. d'orbignyi* was unearthed at the same site in the spring months of two successive years. Although Borgmeier (5) considered this an indication that this species occupies *Dauernester*, such reports tell us only that colonies of the same species have been found in the same nesting place at different times. My records for doryline species in the tropics show for *Labidus* and *Neivamyrmex* as well as for *Eciton* spp. that not infrequently, in different years, different colonies may occupy the same nesting sites. In view of the question of a seasonal interruption of function in relation to possible statary phases, all claims for long-term doryline nesting must be examined carefully.

According to Smith (30), the colony populations of *Neiv. nigrescens* are "moderately large." Although no actual counts have been made, I estimate the worker populations of this species at between 150,000 and 250,000 individuals. Gillespie and Cole (15) describe the workers of *Neiv. nigrescens* as monomorphic and, from a measurement of 250 individuals, as having a size range represented by 0.52—1.50 mm. thorax

length *. The worker population presents a smooth transition from largest to smallest, with the distribution skewed toward the latter. A series representative of the worker range is shown in figure 1.

In advance of the present study I hypothesized (27) for brood production and colony function in *Neivamyrmex* a relationship basically comparable to that found in *Eciton*. Support for this idea is found in my notes on emigrations of *Neiv. pilosus*, *sumichrasti* and *gibbatus* colonies in the tropics, in which great numbers of callow workers often thronged the columns. Also, information has been given to me for *Neiv. nigrescens* in

FIG. 1. — A physogastric queen of *Neivamyrmex nigrescens*, with a series of workers representing the range from maxima to minima. The queen was taken by Dr. W. S. Creighton on March 18, 1950, near El Salto, Durango, Mexico, from a colony found at 8,300 ft. bivouacked beneath a stone under an oak beside a meadow. Length of queen's thorax: 2.55 mm.

the U. S., in which large numbers of mature or nearly mature worker pupae were found, in one case (by E. Ross, in Georgia) in a highly active colony bivouacked under a log, in the other (by C. Rettenmeyer, in Kansas) in a colony which emigrated a few days after maturing worker pupae had been found in the nest. Present results sustain the hypothesis in detail.

Since Wheeler (33) reported the capture of a queen of *Neiv. opacithorax* in 1894 by Schmidt in N. Carolina and of *nigrescens* by himself in Texas, the collection of the queens of some 18 different species of this genus has been recorded. These captures, which have ranged from localities in Iowa and Kansas through the tropics to southern Argentina, need not be described in detail here. However, one fact of great importance to the problem of this investigation should be noticed, namely that about half of

* However, Borgmeier (5) considers the *Neivamyrmex* worker series *polymorphic*. Although this point is subject to discussion, it is clear that *Neivamyrmex* workers are less strikingly polymorphic than those of *Eciton*.

the captures have involved queens in the contracted condition and the other half queens in the physogastric condition. This difference has been found through several species both in tropical and in subtemperate areas.

The taking of physogastric queens of this genus has been reported for 12 species, of which physogastry was incomplete at the time of capture in *Neiv. diana* in Brazil (2), *hetschkoi* in Argentina (9), *minense* in Brazil (2), *nigrescens* in Texas (33), and *raptans* in Argentina (7), and relatively complete in the queens of *angustatum* in Brazil (1), *humilis* in Costa Rica (3), *legionis* in Brazil (21, 9), *nigrescens* in Mexico (Creighton, pers. comm.), *opacithorax* in Tennessee (Cole, *pers. comm.*), *pertyi* (6) and *pseudops* (8) in Argentina, and *spinolai* (5) in Costa Rica. All of these queens were taken from subterranean nests. A transitional stage of physogastry, in the queen of *nigrescens* taken by Creighton, is represented in figure 1.

The taking of queens of this genus in the contracted condition has been reported for 13 species, which are: *Neiv. alfaroi* in Costa Rica (4), *carolinensis* in N. Carolina (13), *d'orbignyi* in Argentina (7), *gibbatus* in Panama (5) *, *hetschkoi* in Argentina (9), *humilis* in Costa Rica (3), *nigrescens* in Texas (33) and in Mexico (20), *opacithorax* in N. Carolina (37), *pilosus* in Costa Rica (22), in Argentina (8), *raptans* in Argentina (7, 9) and *wheeleri* in Texas (10). With the exception of the queens of *gibbatus*, *pilosus* and *pseudops*, which were taken from emigration columns, all others in this list were extracted from the nests of their colonies.

From these results there remains little doubt that normally, as with *Eciton*, the colonies of *Neivamyrmex* spp. have only one functional queen. Among the many cases only three exceptions appear, that reported by Wheeler (33) concerning *Neiv. nigrescens*, by Bruch (7) concerning *raptans*, and by Bruch (9) concerning *hetschkoi*. In each of these instances two queens were found in the same nest, one laying eggs at the time. Here, much as in *Eciton* (26), it is likely that a colony with a mature sexual brood and undergoing fission is involved, with one queen (*i.e.*, the one laying eggs) being the functional queen of the parent colony and the other or others virgin.

It is also clear from the above evidence that queens of many *Neivamyrmex* species may be found in either the contracted or the physogastric condition. The inference plainly is that these two conditions may arise at different times in the same queen, and perhaps alternately as I have found the rule in *Eciton* (23, 25, 27). The conclusion of various authors that contracted queens are 'young, not yet physogastric' would seem wrong as a generalization for this genus as it is for *Eciton* (24, 25).

The fact that in nearly all of a few dozen reported instances queens of *Neivamyrmex* species have been found either physogastric or contracted, with few in a transitional condition, indicates that queens of this genus,

* The queen of *Neiv. gibbatus* reported by Borgmeier (5) was taken by Dr. R. Z. Brown, then my field assistant, from an emigration column at 11:00 p. m., Jan. 19, 1948, on Barro Colorado Island, C. Z. Large numbers of callow workers ran in the column, and a mass of excited workers formed a retinue for the queen.

like those of Eciton, produce distinct broods and are not continuously reproductive. This inference seems to find support in Holliday's (18) statement from her histological study of a partially physogastric queen of *nigrescens*, that

> ". . . on the vagina occurred the receptaculum seminis of rather large size, apparently a necessary adaptation to the large number of eggs to be fertilized. That many of these are mature at a time is indicated by the fact that half of the tubules of each side contains several ripe eggs."

From her dissections, Miss Holliday estimated that the total number of ovarioles in the nigrescens queen "could not be far from 500." From a study of several queens of this species Dr. Roy Whelden (pers. comm.) finds this estimate conservative and judges that at the beginning of an egg-laying period each ovariole may contain an average of at least 10 mature eggs, and also many others in a series of decreasing size and maturity. A prolific reproductive capacity in this queen is indicated by results to be reported in this paper.

No systematic studies have been made on colony function in *Neivamyrmex*. The raiding forays of species such as *nigrescens* are carried out in columns, on chemical trails produced by the workers themselves (33, 31). Smith (30) states that the food consists largely of other insects, including termites, ants and their brood, and beetles. The colony diet, therefore, is essentially carnivorous (37). Smith reports that although ants of this genus tend to be predominantly subterranean (at least in their nesting), the columns of *Neiv. nigrescens* and *opacithorax* frequently appear on the surface, even in full sunlight. The inclusive pattern of colony raiding is unreported, and the relationship of foraging to emigration has not been studied in *Neivamyrmex* species.

PROBLEM

Although it has been generally assumed that colonies of *Neivamyrmex* species, like those of other dorylines, have relatively temporary nests and are nomadic, no regularity has been claimed for their emigrations. The basis of their nomadism has never been studied, although we find the traditional food-exhaustion hypothesis accepted without question by Heape (1) and others. Smith's (30) statement that "The stays are governed largely by the availability of food for them" remains unsupported. On the other hand, by inference from my findings for *Eciton*, Creighton (11) has suggested that the movements of *Neivamyrmex* colonies may be regular and based on circumstances grounded in brood condition.

The first problem of the present investigation was to test the brood-excitation hypothesis for *Neivamyrmex*, favored over the food-exhaustion idea. To test the latter hypothesis, evidence was sought concerning

possible relationships between colony movements or failures to move and local food supply. In view of the brood-excitation hypothesis, evidence was gathered on brood condition in relation to raiding and to emigration, and laboratory tests were made to find what stimulative effects from brood might affect adults differently according to developmental stage.

If the favored hypothesis is supported, and Nearctic dorylines are found to have functional cycles comparable to those of *Eciton*, a second problem arises concerning the continuity of function in the colonies. Wheeler (33) did not find these ants active in the cold months, and it would seem likely that in contrast to the year-around cyclic function of *Eciton* a distinct winter break in function would prevail among dorylines in the Temperate Zones. Therefore the present study, the first of three directed at these problems, was scheduled for the latter part of summer in the hope of sampling colony function both in the regular season and in its possible autumnal changes.

SUBJECT, LOCALITY AND CONDITIONS

The present study is devoted mainly to *Neivamyrmex nigrescens*, the species of this genus which is most widely distributed and most common in the Southern United States (31). This species is represented throughout a large area having mideastern North Carolina and midwestern Nebraska as its northern corners and southeastern Georgia and southwestern Arizona as its southern corners. The area of this investigation was southeastern Arizona near latitude 32° N, on the eastern face of the Chiricahua Mts. at an elevation of about 1,600 m. Also present in this area, and perhaps as common as *Neiv. nigrescens*, are colonies of *Neiv. opacithorax*, a secondary object of study in this research.

The investigation was carried out mainly in the vicinity of the Southwestern Research Station of the American Museum of Natural History in Cave Creek Canyon, from July 6th to Sept. 13, 1956. It thus extended from the height of summer into the time when nocturnal temperatures had begun their annual autumnal decline. Although during the summer in this locality nocturnal temperatures seldom fall to 10°C, after mid-August in 1956, by midnight superficial ground temperatures commonly had fallen below 10°C. and air temperature 6 cm. above the ground to 6-8°C, and in early morning hours the records were even lower. It is not just the latitude of the study area, but ecological conditions peculiar to the altitude and situation, that may be significant for the research. Due to factors related to altitude, the results may resemble more closely those obtainable under conditions farther north in the species range than those for colonies of these species living in zones at the same latitude but nearer sea level.

In the general locality, July and August normally are the two rainiest months of the year; however, in the 1956 season rainfall was unusually

light in August. Prior to mid-August, the Station area was reached nightly by convection currents of warm air rising through the canyon from the desert below. Although Smith (30) concluded that elevations of 2,000 ft. or less are optimal for *Neivamyrmex*, the described conditions holding in the area of the Southwestern Research Station may account for the fact that colonies of both *Neiv. nigrescens* and *opacithorax* were found to be relatively numerous there during the ten weeks of this investigation. Among other conditions favorable to many ants including these dorylines would be included a relatively good although scattered chaparral cover verging into pinyon-juniper and fir-pine associations, and a local geology contributing to a good retention of ground moisture. In addition to the ecological suitability of this area for the dorylines, insects and their brood serving as booty are also plentiful.

METHOD AND PROCEDURES

The method involved longitudinal surveys of behavior and other functions in two or more colonies concurrently and cross-sectional surveys in

FIG. 2. — Locale of the statary bivouac of Rock colony. A pile of stones in the central background marks the initial entrance point, to the right of which the colony nested in an area 1.2 m wide. In the foreground may be seen a section of the inspection lane surrounding the bivouac area; the string in the left background marks a principal raiding route.

other colonies over shorter periods of time, with samples of the brood taken regularly in each case.

In the first three weeks, during July, techniques were developed for studying individual colonies continuously. This involved procedures for tracing the routes of raiding columns and of emigrations with a minimum of disturbance to the ants, an exacting process when the columns ran for some distance under surface cover. As a rule, five surveys of each colony were made nightly,—one shortly after dusk, two others before midnight, a further one before 3:00 a.m. and a final one as appropriate before dawn. Records were taken of items such as activities at the bivouac, the direction and progress of principal raiding systems, and the direction and characteristics of emigration. For a protracted close study of activities, as when inspecting an emigration column for brood, a dim light was used,—otherwise five-cell headlights served for illumination.

To insure observing all columns and particularly emigration columns leading from the nesting site of a colony, a circular inspection lane was cleared around the bivouac center, at a distance of 5 m. or more as might be necessary to detect columns that started out by subterranean routes (fig. 2). This 'cordon' procedure was always used with statary colonies or with others operating under conditions of heavy ground cover. A physical continuity of successive emigrations was established in all cases of colonies continuously on record. After the schedule was standardized, the routine daytime inspection of colonies was minimized except on overcast days.

Brood samples were taken by removing specimens from the emigration columns with a suction bottle. These samples were fixed in Bouin's solution and preserved in 70 % alcohol. As far as possible, sampling was made nightly and was timed on each night so that the limits of the brood size range would be represented.

RESULTS

REVIEW OF PRINCIPAL COLONY RECORDS.

There follow summaries of the main facts concerning events in those colonies from which evidence was obtained bearing both on colony function and on brood condition. Each protocol is followed by a summary and interpretation.

Pugsley colony, Neiv. nigrescens.

On the night of July 12 a heavy emigration column thronged with callow workers, with a minimum of inert pupae carried, was discovered at 10:30 p.m. and observed until its end shortly after 1:30 a.m. White packets suspected to be early brood were also carried. From its origin near the base of a cement wall, the thick column meandered to the *S* 35 m. across an open area to enter a stone wall on the opposite

side, continuing its movement under cover for more than 25 m. to the *E* along this wall to a place where it nested for two days. Raiding was observed from this site on the three following nights, and on July 15 there were indications that at some time after 10:00 p.m. an emigration developed on raiding lines to the *SW*.

This colony is considered equivalent to colonies Lab-B, Thicket, Stone and Bridge, in that the first emigration of a nomadic phase occurred in the presence of a large, mainly eclosed brood of mature worker pupae.

Meadow colony, Neiv. nigrescens.

At 10:30 p.m. on July 15, the two basal columns of a large raid were traced across a field to the colony bivouac under a large stone (fig. 3). As had been observed in raiding colums in this area on the preceding night, the plentiful booty included both brood and winged forms of *Formica spp.* in particular. At 12:15 p.m. the *N* trail

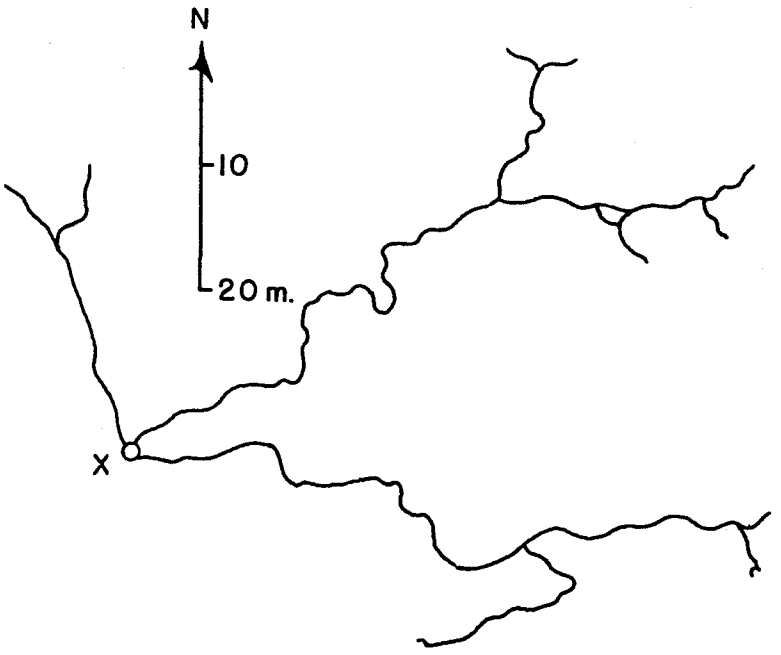

FIG. 3. — The principal raiding trails developed by a colony (Meadow, July 15) entering the nomadic phase, showing the origins of peripheral branches, after five hours of raiding when basal branches have died away. *x*, bivouac under large stone.

system had disappeared, and on the *SE* a wide outgoing column had pushed to a distance of 10 m. where it was then reversed by returning traffic. Overturning the bivouac rock exposed: 1) large windrowed masses of dark-brown adult workers with tens of thousands of light callow workers; 2) a new brood of embryos and a minority of microlarvae of potential workers in three main clusters, of which an estimated 95 % was captured for preservation; and 3) the queen, in a contracted condition, found in a rolled leaf in a mass of workers on one side of center. Captured for fixation were the

queen, most of the new brood of embryos and microlarvae (later numbered at close to 35,000) and perhaps 15,000 of the callow worker brood. Because of these collections, further events observed in this colony must be considered abnormal, but as such are of interest.

On the following nights, raiding columns issued variably from beneath this stone, but there was no emigration until on the night of July 20 the ants moved 21 m. to the *NE* into a stone wall. Here they remained, with nightly raids, until on July 24, after 8:00 p.m., a raiding line to the *E* was crowded with an exodus of workers and darkened callows. Larvae were transported after 10:00 p.m., but were few and a sample was difficult to obtain. There were branches after 40 m., but the most active raiding occurred from branches beyond 60 m. After 10:00 p.m. successive traffic reversals occurred, beginning peripherally, and increased in scope with time. Further reversals entailed increasing traffic disruption, with numerous rushing masses up to 12 cm. wide and often more than 2-3 meters long on the trail. At one collision point about 30 m. back from the raiding front, a mass of ants spread laterally from the trail in an eruption that surged more than 120 cm. upward on the trunk of a small tree. By 1:15 a.m. the reversals had expanded to include nearly the entire line to the old bivouac. (Reversals continued through the night, and only a part of the colony moved to a new site under a stone at 65 m.). On the next night an exodus again developed from raiding on this same line, after 10:15 p.m., with the entire (remnant) colony eventually moving into a stone wall at 70 m. from the bivouac site of July 17. Evening raids followed in this vicinity, with occasional abortive emigrations and one short completed emigration, until after the night of July 29 the ants could not be found.

—What might have been the first emigration of a nomadic phase was blocked by a major disturbance of the colony in which most of the young brood, a considerable part of the mature brood, and the queen were taken. The effect was to reduce further activities, and the absence of the queen evidently increased the difficulty of establishing new bivouacs on exodus, contributing to abortive and variable emigrations.

Rustler's Road colony, Neiv. nigrescens.

At 10:15 p.m. on July 17 this colony had an unbranched column of workers to the *N* from their emergence point among leaves in a dry creek bed, following a meandering course 25 m. across grassy areas to a tree-root mound below which the main colony evidently was bivouacked. Many light-colored callow workers were seen in the traffic, largely directed toward the tree. A system of branching columns extended to the *NE*, and on the most active line from a stone road-fill at 55 m. much booty was lugged back to the bivouac. After 10:45 p.m., an exodus developed from the bivouac on this line to the road-fill area, with large numbers of callow workers running in the column and larvae (identified as potential males) in transport. The movement in wide column continued until after 3:00 a.m., with only booty carried after about 1:00 a.m. Traffic continued until dawn, thinly except for occasional bursts. On July 18, after dusk, there was raiding from the tree-mound on the same line, and after 8:00 p.m. an exodus developed in which further sexual larvae were carried. Interrupted for nearly an hour by rain, this emigration declined after 11:30 p.m. Efforts to trace the colony failed.

—This colony, with a large recently eclosed brood of callow workers and a young brood of sexual-form larvae, was judged to be in the first part of a distinct nomadic phase.

Skunk Hollow colony, Neiv. nigrescens.

On the night of July 20, this colony was located in a bivouac below stones near the creek, raiding to the *SW* more than 55 m in a complex of branches from a long base column. In a large cluster under one of the rocks, thousands of newly eclosed callow workers were clustered with adults. After dusk on July 21 there was a large raid to the *W* and across the creek. After 8:15 p.m. a heavy exodus developed on the base route, while raiding continued on peripheral branches to *N* and *W*. Newly eclosed callow workers thronged the base column, and many hundreds of larvae (potential males) were transported. Until 11:15 p.m. the emigration column ended at 35 m.where it entered a hole on the creek bank from which raiding columns diverged. Thereafter the wide column continued 30 m. farther to the *NW* on one of the branch trails to a preempted ant nest in the ground, the new bivouac. The queen, fully contracted, reached the new site with her retinue shortly before 3:00 a.m.; the emigration was completed shortly after 5:15 a.m. On July 22 after dusk the ants developed a raid to the *W*, with an exodus on the main line after 9:30 p.m. which at 25 m. stopped beneath a stone on the creek bank. After 12:30 p.m. the wide column continued across the dry creek bed under cover of leaves, and entered a hole on the opposite bank; soon reappeared, then disappeared beneath a large mass of brush. On the night of July 23, a thinner column followed the same line, completing the emigration although interrupted by rain. Within 30 min. after the heavy rain and rush of water down the creek, the ants had re-established their trail across the (now muddy) creek bed. The colony could not be traced through the thick grass of a boggy field which lay beyond.

—This colony, evidently beginning a new nomadic phase, was judged to resemble the preceding case as concerned behavior and brood condition.

Laboratory-A colony, Neiv. nigrescens.

From July 12, raids of *nigrescens* were observed nightly around the laboratory, extending in varions directions from the rock fill. On July 22 after 9:15 p. m. a heavy emigration column crowded by newly eclosed workers passed to the *SE* from the laboratory to enter a mound 22 m. from the wall. Later in the movement, a young (potential worker) brood of embryos and microlarvae was carried in packets. On this and the following two nights the colony staged vigorous raids divergently from this site. However no further emigrations occurred until the night of July 25, when an extensive raid towards the *NW*, back into the laboratory rock-fill, was followed after 10:00 p.m. by an exodus in which callow workers (perceptibly darkened) as well as microlarval brood were observed, and the queen (contracted) entered the new bivouac at 12:15 p.m.

—After a succession of days terminating a statary phase observed at the laboratory, the colony started a nomadic phase by emigrating with a callow worker brood and an early larval brood to a new site which was occupied for two days without emigration. On the fourth nomadic day, in late evening, a further emigration ensued. It is probable that this colony moved away unobserved and that a different colony (Lab-B, below) was observed in the following period.

Laboratory=B colony, Neiv. nigrescens.

No raid was observed at the laboratory on the night of July 26; however, on July 27 columns were seen issuing from beneath the concrete steps on the *N* side of the building. On the following afternoon, which was overcast, after 2:00 p.m. a foray pushed from the concrete steps on the *W* side of the laboratory and branched into the clover field, advancing more than 30 m. by 5:00 p.m. Thereafter, on alternate nights, small raids or no raids were observed, until on August 2, which was overcast, a foray to the *NW* developed after 1:45 p.m. (fig. 4) and lasted until after 4:00 a.m. the following morning,

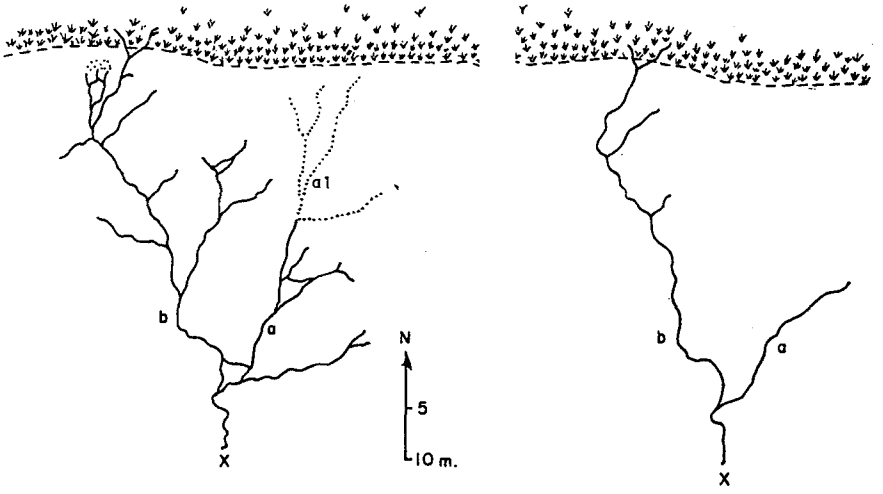

FIG. 4. — One of two trail systems of a colony of *Neiv. nigrescens* in the nomadic phase. *Left*, the trails set up at 9.30 p.m. after four hours of raiding, in which branch *a* is the older component (a_1 now in disuse), *b* the newer. *Right*, the same system at 11.30 p.m. with component *a* now mainly abandoned, *b* now followed by a single column branching profusely in a peripheral zone thickly covered by grass (upper area). *x*, exit from bivouac site in stone wall.

when a thin column still returned with booty. Only small nocturnal raids were observed until August 6, when on an overcast afternoon a foray pushed out to the *W* from a small hole in the *NW* steps used as exit in the three preceding night raids. Then at 3:30 p.m. a thick column was seen, crowded with newly eclosed callow workers, moving 10 m. over the rocks of the laboratory fill to disappear in its border zone. Although the heavy movement stopped at 10:30 p.m., the ants continued to raid during the night on branches probing into the rocks to the *S* of the stopping place. The young brood, doubtless in packets, must have been moved during a period when the observers were engaged elsewhere. On the nights of August 7 and 8, further raids occurred from the same site, extending base lines considerably into the open field to *SW* and *W*, but without an emigration. On the overcast afternoon of August 9 foraging columns extended into heavy grass; then after dusk an emigration began which carried the colony 45 m. to the *W* into a pile of rocks. On the night of August 10 one of three raiding forays led to the *N* into insect holes beneath some stones at 35 m. but no emigration was observed. This line was again in use on the following night, when a vigorous exodus developed to the stones and beyond, in which callow workers were numerous and the first sample of the current young brood was collected. The queen, contracted, passed after 12:00 p.m. Although for some time the ants carried their brood into an insect hole at 43 m., a resurgence developed, and by dawn most of the

colony had settled under stones at 35 m. Shortly after dusk on August 12, a strong exodus with brood carried the main part of the colony into the insect hole at 43 m., from which extensive raiding had developed from early evening to the *NW* and *SW*. The afternoon of August 13 was overcast following rain, and after 3:00 p.m. a foray developed to the *NW* on a previous trail across the open field, taking on much greater vigor at dusk. On this line a heavy emigration column developed after 7:00 p.m., with larval brood soon under transport and the queen (contracted) passing from the old bivouac site at 8:00 p.m. Although rain interrupted the movement at intervals between midnight and 2:00 a.m., the entire colony had transferred before dawn to a preempted ant nest in midfield (field site *x*). The afternoon of August 14 was overcast, and extensive raiding developed over a distance of nearly 40 m. to the *N* and *E* in the field. In the early evening booty was being returned on convergent routes to field site *y*, an abandoned *Pogonomyrmex* nest 25 m. to the *E* of site *x*; then after 8:00 p.m. an emigration developed on the base trail from site *x* to *y*. On August 15, overcast throughout, moderate raiding continued after 10:00 a.m. on lines to the *E* and *N* from *y*, mainly into ant nests in a grassy part of the field; much more vigorously after dusk. After 9:00 p.m., a variable exodus developed from *y*, and under stress of returning traffic resolved itself within an hour into a short transferral of the entire colony over an arcing course of only 2.5 m. to field site *z*, also an abandoned *Pogonomyrmex* nest. Throughout the night a booty-laden column continued its return to *z* from the *NW*. The afternoon of August 16 was overcast and, between rain flurries, traffic from *z* was observed. By 5:20 p.m. a vigorous column extended 25 m. to the *N* to a stone wall bordering the creek, with much booty carried back to *z*. At 9:30 p.m. a booty-carrying column had reached the wall from *z*; however, this column was reversed to *z* within an hour, no further exodus was seen and booty-carriers returned to *z* throughout the night. August 17 was overcast, and all day the ants were active bidirectionally on the trails fom *z*, with a great increase after dusk. Evidently because of interruptions from rain, it was only after 12:10 p.m. that an emigration developed from site *z*, passing to the *N* into the stone wall. This movements, with larvae carried, continued until dawn, as did the return of laden foragers to the new site in the wall. On August 18, in the afternoon, extensive foraging was observed from the wall site into the well-shaded creek bed. By 7:30 p.m. a wide brood-carrying emigration column passed from field site *z* to the stone wall, with three large brood caches en route. After 12:00 p.m. this emigration column went on from the wall across the creek, with the booty-laden column now continuing on a previous raiding line across the lawn beyond to a new site (N—14), deep below leaves at the edge of a great rock near the road, more than 75 m. to the *N* of site *z*. This move had been completed by the entire colony before dawn. Although raiding developed promptly at dusk on August 19, it was not until after 9:00 p.m. that a brood-carrying exodus developed toward the *SE*. With many interruptions, particularly at advance trail-division points, this exodus finally traced a meandering course along the wall and across the lawn over a distance of about 40 m., taking the colony into a stone parapet (site N-15). The emigration continued until after 3:30 a.m., as did the return of laden foragers from the *E* and *N* to site N-15. On August 20, with overcast skies at 2:00 p.m. after a rain, a small foray was seen from site N-15 and from dusk extensive columns developed to the *NE*, soon mounting the bank to the road and dividing variously on the road and on the other side. Fortunately no automobile traffic disrupted these events, and by 8:30 p.m. the larva-carrying exodus had established a route across the road and up the steep rock face on the opposite side. At 10:00 p.m. the queen (contracted) appeared and was captured for fixation. The emigration was soon re-established, now terminating at a site (N-16) about 35 m. to the *NE*, under a great rock atop the hill. Because of the queen's capture, this colony thereafter was considered abnormal. However, due to an important relationship to Thicket colony that developed, a summary of subsequent events follows.

On August 21, in the evening, there was raiding to the *NW* and *N* from site N-16, but no emigration occurred. In the evening of August 22 complex movements developed, including extensive back-tracking across the road to site N-15; later, after

3:00 a.m., a movement with brood branched from the back-tracking route to a new site (N-18) 25 m. to the *W* of N-16. With trail-following again complicated on the evening of August 23, a resumption of the exodus with brood after 2:00 a.m. led beyond site N-18 to a new site (N-19) under an old stump. These movements continued on the evening of August 24, with raiding from sites N-16 and N-19, and an abortive back-tracking with brood to site N-15. Back-tracking was also observed from site N-15 to the *W* through site N-14 and to the *S* toward the creek, where a fusion with the Thicket colony (now also queenless) evidently was in progress. Throughout the night of August 25 these movements continued, with an extensive raid to the *N* from the stump, site N-19, where most of the colony was still located. During the night of August 26 there was a continued back-tracking shift toward the S, and a fusion with the Thicket colony. Although raiding continued from the stump on the hill (site N-19), after 12:30 p.m. there was an emigration with brood (now entering the prepupal stage) from the N-19 site to site N-18, and to some extent from the rock to site N-15 across the road. Throughout the night of August 27, as also on the night of August 28, these movements went on variably. The shift to the *S* kept going throughout the night of August 29, with a drift through site N-14 back toward the creek and continued fusion with the Thicket colony. After the night of August 26 there was no extensive shifting of brood (apparently still centered at sites N-19 and N-18) until the night of August 30, when a broad exodus column passed from site N-19 across the road to site N-15, carrying pupal brood as well as booty. On the following nights there were complex shiftings on the trails, with a drift into site N-15 and further junction with Thicket colony. On the night of September 3, all trails between N-13 and N-19 had thin variable traffic, but no brood was transported. After September 5, columns were seen nightly, emerging from beneath the Lodge (70 m. to the *W* of N-15). The fused Laboratory-Thicket colonies may have settled there before September 10, when nocturnal activities ceased in this area except for brief and limited forays in the early night.

—Periods A and B of the laboratory observations probably involved different colonies, but period B concerned only one colony. This colony at first completed a statary phase at the laboratory, with limited raiding, then entered a nomadic phase in which extensive nightly raiding was common and nocturnal emigrations were almost the rule. The nomadic phase began with the eclosion of a large brood of mature worker pupae, and as it continued a new brood of potential workers advanced from the microlarval stage toward the prepupal stage. The capture of the colony queen on the 16th day of this nomadic phase seemed to disrupt normal colony function. Instead of the three or four emigrations which might otherwise have occurred thereafter, prior to the attainment of early pupation in the brood, there ensued a variable backtracking and a more or less complete fusion with the Thicket colony.

Creek colony, Neiv. nigrescens.

At 10:30 p.m. on August 6 this colony was found engaged in a large raid and an emigration of more than 50 m. to the *N* from the South creek (see fig. 5). Raiding was interrupted and the emigration was delayed beyond a major trail division near the meadow by persistent major conflicts with three large colonies of *Iridomyrmex* sp. nesting there (points *2a*, *b*, and *c*, fig. 5). By 12:00 p.m. most of a large recently-eclosed brood of callow workers had run the course from the old bivouac (*x*) to a cache beneath

a large rock at *2*, and most of a brood of young worker larvae had been shifted to caches on the trail near *2*. At 3:30 a.m. traffic was still variable around and beyond trail division *2*, with indications that the emigration was continuing by degrees to site x_1. Later in the night, most of the colony moved with the broods to nest within a large wooden beam lying in the meadow (site N-6) about 64 m. from site x. At 8:15 p.m. on August 6 the emigration was completed by transportation to site N-6 of booty cached near the trail-division at *2*, from which raiding continued during the early night. Also, from shortly after dusk a large raid had progressed from x_1 to the *SW* across the field, with several major branches. In the early hours a large booty cache developed under a stone close to that under which the Meadow colony was

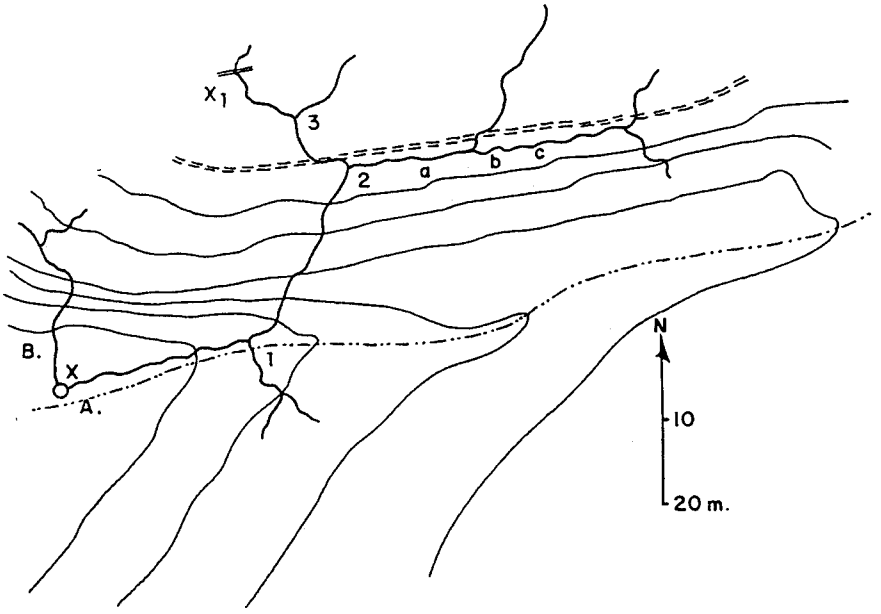

FIG. 5. — Sketch of two principal raiding systems (*A*, *B*) and the emigration route (x to x_1) of a colony of *Neiv. nigrescens* (Creek, August 6) in the early nomadic phase. Explanation in text. x, bivouac of the day, under stone on creek bank, being abandoned as colony emigrates to x_1, new bivouac within a large wooden beam.

bivouacked on July 14-15, and a 15-m. section of former Meadow Trail to this site was in use. At 11:20 p.m. a booty-laden emigration column had developed from x_1 to this point, 35 m. distant. Continued emigration beyond this cache was delayed by interference from traffic returning on several raiding lines converging here; however, after 12:15 p.m. the exodus pushed on to the *W* to the new site (N-7), a preempted ant nest under a stone on the creek bank, 63 m. from site N-6. A raid developed on the following evening on short lines to the *E*, *W*, and *N*, and booty-laden traffic returned to site N-6 until after 4:00 a.m., but no emigration occurred. The afternoon of August 9 was overcast, and raiding expanded beneath the leaves, reaching out more than 10 m. by dusk. Beginning shortly after nightfall, an emigration developed by stages through a complexly branched raiding system with numerous caches of brood and booty, to site N-9 about 46 m. to the *SW* of N-7. On two lines extending beyond N-7 to *W* and *S*, booty-laden traffic returned until after 5:15 a.m. The principal raid on the evening of August 10 extended to the *W*, and despite interruptions by rain an exodus carrying booty and brood had pushed farther along this line on the creek bank, nearing a

booty cache under a stone at 31 m. where the new bivouac (N-8) was established. To this site thin booty-laden columns returned until shortly after dawn. The afternoon of August 11 was overcast, and at 3:00 p.m. the ants were raiding to the *W* on several branching lines. Vigorous foraging in the evening initiated an exodus which by 10:00 p.m. had pushed out more than 40 m. along the creek bank, then bent sharply up to the *NW* on a branch trail where a brood cache was being established under a large rock. By 3:30 a.m. the exodus had pushed 15 m. farther uphill to the road-fill, on a peripheral trail in use at 10:15 p.m., to site N-9 at 47 m. from N-8. With low temperatures prevalent after dusk on August 12, the raid on complexly branched lines among the rocks near N-9 was almost entirely under surface cover, and no emigration took place. A continuation of raiding on some of the same base-lines after dusk on August 13 led into an emigration to the *SW* which ran beneath rocks through nearly the entire course of 51 m. The new bivouac site (N-10) covered more than 1 sq. m. in insect nests below adjoining rocks. Although this general area, a high creek bank, was rock-covered, vigorous raiding developed only after dusk, with few indications of daytime raiding. In the evening emigration of August 14, a distance of only 8 m. was covered (to site N-11) in several stages of brood-shifting from one to the next of three caches beneath large rocks, with signs of extensive feeding of larvae. Just before 10:00 p.m. there was a lasting reversal of the exodus by rain. The evening emigration of August 15 carried over a distance of 30 m. to site N-12, again with a relaying of larval brood through two or more intermediate cache points at which brood-feeding occurred. After dusk on August 16 there were indications of raiding among the rocks on numerous relatively short divergent lines, with much shifting of brood under rocks around the bivouac site, but without any emigration. The afternoon of August 17 was overcast, and short raiding columns from the bivouac were observed. Raiding became much heavier after dusk with much booty returned during the night. A heavy exodus to the *E* began about 2:00 a.m., but was soon reversed and there was no emigration. On the evening of August 18 a brood-carrying column was observed working its way to the *E* and *NE* through the raiding zone, ending at 11:10 p.m. in a large brood cache beneath rocks at 45 m. Still moving at 4:00 a.m., this column then led under a large rock (site N-15) 3 m. farther on, to which laden foragers returned in two converging lines. Raiding after dusk on August 19 continued the development of one of these lines uphill at angles to the *N* through the rocks, and an emigration which developed on this line after 9:00 p.m. followed almost the exact route taken by this colony in its downhill course on August 13. The movement carried over a distance of 58 m. to site N-16, close to the site occupied on August 11-13. Next afternoon, digging disclosed that the colony had its nearly mature larval worker brood packed into the many chambers of an abandoned ant nest, to a depth of more than 50 cm. below a large rock. The disturbance may have stimulated an earlier exodus that evening, leading across Rustler's Road into a raiding zone on the opposite bank. At 4:00 a.m. the emigration ended there with the new bivouac (site N-17) established beneath some large rocks. The night of August 21 found the colony raiding until after 4:15 a.m. on numerous short lines beneath many rocks near the bivouac, and some shifting of brood was observed (probably with brood-feeding), but no emigration took place. Development of the *NE* raiding system continued from dusk on August 22, and after 10:15 p.m. an emigration developing on the principal trail in this direction carried nearly 40 meters uphill to the exposed entrance of an ant nest on the rocky slope. This emigration continued after nightfall on August 23 and was completed shortly before 1:30 a.m., with the transport of the remainder of the brood, now mainly or entirely in the early pupal condition.

The colony remained at this site until Sept. 4, with no raids observed on the nights of August 24 and 25, and September 1, and relatively small raids on the other nights. The successive forays all developed rather slowly and variably, emerging from different insect holes within a radius of 4-5 m. A small raid to the *E* on the night of September 4, extending a route used on the preceding night, changed at some time

after 11:00 p.m. into a heavy emigration across the bare hillside into an insect hole under leaves at a distance of 23 meters. A large brood of only faintly pigmented worker pupae was carried in the column, but no young brood was seen despite a close watch. The queen, followed by a large retinue of workers, appeared in the column shortly after 1:00 a.m. Nearly maximally contracted, she was collected at once for fixation. (This unforseen event displaced a plan to dig into the bivouac on September 7 to capture the queen and inspect the brood.) The colony remained at the new site, with weak nocturnal raids, until it was last visited on the night of September 12.

—When this colony was first seen, it was then at about the 5th day of a nomadic phase, judging from the pigmentation of the callow-worker brood and the size range of the larval = worker brood. Nocturnal raiding persisted at a fairly high level, with emigrations ensuing on most of the nights, as the young brood passed through its larval stage of development. When most or all of the brood had reached the early pupal stage, the colony entered a statary phase of low raiding activity and without emigration except for the movement which occurred on the night of September 4. The colony otherwise evidenced a low excitement level in the entire period following August 23, and this movement may have been due to an exceptional disturbance (see Note 4). It is probable that raiding would have increased considerably in vigor and the colony would have emigrated soon after September 12, or when the pupal brood had matured fully. The non-physogastric condition of the queen, together with the absence of eggs, indicated a failure to deliver a new brood at the predicted time midway in the statary phase.

Bridge colony, Neiv. nigrescens.

This colony was first observed at 11:40 p.m. on the night of August 9, engaged in a large raid and in an extensive emigration to the *E* in the lower dry creek bed. A potential all-worker larval brood was carried in the column, or heaped with booty in one of numerous large caches. At 12:50 p.m. the emigration column, moving through the advanced zone of raiding, led to a log in a boggy area. At 1:00 a.m. a large cluster was visible in a 7 cm. high space beneath this log, into which the emigration column emptied; however, the emigration later continued 12 m. to the cement pier of an old footbridge within which the colony settled. On the following three nights there were moderately developed raids, but no emigrations. The raid of August 12 was completed before 3:00 a.m. Next evening, in the course of a larger raid, a heavy brood-carrying emigration column moved to the *S* across an open grassy area. At 8:00 p.m. the first brood-carriers had reached a point 25 m. from the old bivouac, and at 9:00 p.m. the colony was settling beneath a pile of logs. With one lengthy interruption by rain, the emigration continued until after 5:00 a.m.; then to the *NE* raiding had ceased, but ants were still returning from the *SE*. August 14 was somewhat overcast, and at 10:30 a.m. thin columns extended to the *SE* from the bivouac. A large raid developed that evening to the *SW*, and at 8:30 p.m. a vigorous emigration column extended 45 m. to where the ants were entering an insect hole beneath a stone. Several short raiding branches with terminal swarms extended from this point under the dry leaves. On the following night, after raiding began, emigration occurred similarly, arcing *SE* to a trail division and brood cache at 25 m., and by 1:30 a.m.

extending to a point on the stony hillside at 35 m. where a large cluster and brood cache had formed under a rock. At 4:30 a.m. the emigration extended to a rock 3 m. beyond the previous point, with brood being deposited in a large booty cache there. On both of these nights, nearly the entire emigration passed beneath leaves and other ground cover. Extensive brood shifting beneath the rocks occurred on the next afternoon. This action continued in the evening, and around 10:00 p.m. an emigration started to the *NE* on the most vigorous line of raiding, running along the contour into a cavity below a stump. The raid of August 17 was a large one, and by 11:30 p.m. an emigration column had developed through the *E* trail system uphill and along the sharp crest. By 2:00 a.m. the larva-carriers had reached a point in the upper meadow at which an insect hole was entered, as raiding continued beyond. With several brood caches forming, the emigration continued until nearly 6:00 a.m., when it led on to a site beneath a rock at 35 m. On the afternoon of August 18, with overcast skies, a thin emigration column continued on this route. At 10:00 p.m. this emigration was vigorous, and on the larger of two raiding systems from the new site, a brood-carrying emigration column passed on 40 m. to the *NE* to a similar bivouac site on the stony plateau. At 3:30 a.m. the resumed emigration from the site of August 17 had ended, but the advance exodus ended beneath a stone at a tree 3 m. from its former terminus. At 10:00 p.m. on August 19 the pattern of the previous evening was approximated, with both continued emigration from the old site and an advance emigration to the *E* through the principal raiding system to a new site beneath some rocks in a little draw. At 3:45 a.m. this emigration continued, but all raiding had ceased. On August 20, although a vigorous raid developed in two directions after dusk, emigration was limited to a shifting of brood over a surface distance of only 3 m. This movement continued at 3:45 a.m. after all raiding apparently had ended. There was no emigration on the night of August 22, although forays developed on short lines in various directions. All ants had returned by 3:45 a.m. The principal raid of August 23 evening was to the *E*, and after 8:00 p.m. an emigration developed through this system, over an arcing, irregular course. At 3:45 a.m. this movement continued to the new bivouac site, an insect nest under stones at 76 m., with a heavy return to this place on two advance raiding lines. At 8:05 p.m. on the following night a continuation of this emigration was in progress, with one very large brood cache under a stone 15 m. from the bivouac of August 23. This movement was completed by 1:15 a.m. without any further advance beyond the site occupied by a part of the colony on the preceding night. At the time of this final transfer, the brood had entered the early pupal stage.

The colony remained at this site during the following 18 days, in which only relatively small raids developed on most of the nights, but without forays on the nights of August 31 and September 8. The successive raids led off in different directions from different exit holes scattered within a radius of 3 meters. The forays of September 9 and 10 seemed to be more vigorous and extensive than any others of this period.

The first evening foray of September 11 was a moderate one to the *W*, the second was a stronger outburst arcing to the *NW*, and on the line of the latter a vigorous emigration developed after 8:00 p.m. The column was thronged with callow workers, all at first running independently, but after 8:30 p.m. with a minority of them inert and transported. The queen (fully contracted) appeared at 10:20 p.m. followed by a long retinue, and was collected for fixation. The thick column including callows stopped shortly after 12:00 p.m., when the temperature 5 cm above the ground was 8.7°C and within the surface soil 14.5°C. The emigration was completed on the following evening. In the entire movement, no brood was found except that of mature pupal workers.

—Judging from the condition of the brood, this colony when first discovered had reached the seventh or eighth day of a new nomadic phase. This phase continued with the further maturation of a larval worker brood and ended when this brood attained the early pupal stage.

The colony then entered a statary phase, with only small raids and no emigrations until the current brood reached pupal maturity. In the emigration coincident with that change in colony condition, no young brood was found.

Thicket colony, Neiv. nigrescens.

On the nights of August 17, 18 and 19 columns seen raiding in the upper creek area were differentiated from those of the Laboratory-B colony and were traced to the *SE* cement post of the footbridge. The evening raid of August 22, which was much more extensive than before, originated from the *SW* post of the bridge, and expanded mainly across the field recently vacated by the Laboratory-B colony. By 9:25 p.m. a broad exodus developed on this line in which a mature pupal worker brood appeared, most of it inert and transported by adult workers. For several hours this column discharged into a small hole, the entrance to a preempted ant nest, near a trail division point 38 m. out in the open field. The queen, fully contracted, appeared at 10:50 p.m. and was collected for fixation. After 12:00 p.m. small packets of new brood began to appear in the column, and continued although sparsely until the end after 1:00 a.m. Despite a continuous watch, only about 2,500 pieces of such brood were taken, very small in numbers for the species. After 7:15 p.m. the following evening the exodus continued on the same line, with callows numerous, now most of them running independently. No young brood was seen in this movement, which after 3 hours was replaced by a thin, variable line between the bridge and field nest, thereafter a continuous feature at night. This and further behavior was considered abnormal.

Back-tracking continued on the following three nights, when moderate raids developed from the field nest to the *W* and *S* particularly, but without emigration. After 9:00 p.m. on the night of August 27 the column thickened to an exodus from the field nest to the *SE* bridge pier. This column, crowded with callow workers, first entered the pier, then continued across the creek bed on an old raiding trail of this colony which crossed various known trails of the Laboratory-B colony. (A close watch was kept for young brood, but less than 250 microlarvae were taken.) Through this complex of trails, ants from the Thicket colony reached and entered the same small hole in the cement wall used by the Laboratory-B colony (N-15) one week before, at a site now occupied by part of that colony. A fusion of these two queenless colonies, evidently in prospect, was indicated on the following nights by the presence of occasional callow workers (which could only have come from the Thicket colony) in the lines on the hill to the *N* of the road, between sites N-16 and N-18 of the Laboratory-B colony. A widespread following of these and related trails by the continuous columns of these colonies, undergoing fusion, was observed on the following nights until September 12.

—This colony was found during the last week of a statary phase, and its queen was captured on the first emigration of the succeeding nomadic phase, when a large eclosing worker brood was present. There was also a new brood, but its numbers seemed unusually sparse for the species. There was no further emigration until three nights thereafter, when an extensive movement on the back-trail carried this colony into fusion with the Laboratory-B colony, also queenless.

Rock colony, Neiv. nigrescens.

When found on the night of August 26, this colony was engaged in a vigorous raid of two trail systems mainly to the *W*, and bivouacked under a large rock in a grove about 400 m. to the *E* from the current site of the Creek colony. No emigration occurred, despite lengthy eruptions at two different times. At 6:00 a.m. next morning, thick columns were still returning to the bivouac with booty, including adults and pupae of *Formica spp.* in particular. In the course of a large raid on the following night, mainly on two systems to the *SW* and *NE*, an emigration developed after 11:00 p.m. in which a large brood of early pupal workers was transported. The movement progressed by stages through two or more caches under rocks, into a preempted nest of fungus-growing ants under the rocks at 14 m. The raid of the following evening, although at first heavy, fell off sharply after 10:00 p.m. and no emigration occurred.

The colony remained at this site (fig. 2) with relatively small divergent raids on some of the nights (and no raid on August 31), until it was excavated on September 4. Its nest, about 1 m. broad and nearly as deep, occupied most of the galleries and chambers of the dispossessed myrmecine colony, the remnants of which huddled in peripheral chambers. Below a surface layer of dry soil about 12 cm. deep, the dorylines were clustered thickly with their pupal worker brood in several dozen chambers distributed through a thick root mass in light, humid soil to a depth of about 95 cm. The queen, nearly maximally contracted, was found near one side about 30 cm. down. A thoroughgoing search of the entire nest disclosed no eggs or other young brood. When last seen on the night of September 11 the colony was still clustered with its pupal brood under stones at the bottom and one side of the excavation, and had a thin single column over the parapet to the *E*.

—This colony when found was completing a nomadic phase, with an all-worker brood at the early pupal stage of development. After one week in the statary condition, its nest was excavated so that the queen could be captured and the brood thoroughly inspected. As no brood other than the one then in the mid-pupal stage was found, and as the queen was non-physogastric, although the colony would have emigrated from this site on the eclosion of the advanced brood, a continuation of nomadic function would have been doubtful.

Stone colony, Neiv. nigrescens.

When discovered on the night of August 30, this colony was raiding on a long, branching trail-system extending more than 30 m. to the *E* from its bivouac in an old foundation near the upper spring. Next night there was a relatively light raid to the *NW*, and on the night of September 1 a somewhat heavier raid to the *W*. On September 2, at 8:15 p.m., a full emigration column meandered through leaves and stones 35 m. to the *W* on the principal trail of the previous evening's raid. In this column, for several hours, light-colored callow workers predominated, with a relatively small proportion of mature worker pupae carried by workers. Despite a continuous inspection of the column, there was no sign of young brood. The queen (contracted) was permitted to pass in this movement, but was taken for fixation when she passed at 9:05 p.m. in the next emigration, on September 5. Raiding on the evenings of September 3 and 4, although rather heavy, was relatively limited both in distance and in duration. At one point in the latter raid, a mass 1 m. wide operating in vines

and brush spread upward over the trunk of a large juniper tree for a distance of nearly 2 m. Back-tracking began after 8:00 p.m. on September 6, and somewhat later a wide emigration column thronged with callow workers surged back for 20 m. toward the first nomadic bivouac. During the following three days the colony remained in the vicinity, with a short emigration on the night of September 8, first back-tracking, then reversed toward the site of September 5. At 9:00 p.m. on September 9 a mixed column was seen back-tracking from the first nomadic bivouac; however, on the following nights the ants could not be found in the vicinity.

—This colony was observed during the last 3 days of a statary phase, also in the first four days of a nomadic phase which ensued on the eclosion of a large pupal worker brood. The case resembled the Rock, Creek and Bridge colonies in that no young brood was found at the time. The failure of emigration on the second and third nights of the nomadic phase was not unusual under the conditions; however, back-tracking and difficulty in resettling observed on the following nights, as with the Meadow colony, was attributed to the removal of the queen.

Lodge colony, Neiv. opacithorax.

On the night of July 12, when this colony was found at the Lodge, at 3:00 a.m. a heavy column emerged from a short flight of stone steps and moved along the base of a stone wall for 3 m. in the open and then into the wall, transporting a larval (sexual-form) brood. This movement continued past 5:00 a.m. After 8:00 p.m. on July 13, a bidirectional column was first seen, then a thicker column 8-10 mm. wide transporting brood as on the previous night. This column was traced 15 m. to the *N*, reappearing three times from the stone wall before it disappeared into thick grass. Traffic thinned out after 11:00 p.m.

—This colony was nomadic, with a large brood of sexual-form larvae.

Spring colony, Neiv. opacithorax.

On August 8 at 11:00 p.m. this colony had a complex raid on trails branching to the *SW* in the field beyond the upper spring, and a long meandering emigration column extending 40 m. to the *NE* where a large cache of brood and booty was found beneath a stone on the creek bank. Thousands of potential worker larvae (range 0.58-3.6 mm.) were transported in the column.

—This colony was nomadic, in a highly vigorous condition of activity with a potential worker brood well advanced toward larval maturity.

RAIDING

In the locality of this investigation, the raiding columns of *Neiv. nigrescens* usually and of *opacithorax* always issued at dusk and foraging continued during the night, often to dawn. In the former species there

were relatively few exceptions save on overcast days, when raiding sometimes occurred but then very subdued in comparison with nocturnal forays. At rare intervals in this species, usually when a colony was highly excited as in the presence of a newly eclosed worker brood, raiding might occur in full sunlight. This generalization holds for the area of study, in which a mixed cover seldom held light at ground level to a low intensity except on overcast days. In contrast, in the forests of Central America, Mexico, and Trinidad I have frequently observed vigorous daytime raiding in *Neivamyrmex* species such as *pilosus*, and at times over a considerable area.

Two principal conditions of raiding may be distinguished, that of a colony in the *nomadic* condition and that of a colony in the *statary* condition. Nomadic raids tend to begin earlier, usually as dusk approaches, involve much greater numbers and more branching columns generally with larger terminal groups, and are usually characterized by an emigration over one of the principal raiding trails. Raiders from a nomadic colony tend to be much more excitable than in a statary colony so that outbursts generally are stronger and more lasting. The evening exodus from a statary colony typically holds its peak only for a few minutes, after which the basal column is thin until the laden return begins. In contrast to the reduced level of statary colonies, the output of a nomadic colony may remain at peak for two hours or more, and in the periphery greater numbers usually are brought to bear more quickly upon any excitation center at which new booty is found or stiff resistance is met. In the latter, persistent excitement is greater on trails both in the raiding front and in the rear than in the former. Raiders from a nomadic colony generally take a larger proportion of adult insects such as ant workers and sexual forms, beetles and the like, than those from a statary colony, of which the booty tends to be the soft-bodied brood mainly of ants.

In the less frequent instance when a colony of *Neiv. nigrescens* has settled at or beyond the limit of its previous raiding zone and new, unworked territory confronts it, a characteristic pattern of initiating a foray is observed. Ants then crowd out in several directions, and as this mass advances it splits variously and is succeeded on the same terrain by a network of columns and finally by branching columns (fig. 3, 4 and 5). Orientation is chemotactual, and, as the zone of raiding is extended, anastomosing columns remain of which the strongest radii continue to follow chemical traces behind the advance. In figure 4 one trail system of a nomadic colony is represented as observed about four hours after raiding began at dusk. Dotted lines in the periphery of system *a* indicate trails abandoned as heavier booty found elsewhere drained ants from the area first exploited. In the sequel, sketched 90 minutes later, and after a rain, system *b* is now abandoned but *a* has entered a zone thickly covered with grass, where the raid advances with a profuse branching of columns.

The raid of a colony of these *Neivamyrmex* species thus advances in

three stages: 1) spreading groups in the forefront, succeeded by 2) areas of dividing, anastomosing columns and finally 3) a single long base column with terminal branches. The advance groups may be anywhere from a few centimeters to a meter or more in width, their survival as masses in given terrain depending particularly upon the intensity of raiding and the local booty supply. Usually, as the sketches shown in figures 3, 4, and 5 indicate, secondary branches disappear from use in the course of time and only the base trails remain in use. The pattern of nomadic raiding systems varies according to the topography and the distribution of booty. Two large branching-trail systems, each with its principal or base trail leading from the bivouac, may remain in use for hours, one of these may disappear and a new one develop, or one alone may persist. The advance from the bivouac may be slow or rapid according to conditions, and after some hours may extend only 30 or 40 meters with numerous long branches or more than 60 meters with fewer branches in use.

Similarly, although on a smaller scale, the raids of *Neiv. opacithorax* involve one or more systems of columns on branching chemical trails.

Storage heaps or caches of booty usually develop at trail branches in the zones of more productive raiding. In these the booty may be left for hours, heaped under cover, before it is removed to the rear or forward depending on how the emigration develops. In the raid of the Creek colony on the night of August 6, represented in figure 5, an early cache under a small stone at junction *1* was removed and smaller ones at 2*a*, *b*, and *c* disappeared before 11:30 p.m. as the emigration moved forward, but a large one at junction *2* remained throughout most of the night.—When in the route of emigration, booty caches may also become temporary depots where larvae are deposited and consequently where extensive feeding can occur.

Under the conditions of this investigation, the regular, extensive raids of this species occur at night, and raiding columns were not seen on the surface in the daytime except on overcast days. When a colony is in a highly excited condition, as at the beginning or near the end of a nomadic phase, subterranean raiding may occur to an appreciable extent in the daytime, although as a rule only relatively close to the bivouac when subterranean channels are available. It is unlikely that these ants usually get out very far from the bivouac except at night, and then only on the surface or under ground cover such as leaves and stones. At times large sections of a raid or even an entire raid may be active beneath surface cover. The columns tend to run along beneath objects such as fallen limbs rather than on the upper surface, as is common with the columns of *Neiv. pilosus* and others in tropical forest. As an exception, when the Bridge colony was raiding in a boggy area on the nights of August 10, 11 and 12, its columns often followed the tops of logs and fallen limbs; however, in a dry area on the following night, the columns ran below limbs and the raid largely developed under leaves and other ground cover. These ants seldom leave the ground in their raiding, and then as a rule

only when considerable numbers surge forward simultaneously in a limited space, as with the Stone colony on the night of September 4.

Under statary conditions the raids are smaller and less vigorous than in nomadic colonies, and on some nights raiding is brief or absent. The raids on successive nights then tend to be in different directions, although at times, after intervals of disuse, the same base route may be extended. The various routes taken by the Creek colony and by the Bridge colony during their statary phases were roughly axial from the bivouac center, although few forays of the former colony mounted the steep hillside, and none of the latter probed far into two sectors evidently deficient in booty.

THE QUEEN OF *NEIV. NIGRESCENS*

Morphological studies by Holliday (18) and Whelden (pers. comm.) on the queen of this species indicate that a large number of eggs may be matured at one time. In this study the number found in one distinct brood, that of the Meadow colony, was more than 37,000. Judging from the earliest brood ranges obtained (*i.e.*, at the outset of the nomadic phase) a few days and probably not more than one week suffice for the actual laying operation. A short-term output of this magnitude would not have been suspected for the relatively diminutive queen of this species, whose total body length with contracted gaster is only 12-14 mm. Under the conditions of this investigation, the interval between broods was about 30-35 days. As in *Eciton*, a succession of all-worker broods is the rule, and sexual broods appear to be exceptional.

The queen remains in the nest except for the time when she runs in the emigration column to a new bivouac site. This event, described by Reichensperger (21) for an emigration of *Neiv. pilosus* witnessed in Costa Rica, was observed many times in this investigation. The queen's passage always occurred at night and in all cases she ran the full route under her own power, moving along steadily with a thickened column of highly excited workers pressing around and after her. Although the workers are strongly attracted to the queen and greatly excited when in her vicinity, they seldom run over her in the emigration to the extent that she is hidden from view, as is common in *Eciton burchelli* and frequent in *hamatum*.

Seven queens of *Neiv. nigrescens* were captured and preserved in Bouin's fixative for histological study by Dr. Whelden. With the exception of the Meadow queen, collected for evidence on the queen's condition in relation to brood in the regular season, all of these queens were captured late in the project. With the Meadow queen two broods were found, one potential worker brood in the embryonic and microlarval stages, and one callow all-worker brood, mainly eclosed. Both of these broods may be attributed to the function of the one queen, and the spacing may be considered representative. Fom Dr. Whelden's findings, this queen,

contracted maximally when taken, would have produced a further brood in due time.

The remaining six queens were taken when the work was in its last stage, two (Thicket and Bridge) for additional evidence on the queen's condition at the beginning of the nomadic phase, one for her condition early (Stone) and one late (Laboratory-B) in the nomadic phase, and two for her condition before (Rock) and after (Creek) the time hypothesized for regular egg-laying midway in the statary phase.

In this queen series there were major departures from expectations. All of these queens were maximally contracted or nearly so at the time of capture. In strong contrast to the Meadow queen, of the two other queens taken at the outset of a nomadic phase only the Thicket queen had produced a new brood, and this was found abnormally low in numbers. But neither Bridge nor Stone, when the queens were captured early in September as a nomadic phase began, had any young brood so far as could be ascertained. As for queens in the statary phase, both the Rock and Creek queens were nearly maximally contracted when taken, and in neither colony were any eggs found, despite a careful search in the excavation of the Rock statary nest and a close watch on the sporadic emigration of Creek colony. From the presence of a maturing pupal all-worker brood, it may be inferred that in the preceding statary phase both of these queens had passed through physogastry (fig. 1) and egg-laying.

From his histological studies of the last six queens, all taken after August 20, Dr. Whelden found no indication that any one of them was maturing a new brood. However, from the results on regular colony function and reproduction earlier in the season, the Rock queen should have been physogastric and laying or nearly ready to begin laying eggs, the Creek queen should have completed or nearly completed the laying of eggs, and the Thicket, Bridge, and Stone queens should each not only have laid the eggs of one brood within about two weeks previously, but also should have entered the early stages of producing a further generation. The results support the conclusion that although all of these seven queens had been normally reproductive at least up to times within a few weeks preceding their capture, a termination of reproduction had set in for every one of them, except the Meadow queen. For the Thicket queen, what would probably have been her last brood of the season evidently was curtailed. These and other considerations indicate that this period marked a termination of reproduction for the current year in these queens and their colonies.

The workers of *Neiv. nigrescens* are strongly attracted to their queen. This is indicated by observations of behavior on the emigrations, of worker responses to queens temporarily housed in laboratory nests or to queens returned to their colonies after detention periods up to 24 hours, and (in the cases of the Meadow and Rock colonies) of clustering responses observed in the nests. A further fact indicates the major role played by the queen in the unified function of her colony.

This concerns the response of a colony to an absence of its queen exceeding about twelve hours. After the Thicket, Stone and Laboratory-B queens had been captured, in each case a definite back-tracking on earlier emigration trails was seen on the following night and two or more nights thereafter. Such behavior seems attributable to the effect of the queen's protracted absence, as it was not otherwise observed in nomadic colonies of this species. Also, as indicated in the colony protocols, an abnormal pattern of behavior appeared in the Meadow colony, and in the Stone and Laboratory-B colonies as well, in the form of a difficulty to establish nest sites in the course of back-tracking emigrations. No back-tracking was observed in the Rock and Creek colonies, which were statary when the queen was captured, and the Bridge colony was not observed on the nights following the queen's capture.

There is no indication that normal (*i.e.*, queenright) colonies of this species are likely to fuse. However, the cases of the Thicket and Laboratory-B colonies indicate that under certain conditions, when back-tracking leads one colony into the trails of another, a fusion can occur. As both of these colonies lacked queens, some change or set of changes due to the absence of queens may be held responsible.

HABITAT AND NESTING

The area of the Southwestern Station in Cave Creek Canyon seems to be a very suitable habitat for certain *Neivamyrmex* species, from the fact that within ten weeks in this investigation more than 12 colonies of *Neiv. nigrescens* and 6 colonies of *opacithorax* were found operating within a zone of about 1,000 meters there. This spring-fed area presents a good range of nesting sites in dry to moist ground of varying composition, with a fairly good cover, and a large population of ground insects serving as booty. The typical pattern of operations in a nomadic colony is to raid the nests of ants and other insects from one site over a sector from 30 to 70 meters long, then to move on the same night into the subterranean diggings of one or more of the adjacent pillaged colonies or into some natural cavity. Colonies of *Formica* spp. and other ants are often thus dispossessed, the survivors usually huddling in the environs until the dorylines have moved on.

Although evidently the colonies of *Neiv. nigrescens* may extend their captured subterranean nesting sites to some extent through secondary excavation, typically they do not make their way along underground routes for more than a few meters. Although in nomadic raids the columns frequently run for considerable distances beneath ground cover, actual subterranean routes are infrequent and limited in extent. In statary raids, however, underground channels leading out from the nest commonly are utilized or developed to the extent that successive raids may originate on the surface at points several meters apart.

All nests involved in the present study were subterranean, often in the ground beneath stones as in the forcibly seized quarters of other ants, or with only the entrance holes exposed. The statary nest of Rock colony, excavated in detail on Sept. 5, occupied the central galleries and chambers of a fungus-ant's nest 1.2 m. broad and 1 m. deep, from which survivors had flet into peripheral zones with salvaged brood. Nomadic colonies of this species seem to cluster more numerously in central cavities, with their brood closer to the surface than in statary colonies, the nest patterns of which seem to be more extensive in breadth and depth.

THE BROODS

In this investigation, the broods of both *Neiv. nigrescens* and *opacithorax* were found to occur in successive distinct generations. In the Meadow colony of the former species a major part of the brood estimated at more than 90 % was captured, and a randomized half of this collection numbered 17,354 individuals, which, doubled and including 2,336 specimens taken

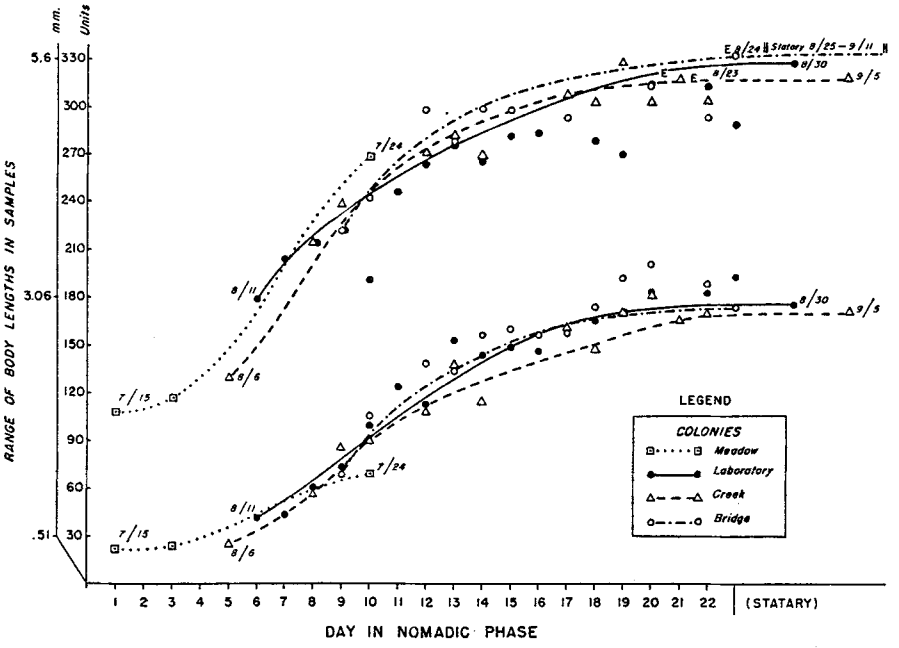

FIG. 6. — Maximal and minimal body lengths in brood samples taken from four colonies of *Neiv. nigrescens* at successive times from the early larval to the pupal stage of development. *E* on the curve of maxima marks the last emigration of the nomadic phase. The curves are synchronized on an empirical basis, and are smoothed in view of irregularities in sampling.

later from the colony remnant, indicates a total brood population of more than 37,000. From calculations based on repeated observations of the

same broods in successive colony emigrations, the strong impression was gained that under the conditions of this investigation this brood magnitude is usual for the species. These large broods, which are the rule, contain only potential workers. Evidently sexual broods appear infrequently and are much smaller, as in *Eciton*.

The concept of specific broods, each consisting entirely of individuals at nearly the same age, was invariably supported by the brood samples taken in this study. In the earliest large sample, that of the Meadow colony mentioned above, a randomized half numbering 17,354 individuals contained 95.5 % of embryos not exceeding 0.5 mm. in length and only 4.5 % of microlarvae up to 1.5 mm. in length. Figure 6 shows that successive samples taken from the larval broods of each of four colonies all present distinct upper and lower limits indicating a definite range of sizes increasing with further development.

The time interval between brood members first to eclose at pupal maturity and those last to eclose is estimated at about three days; probably an appreciably shorter time than the duration of egg-laying. The population curve of all-worker broods of this species is unimodal and skewed toward the smaller sizes. The largest members of the brood are the first to attain larval maturity, the first to attain the pupal condition, and the first to eclose as callows; the smallest members are the last in each case.

It is estimated that in the season of study, new broods were initiated regularly in the colonies at intervals of somewhat more than 35 days. The developmental period of a given brood from the egg to the mature pupal stage required a period of about 45 days, and an overlapping of broods therefore was the rule. The cases of the Meadow, Laboratory-A, Laboratory-B, Bridge, Thicket and Creek colonies of *Neiv. nigrescens* show that, in the regular season, a colony with a newly eclosed brood of worker callows also has a potential all-worker brood at the embryo-microlarval stage. If for the conditions of this study the case of the Bridge colony may be taken as representative, a procedure supported by comparison with the other cases in figure 6, the duration of brood development may be set at a value of nearly 50 days for these cases, on the assumption that egg-laying ended from 5 to 8 days before the nomadic phase began.

It is well known that the post-larval stages of brood development in *Neivamyrmex* species are naked. An interesting fact hangs thereon, namely, that when all-worker broods are present the last brood stage normally seen in colony emigrations before the colony enters the statary condition is early pupal, as in the case of the Bridge, Rock, and Creek colonies. Later stages preceding eclosion were taken in the Laboratory-B colony only by virtue of disturbance due to capture of the queen, in the Creek colony an abortive emigration, and in the Rock colony excavation of the statary bivouac. This interesting result will be considered in the Discussion.

In the two-day studies of the Rustlers' Road and Skunk Hollow colonies,

sexual-form larval broods were found as well as callow all-worker broods evidently only recently eclosed. Larval samples of about 25 specimens ranged from 6.5 to 8.7 mm. in body length in the former and from 6.4 to 7.8 mm. in the latter. From inspections of the emigrations, it was judged that neither of these broods numbered more than one or two thousand individuals at the most.

In the case of *Neiv. opacithorax*, two colonies were found with larval broods under transport in colony emigrations. The brood of Spring colony was estimated in the few tens of thousands and was clearly a potential all-worker brood, a large sample ranging 0.85-2.97 mm. in body length. The brood of Lodge colony seemed far less numerous and evidently included only sexual-form larvae, ranging 2.1-3.2 mm. in body length.

Notwithstanding the nightly practice of overturning rocks and other potential bivouac cover at every opportunity, no sexual brood of any species was found except for the two larval broods noted above and the winged males of seven *Neivamyrmex* species taken at the lights.

THE EMIGRATIONS

In this investigation more than sixty emigrations of colonies of *Neiv. nigrescens* were observed. All of these colony movements occurred at night, and all as sequelae of raids. A case representing the relationship is sketched in figure 5. Typically, raiding activities went on for 2-3 hours or more before the emigration began with the emergence of a column moving outward from the bivouac including carriers of booty, brood from microlarval to semipupal stages, or with a mature brood mainly seen as callows running in the column, a minority transported as inert pupae. Emigrations seldom started within two hours after dusk when raiding began but usually were under way before midnight, or roughly within six hours after raiding began. Except with important interruptions as from rain or (late in the season) low temperature, the exodus from the old bivouac usually continued until it was finished or until dawn. The entire movement probably required about 6 to 8 hours as a rule. If not completed before daybreak, emigrations were continued on the following night, usually with an early beginning. Such a resumed emigration often went on simultaneously with an emigration from the current advanced site to a new bivouac. Even under the most disruptive conditions, such as heavy rain, or low temperature after midnight late in the season, no queenright colony was found to require more than two nights to carry out a change of bivouac. Also, no queenright colony ever emigrated along the back-trail, although, as with the Creek colony on August 19, an older section of trail might be followed if the colony happened to cross it after a period of days.

The emigration of *Neiv. nigrescens* involves a column of from 1-2.2 cm. in width, usually with a minority of returning traffic at the borders of

the procession, especially near the old bivouac or near the new site. In the early nomadic days, callows usually crowd the column until all have passed, and the young brood carried in packets may be expected during the latter part of the callow procession. When the larval brood is more advanced, its transportation generally starts within about one hour after a consistent exodus has begun. The queen, who runs the entire distance, always with a retinue of excited workers, usually makes her journey at some time after the emigration is roughly one-third completed.

The emigration always occurs over a principal trail developed from the bivouac in raiding (see figure 5). Often as the foray advances, the exodus moves up behind the forefront of raiding by stages, with the brood deposited in successive booty caches. Even when the exodus is fairly steady, the foray ahead of it presents a variety of traffic hindrances to the outgoing movement. Delays often occur at successive principal trail junctions where booty caches may afford opportunities for feeding by callows or by larvae. The emigration then is likely to forge ahead on the branch line presenting the lower pressure of returning traffic. For these reasons, establishing a new bivouac is often a variable and lengthy process.

While the nights remained temperate, emigrations were normally stopped only by their completion, by heavy and continued rain, or by the coming of daylight. However, in late August and early September in the area of study, nocturnal temperatures had fallen steadily to a point at which, by 2:00 a.m. in the more exposed places, the temperature was below 10° C. at the ground surface and only about 6-8°C. at 6 cm. above the ground. On such nights, at increasingly early times, raiding would slow down and presently stop, as would emigration. Emigrations requiring a second night for completion then were seen with greater frequency, particularly with colonies (e.g., Bridge) operating in more exposed areas. At times an emigration was completed on the second night without any further advance (e.g., Creek, August 23); at times the remainder of the colony would move up while an advance to a new site was under way (e.g., Bridge, August 18).

The distance of an emigration varied considerably. The shortest emigration observed in this study was a move of only 2.5 m. by the Laboratory-B colony on Aug. 15, the longest was one of 76 m. by the Bridge colony on August 23. The distances covered in successive emigrations by the Creek colony during the main part of a nomadic phase are listed in Table I. The emigrations of this colony, which may be taken as representative of the species under these conditions, ranged between 6 and 64 meters, with an average near 40 meters.

The new bivouac site reached in the emigration usually lay at a trail division somewhat short of the limits of raiding, but sometimes it was considerably short of that point, as in the case of the Creek colony on August 20. Occurrences in the emigration affecting the distance of the advance depend to a considerable extent upon the pattern of raiding. A frequent cause of shortened emigration is a heavy and continued return of

TABLE I.—DISTANCE COVERED IN SUCCESSIVE EMIGRATIONS OF CREEK COLONY, *Neiv. nigrescens.*

NOMADIC DAY (estimated).	DATE.	DISTANCE OF EMIGRATION.	NO EMIGRATION.
N-5	August 6	65 meters	
6	7	63 —	
7	8	...	X
8	9	46 —	
9	10	31 —	
10	11	47 —	
11	12	...	X
12	13	50 —	
13	14	6 —	
14	15	41 —	
15	16	...	X*
16	17	...	X*
17	18	36 —	
18	19	41 —	
19	20	18 —	
20	21	...	X*
21	22	40 —	**

* Local shifting of brood.
** Emigration completed over the same route.

booty-laden columns to a trail-junction cache at which the exodus has been halted. If such a place does not adequately accommodate the colony as its new bivouac, a further shift into the forward zone may occur once the pressure of return traffic is sufficiently reduced. Emigrations by stages, after this fashion, were often observed in this investigation.

THE FUNCTIONAL CYCLE

The hypothesis of a distinct statary condition (23) in *Neiv. nigrescens* is supported by the results summarized in section *A* of Table II. These results indicate the existence of a phase of reduced colony activity and low excitement in which emigrations do not occur, coincident with the time when the brood is passing from the early pupal to the mature pupal condition. Among the colonies listed in Section *A* of Table II, Bridge represents the full course of this phase, Creek and Rock the beginning and principal part, and Stone and Thicket the terminal part.

The hypothesis of a distinct nomadic condition in *Neiv. nigrescens* is supported by the results summarized in section B of Table II. These results reveal the existence of a phase of vigorous colony activity and heightened excitement in which emigrations occur regularly, beginning with the eclosion of a mature pupal brood and normally ending at the time when the next generation reaches the early pupal condition. The

TABLE II.—NOMADIC AND STATARY FUNCTIONAL CONDITIONS AS INDICATED BY DISTINCTIVE CONDITIONS IN BROOD, EMIGRATIONS AND RAIDING *.

A. *Neiv. nigrescens*, statary condition.

COLONY.	BROOD CONDITION.	RAIDS.	EMIGRATIONS.
Creek	p to PP	14, all weak, in 17 days	1 in 17 days
Thicket	P to PP	3 weak in 3 days	0 in 3 days
Bridge	p to PP	15, all weak, in 17 days	0 in 17 days
Rock	p to P	6, all weak, in 9 days	0 in 9 days
Stone	P to PP	3, all weak, in 3 days	0 in 3 days
	TOTALS.	43 in 49 days	1 in 49 days

B. *Neiv. nigrescens*, nomadic condition.

Creek	Call., ml to p	15 strong, 3 med. in 18 days	13 in 18 days
Thicket	Call., ml	1 strong in 1 day	1 in 1 day
Bridge	Call. + L to p	15 strong, 1 med. in 16 days	12 in 16 days
Bridge	Call.	1 strong in 1 day	1 in 1 day
Pugsley	Call., ml	1 strong in 1 day	2 in 4 days (days 1,4)
Rock	p	2 strong in 2 days	1 in 2 days
Stone	Call.	4 strong in 4 days	2 in 4 days (days 1,4)
Lab. (A)	Call., ml	4 strong in 4 days	2 in 4 days (days 1,4)
Lab. (B)	Call., ml to L	13 strong, 2 med. in 15 days	13 in 15 days (none: days 2,3)
Skunk Hollow	Call. ☿☿, ♂ L	2 strong in 2 days	2 in 2 days
Rustlers Road	Call. ☿☿, ♂ L	2 strong in 2 days	2 in 2 days
	TOTALS.	69 in 69 days	51 in 69 days

C. *Neiv. opacithorax*, nomadic condition.

Lodge	Call. ☿☿, ♂ L	not obs.	2 in 2 days
Spring	☿ L	1 strong in 1 day	1 in 1 day
	TOTALS.	1 in 1 day	3 in 3 days

* Symbols: ml, embryos and microlarvæ; L, larvae; p, prepupæ; P, pupæ; PP, eclosion of mature pupæ; Call., callows. ---Broods are all-worker broods unless otherwise indicated.

Thicket, Laboratory-A and Pugsley records represent the initiation of this phase, Laboratory-B the initiation and principal part of the phase, Creek and Laboratory-B the principal part from just after the initiation to the completion, and Rock the completion. The Stone and Bridge records are considered representative of the initiation of this phase under exceptional seasonal conditions in which no young brood is present whose larval development would support a continuation of nomadism and whose attainment of the early pupal condition might be related to the processes normally terminating the phase (see figure 6).

In Sections *A* and *B* of Table II, the Creek, Bridge and Rock records represent the transition from the nomadic to the statary condition, with the first two showing that a nomadic sequence may precede. The Thicket, Bridge, Stone and Laboratory-B colonies represent the transition from the statary to the nomadic condition, with Laboratory-B demonstrating that a nomadic sequence may follow.

The records of the Bridge and Creek colonies each represent a nearly complete nomad-statary cycle. It may be inferred from the reliable indication of brood condition (fig. 6) that each of these colonies when found was already a few days advanced in the nomadic phase. It is apparent that each of these two colonies passed through virtually one complete cycle while under study.

Section *A* of Table II shows that in 6 of 49 nights in which six colonies with pupating broods were observed, no raiding occurred, and that raiding was rated as relatively weak in the others. This is a definite indication of a low level of colony activity, as is the fact that an emigration occurred in only one of the 49 cases. The one case occurred in the Creek colony after 12 nights with weak raiding and no emigrations, and was followed by 8 nights in a similar condition at the new site. Such an emigration is to be considered exceptional, particularly as a raid had started slowly and variably earlier in the evening, as do statary raids normally *

These results contrast sharply with those in Section *B* of Table II, in which it is seen that raiding was rated as strong or at least medium in 69 of the nights with colonies having callow or larval to early pupal broods, and that emigrations occurred in 51 of the 69 cases. Various conditions relevant to certain of the failures to emigrate at such times may be mentioned. First of all, in four of these cases, an emigration occurred at the eclosion of a mature pupal brood but no further emigrations took place until the third night thereafter. It is possible that brood condition, alike in all four cases, had much to do with the interesting similarity in behavior, and we shall return to this point. The 10 remaining failures to emigrate under these conditions occurred sporadically and without indications of a reduced level of excitement in the colonies. For instance, in the Bridge colony, three successive nights without movement came at

* Earlier in the evening, forays into a sector near the bivouac evidently had aroused extensive combat with two large colonies of *Pheidole* spp. nesting on that side. These ants may have spread into the doryline bivouac along subterranean channels, arousing an abortive emigration.

a time when raids were vigorous and highly productive, but involved many short and complexly branching trails. Comparable conditions existed in the Creek colony in two of the instances of failure to emigrate in the nomadic series. In these last cases, as also in the failure of specific emigration in the Bridge colony on August 22, much shifting of brood occurred along covered channels close to the bivouac. These cases will be considered in the Discussion.

The last two cases in Section *B* of Table II represent the coincidence of a condition of high arousal and of emigration in the colony, with the presence of a sexual brood in the larval stage. Unfortunately these colonies were on record only briefly, as were two cases of emigration in *Neiv. opacithorax* presented in section *C* of Table II, both colonies highly active with larval broods containing potential sexual forms in one and workers in the other.

Altogether, the results presented in Table II may be taken to indicate a close relationship in *Neiv. nigrescens* between condition of the brood and functional pattern of the colony. The prevalence of this correspondence of conditions through definite sequences of days in certain colonies representing successively the two different phases, and the reversal of each phase into the other under appropriate conditions of brood metamorphosis, are strongly indicated.

It is very interesting to note that the termination of a nomadic phase occurs not at larval maturation, as in *Eciton*, but only later when most of the brood has entered the early pupal condition. This important difference will be considered in the Discussion.

From the present results, the duration of the activity phases may be set very roughly, and only for the conditions of this investigation, at about 21-22 days for the nomadic phase and about 18 days for the statary phase. The correlation of brood curves in figure 6 indicates that in both the Bridge and Creek colonies nomadic function had begun a few days before these colonies were discovered in August. Although the curves in this figure lack common origin points and are synchronized on an empirical basis, the errors probably do not exceed one or two days. Only one completed statary phase was obtained,—that of the Bridge colony,—however, other results indicate the reliability of this case. For both phases, therefore, the above estimates are offered as good approximations of the respective time values for colonies operating in the locality of study under the prevalent seasonal conditions.

DISCUSSION

From results for *Neivamyrmex* colonies under the conditions of this investigation, a reversible functional cycle prevails in the active season, describable as a nomad-statary cycle and theoretically equivalent to that found in *Eciton*. As in *Eciton*, cyclic function is continuous under appro-

priate seasonal conditions. However, in *Neivamyrmex* under Nearctic conditions, it is probable that the sequence of colony functional cycles is interrupted completely between autumn and spring.

From our present results, cyclic behavior in *Neivamyrmex* has its basis in reproductive functions, much as in *Eciton*. These two doryline genera seem equivalent in the effect of the two principal brood-excitatory factors promoting phasic changes in function: 1) a callow-excitatory factor initiating nomadism, and 2) a larval-excitatory factor continuing the phase. These major similarities prevail in function despite the fact that the *Eciton* species studied are terrestrial in nesting and regularly diurnal in raiding, the *Neivamyrmex* species hypogaeic in their nesting and mainly nocturnal in surface activity. The hypothesis that homologous factors underlie the functional cycles of *Eciton* and *Neivamyrmex* seems to find support in these findings.

Two secondary characteristics distinguish the functional cycle of the investigated *Neivamyrmex* species from comparable aspects of *Eciton* function. The first is that, after an initial vigorous emigration on the eclosion of a mature pupal brood, emigration evidently goes into abeyance until about the fourth night. The resemblance of this occurrence to the early drop in nomadic function in *Eciton*, after a vigorous beginning (27, 28) seems unmistakable, and both phenomena may involve comparable processes associated with the overlapping of the mature pupal and young broods. The interesting difference is that although colony function in *Eciton* is somewhat reduced at a corresponding time, emigration does not stop, normally. The hypothesis may be advanced that in *Neiv. nigrescens* two factors are involved, the first postulated as a change in the responses of workers to the callow brood just after the initial highly excitatory eclosion episode, such that the colony although still very excited holds the same underground site without emigrating. The second factor postulated is a slower rise of the larval excitatory effect than in *Eciton*, related to a more retarded condition of the young brood. Results in the present study indicate that on the second and third nomadic days the bulk of the young brood is still in the embryonic and earliest microlarval stages. Tentatively, the break that appears characteristic of the early part of the nomadic phase in these *Neivamyrmex* is thus attributed to a temporary change in the worker-brood relationship, involving an inhibition of emigration by the specific post-eclosion influences of a callow brood together with a low stimulative effect from the young brood.

The second difference from *Eciton* is a striking one, related to properties centering around the absence of cocoon-spinning in the mature larval brood of *Neivamyrmex*. In this investigation, nomadic function continued in colonies of *Neiv. nigrescens* past the stage of maturity and straightening in the larval brood, and the statary condition did not ensue in the colonies until the naked brood entered the early pupal stage. This result is confusing at first, as the mature larvae soon lose the property of motility

and the *tactual* aspect of their stimulative effect on the worker population is inevitably reduced and greatly changed. For *Eciton*, I have held that the tactual stimulative effect of an active larval brood is a major factor promoting nomadism after the early part of the phase. However, in addition to the tactual factor in such trophallactic relations, a chemical factor must also be postulated (23, 27), which in *Eciton* falls greatly in strength at larval maturity. From the fact that in *Neiv. nigrescens* nomadism continues past the stage of larval maturation in the brood, an important difference would seem to exist between these dorylines and *Eciton* in respect to the brood-adult relationship prevalent at this time.

It seems that in *Neiv. nigrescens* the brood-stimulative effect somehow is held at a high level past larval maturation, despite a drastic reduction of the tactual factor. Laboratory tests of worker responses in this species to the inert brood stages between larval maturity and entrance into the pupal stage support the hypothesis that the stimulative factor critical for the maintenance of high worker excitement and nomadic colony function is chemoceptive, and presumably both gustatory and olfactory. The results suggest that the chemical effects involved are peculiar to this stage. The hypothesis is advanced that, during post-larval metamorphosis, products of stage-specific secretory and other metabolic functions are effective for which the organic basis is greatly limited or even absent in *Eciton*.

The reproductive properties of the relatively diminutive queen of *Neiv. nigrescens* are prodigious although not equal to those known for *Eciton* species. In the functional season this queen is capable of producing distinct broods at regular intervals, each new generation evidently initiated before the time-limited delivery of the preceding one as eggs has occurred, much as indicated for the *Eciton* queen by Hagan's (16) findings. For a reproductive individual of such limited body size to produce potential all-worker broods of around 40,000 individuals at intervals of no more than 40 days (as under the conditions of this investigation) is certainly impressive, but in keeping with the known properties of the doryline adaptive pattern (23, 27).

The conclusion held for *Eciton* (25, 27) that the timing of the queen's reproductive rhythm is not mainly dependent upon endogenous processes, but rather upon a complex set of interrelationships between the queen and the colony situation, seems also valid for *Neiv. nigrescens* as represented in this investigation. In this doryline also, the regularity of brood generations produced by the queen seems attributable to an interplay of exogenous and endogenous factors affecting the queen's reproductive functions. But it is possible that under Nearctic conditions the temporal control of reproductive processes in the doryline queen and colony may differ according to the state of brood development and related feed-back processes keyed to prevalent seasonal conditions in temperature and food supply particularly. This possibility remains to be tested.

Present evidence indicates a termination of reproductive function in the autumn. But the cessation of seasonal reproductive processes in the queen may not occur quite as abruptly as certain cases in this study would indicate. At a time dependent upon locality and altitude, a transitional interval may ensue before full dormancy sets in, when reduced broods are produced by the queen but are lost perhaps through worker cannibalism. Such a condition was possible in the Thicket, Bridge and also the Stone colonies, but seems very unlikely in the cases of the Rock and Creek colonies. The last cases instead support the concept of a definite threshold of exogenous stimulative and trophic conditions below which the queens become non-functional.

The latter interpretation seems to account best for the general results. In Arizona, at an elevation of one mile, the duration of nightly colony raiding seemed to be steadily reduced after late August, particularly through falling temperature which stopped surface activities at increasingly early times. Then the food intake of the colony might clearly undergo a rapid decrease as not only the nightly foraging time became greatly curtailed but also raiding activities became increasingly sluggish. For the colonies involved in the longitudinal surveys of this study, it is probable that functional phases begun under the trophallactic effect of broods maturing after late August would have ended before one month, and would have been succeeded by a non-cyclic, dormant, over-wintering condition. It is probable that this condition would have arisen as a normal seasonal change, even had these colonies retained their queens.

As it was in the autumn of 1956, with the six queenless colonies left in the Station area of Cave Creek Canyon, the prospects for a later resumption of cyclic function must have depended not only upon surviving the winter but also upon the chances of fusion with queenright colonies of their species upon reactivation in the spring.

SUMMARY AND CONCLUSIONS

An investigation was made of behavior and biological function in several colonies of the Nearctic doryline species *Neivamyrmex nigrescens* at an altitude of 1,660 m. in Arizona. In that locality this species is subterranean in its nesting and is nocturnal in its raiding and emigrating, except for surface forays on overcast days. Under appropriate stimulative conditions in the colony, a vigorous raid provides a basis for an emigration during the same night.

These dorylines resemble *Eciton* species of the tropics in having a distinct nomad-statary cycle. This cycle in colony function is dependent upon critical stimulative effects from the successive immense, distinctive all-worker broods, and thus is repetitive in each colony during the active season.

In these army ants each nomadic phase is set off, as in *Eciton*, by a massive stimulative effect introduced upon the eclosion of a mature pupal brood, and is then maintained by stimulative excitation from a new brood in the larval stage. In striking contrast to *Eciton*, the nomadic phase in this *Neivamyrmex* species does not end at larval maturity, but only later when the current brood reaches the early pupal stage. No cocoons are spun by mature worker larvae in this genus, and the high excitatory

effect evidently is continued through an intensive chemotactic excitation characteristic of the developmental period between larval maturity and attainment of the early pupal condition.

Onset of the statary phase is attributable to an abrupt fall in the potency of brood stimulative processes as the brood begins to enter the pupal stage.

In the locality of study, the functional season terminated during September, evidently at a time after the colony queen had ceased to produce mature eggs in large broods. This change may depend upon a seasonally conditioned reduction of stimulative and trophic conditions in the colony below a specific threshold essential for normal reproductive function in the queen.

It is concluded that the factors underlying a regular cyclic function in colonies of *Neivamyrmex nigrescens* during the active season are basically equivalent or even homologous to those operative in *Eciton* species, and that the differences may be considered secondary.

RÉSUMÉ ET CONCLUSIONS

Une enquête a été effectuée sur le comportement et sur la fonction biologique chez plusieurs colonies de l'espèce néarctique de fourmi doryline *Neivamyrmex nigrescens*, à l'altitude de 1 660 m dans l'État américain de l'Arizona. En ces lieux, l'espèce est souterraine quant à ses nids et est nocturne quant à ses raids et déménagements, sauf en cas de razzia par temps couvert. Dans des conditions appropriées d'effet stimulant dans la colonie, un raid très violent sert de base à une émigration au cours de la même nuit.

Ces dorylines ressemblent aux espèces *Eciton* des tropiques, en ce sens qu'elles sont soumises à un cycle caractéristique nomadisme-sédentarité. Ce cycle fonctionnel de la colonie dépend des effets stimulants critiques provenant des immenses couvains distinctifs composés uniquement d'ouvriers, et il se renouvelle donc dans chaque colonie pendant la saison d'activité.

Chez ces fourmis guerrières, chaque phase de nomadisme est déclenchée, comme chez *Eciton*, par un effet stimulant massif dont l'origine se trouve dans l'éclosion d'un couvain nymphal parvenu à maturité, et elle se maintient ensuite par l'excitation stimulante due à un nouveau couvain à l'état larvaire. Par un contraste saisissant avec ce qui se passe chez *Eciton*, la phase nomadique chez cette espèce de *Neivamyrmex* ne prend pas fin lors de la maturité des larves, mais seulement plus tard lorsque le couvain en cours de développement est arrivé au stade nymphal. Chez ce genre, les larves mûres d'ouvriers ne tissent pas de cocons, et la cause excitatrice si vive se poursuit évidemment sous l'influence d'une intense excitation chémotactile, qui est caractéristique de la période de développement située entre la maturité larvaire et l'arrivée de la première forme nymphale.

Le déclenchement de la phase de sédentarité doit être attribué à une brusque diminution de puissance des facteurs stimulants chez le couvain, tandis que celui-ci commence à entrer dans le stade nymphal.

A l'emplacement des études effectuées, la saison d'activité fonctionnelle

s'est terminée dans le courant de septembre, à une époque qui se situe évidemment après que la reine de la colonie eut cessé de produire des œufs mûrs en importants couvains. Ce changement dépend peut-être d'une réduction, en temps opportun, de facteurs stimulants et trophiques dans la colonie, en deçà d'un seuil spécifique qui est essentiel à l'exercice normal de la fonction reproductrice de la reine.

En conclusion, les facteurs qui sont à la base d'une fonction cyclique régulière chez les colonies de *Neivamyrmex nigrescens*, pendant la saison d'activité, sont sensiblement équivalents ou même homologues de ceux qui entrent en opération chez les espèces d'*Eciton*, et les différences peuvent être considérées comme secondaires.

Zusammenfassung.

Verhalten und biologische Function in mehreren Kolonien der nearktischen Ameisen-Art *Neivamyrmex nigrescens* (Unterfamilie Dorylinae) auf 1 660 m. Seehöhe in Arizona wurden untersucht. Dort nistet diese Art unterirdisch und unternimmt ihre Raubzüge und Auswanderungen zur Nachtzeit, ausgenommen Oberflächen-Razzias an bewölkten Tagen. Unter geeigneten Stimulationseffekten innerhalb der Kolonie löst ein kräftiger Raubzug fast unfehlbar Auswanderung noch in derselben Nacht aus.

Diese Dorylinen ähneln tropischen *Eciton*-Arten in ihrem deutlich nomadisch-statischem Zyclus. Dieser Zyclus in der Function der Kolonie hängt von kritischen Stimulationseffekten aufeinanderfolgender, sehr großer, deutlich nur aus Arbeitern bestehender Bruten ab, und wiederholt sich so in jeder Kolonie während der Aktivitätsperiode.

Wie in *Eciton* so wird auch in diesen Dorylinae jede nomadische Phase durch den massiven Stimulationseffekt des vollen Heranreifens einer Puppenbrut eingeleitet und dann durch stimulative Erregung durch eine neue Brut im Larvenstadium wach gehalten. Im auffallenden Gegensatz zu *Eciton* endet jedoch in dieser *Neivamyrmex*-Art die nomadische Phase nicht mit der Larvenreife, sondern erst bis die jeweilige Brut das pupale Stadium erreicht. In dieser Gattung spinnen die reifen Arbeiterlarven keine Cocons ; der starke Erregungseffekt wird offenbar durch intensive chemotaktische Erregung, eine eigenartige Begleiterscheinung der Metamorphose, aufrechterhalten.

An der untersuchten Örtlichkeit endet die Functionsperiode im September, offenbar sobald die Königin der Kolonie aufgehört hat, neue Bruten hervorzubringen. Möglicher Weise hängt diese Veränderung von einer jahreszeitlich bedingten Verminderung der stimulativen und trophischen Bedingungen unter eine kritische Schwelle ab.

Hieraus wird gefolgert, daß die der regelmässigen zyklischen Function in Kolonien von *Neivamyrmex nigrescens* während der Aktivitätsperiode zugrunde liegenden Faktoren im wesentlichen den in der Gattung *Eciton* wirksamen gleichwertig oder selbst homolog sind und daß die Unterschiede als sekundär werden können.

References

1. 1930. Borgmeier (Th.).—Duas rainhas de *Eciton* e algumas outras Formigas Brasileiras (*Arch. Inst. Biol.*, **3**, 21-40).—2. 1939. Nova contribuição para o cohecimento das formigas neotrópicas (*Rev. Entom.*, **10**, 403-428).—3. 1948. Die Geschlechtstiere zweier *Eciton*-Arten und einige andere Ameisen aus Mittel- und Suedamerika (Hym. Formicidæ) (*Rev. Entom.*, **19** [1-2], 191-206).—4. 1949. Formigas novas ou pouco conhecidas de Costa Rica e da Argentina (*Rev. Bras. Biol.*, **9**, 201-210).—5. 1955. Die Wanderameisen der Neotropischen Region (Hym. Formicidæ) (*Studia Entomologia*, Nr. **3**, Petropolis, R. J., Brasil, Ed. Vozes Limitada).

6. 1922. Bruch (C.).—Estudios mirmecológicas (*Rev. Mus. La Plata*, **26**, 175-211).—7. 1924. Descripción de la reina *Eciton* (*Acamatus*) *hetschkoi* Mayr. (*Physis*, **7**, 232-235).—8. 1928. Estudios mirmecológicos (*An. Mus. Nac. Buenos Aires*, **34**, 341-360).—9. 1934. Las formas femeninas de *Eciton* (*An. Soc. Cien. Argent.*, **118**, 113-135).

10. 1932. Creighton (W. S.).—A new female of Acamatus from Texas (*Psyche*, **39**, 73-18).—11. 1950. The ants of North America (*Bull. Mus. Comp. Zool.*, **104**, 1-585).

12. 1910. Emery (C.).—Sous-famille Dorylinæ. Wytsman's Genera Insectorum (*Fasc.* **102**, 1-34).

13. 1899. Forel (A.).—Excursion myrmécologique dans l'Amérique du Nord (*An. Soc. Ent. Belg.*, **43**, 438-447).

14. 1915. Gallardo (A.).—Observaciones sobre algunas hormigas de la República Argentina (*An. Mus. Nac. Hist. Nat. Buenos Aires*, **27**, 1-35).

15. 1950. Gillespie (D. S.), Cole (A. C.).—Measurements in the worker caste of two species of ants (*Amer. Midl. Nat.*, **44**, 203-204).

16. 1954. Hagan (H.).—The reproductive system of the army ant queen, *Eciton* (Eciton). Part 2. The oocyte cycle (*Amer. Mus. Novitates*, No. **1665**, 1-20).

17. 1931. Heape (W.).— *Emigration, migration and nomadism*, Cambridge, Heffer.

18. 1904. Holliday (M.).—A study of some ergatogynic ants (*Zool. Jb., Syst.*, **19**, 292-328).

19. 1912. Ihering (H. von).—Biologie und Verbreitung der Brasilianischen Arten von Ameisen (*Ent. Mitt.*, **1**, 226-235).

20. 1926. Mann (W. M.).—Some new neotropical ants (*Psyche*, **33**, 97-107).

21. 1930. Reichensperger (A.).—Ein Nest und die Kœnigin von *Eciton* (*Acamatus*) *legionis* Sm. (*Zool. Anz.*, **69**, 113-125).—22. 1939. Beiträge zur Kenntnis der Myrmekophilenfauna Costa Ricas und Brasiliens VII, nebst Beschreibung der Königin von *Eciton* (*Acamatus*) *pilosum* (*Zool. Jb. Syst.*, **73**, 367-446).

23. 1938. Schneirla (T. C.).—A theory of army-ant behavior based upon the analysis of activities in a representative species (*Jour. Comp. Psychol.*, **25**, 51-90).—24. 1944. The reproductive functions of the army-ant queen as pace-makers of the group behavior pattern (*Jour. N. Y. Entom. Soc.*, **52**, 153-192).—25. 1949. Army-ant life and behavior under dry-season conditions. 3. The course of reproduction and colony behavior (*Bull. Amer. Mus. Nat. Hist.*, **94**, 5-81).—26. 1956. A preliminary survey of colony division and related processes in two species of terrestrial army ants (*Insectes Sociaux*, **3**, 49-69).—27. 1957. Theoretical consideration of cyclic processes in doryline ants (*Proc. Amer. Phil. Soc.*, **101**, 106-133).—28. 1957. A comparison of species and genera in the ant subfamily Dorylinæ with respect to functional pattern (*Ins. Soc.*, **4**, 259-298).

29. 1954. Schneirla (T. C.), Brown (R. Z.), Brown (Frances).—The bivouac or temporary nest as an adaptive factor in certain terrestrial species of army ants (*Ecol. Monogr.*, **24**, 269-296).

30. 1927. Smith (M. R.).—A contribution to the biology and distribution of one of the legionary ants, *Eciton schmitti* Emery (*Ann. Ent. Soc. Amer.*, **20**, 401-404).—31. 1942. The legionary ants of the United States belonging to *Eciton subgenus Neivamyrmex* Borgmeier (*Amer. Midl. Nat.*, **27**, 537-596).

32. 1905. Vosseler (J.).—Die ostafrikanische Treiberameise (Siafu) (*Pflanzer*, *Jg.* 1, Nr. **19**, 289-302).

33. 1900. Wheeler (W. M.).—The female of *Eciton sumichrasti* Norton, with some notes on the habits of Texas Ecitons (*Amer. Nat.*, **34**, 563-574).—34. 1908. The ants of Texas, New Mexico and Arizona (*Bull. Amer. Mus. Nat. Hist.*, **24**, 399-485).—35. 1913. *Ants, their Structure, Development, and Behavior*, New York, Columbia Univ. Press).—36. 1921. Observations on army ants in British Guiana (*Proc. Amer. Acad. Arts Sc.*, **56**, 291-328).

37. 1901. Wheeler (W. M.), Long (W. H.).—The males of some Texas Ecitons (*Amer. Nat.*, **35**, 157-173).