

Recruitment and Food-Retrieving Behavior in *Novomessor* (Formicidae, Hymenoptera)

I. Chemical Signals*

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Summary. 1. *Novomessor cockerelli* and *N. albisetosus* have been considered by previous authors to be individual foragers. This investigation, however, has demonstrated that workers of both species employ recruitment techniques when they encounter large prey.

2. *Novomessor* workers usually carry large food items in a cooperative action directly to the nest.

3. The chemical communication system employed during foraging was investigated in laboratory and field experiments. Secretions released from the poison gland proved to be the most effective recruitment signal.

4. In order to summon nestmates to large food objects, *Novomessor* employs the following two different recruitment techniques.

Short-range recruitment: After discovering the prey, the scout releases poison gland secretion into the air. Nestmates already in the vicinity are attracted from as far away as 2 m and move upwind toward the prey.

Long-range recruitment: If short-range recruitment does not attract enough foragers, a scout lays a chemical trail with poison gland secretion from the prey to the nest. Nestmates are stimulated by the pheromone alone to leave the nest and follow the trail toward the prey.

5. The trail pheromone is short-lived, and trail laying consequently does not lead to mass communication. Instead, the pheromone releases a short pulse of outrushing ants, usually numerous enough to subdue the prey and to carry it home when the ants act jointly.

6. In several field experiments, we demonstrated that these recruitment and prey-retrieving techniques enable *Novomessor* to counteract interference competition by mass-recruiting ant species.

* Dedicated to Prof. Dr. M. Lindauer on the occasion of his 60th birthday

Introduction

In most ecological studies of foraging behavior in ants, surprisingly little attention has been given to the social organization of recruitment and food-retrieving behavior. Yet the possession of one kind of recruitment system as opposed to another reflects adaptations by individual species to a particular foraging strategy. As a consequence, the ecology of most ant species cannot be fully understood, and may even be misconstrued without a detailed knowledge of their social food-retrieving mechanisms. This special requirement of behavioral analyses has been exemplified by recent studies of the foraging strategies of *Novomessor cockerelli*, a very common ant in the southwestern deserts of the United States of America. Whitford (1976) as well as Davidson (1977), adopting the terminology of Bernstein (1975), characterize *N. cockerelli* as "individual foragers... where the individuals search and collect food independent of each other," as opposed to "recruit foraging, where individual scouts search independently, but the actual collection of food is a highly coordinated group effort" (Bernstein, 1975). Our field studies and experimental analyses of the foraging and recruitment behavior of *Novomessor* do not support this characterization. We have discovered that *Novomessor* employs a rather complex communication system employing chemical (part I) as well as vibrational signals (part II) to organize the retrieval of prey objects. Further, our ecological studies demonstrate that this particular foraging strategy is an effective adaptation in interspecific foraging competition.

Material and Methods

The genus *Novomessor* comprises only three species: *N. albisetosus*, *N. cockerelli*, and *N. manni*. The first two species are rather common in the Southwestern United States and Northern Mexico (Creighton, 1950, 1955) while the latter has been collected along the Pacific coast of Mexico (Kannowski, 1954).

Novomessor was originally described under *Aphaenogaster*, and recently W.L. Brown (1974) suggested that it should be placed back in that genus. In the course of our comparative study of communication mechanisms in *Novomessor*, we discovered an exocrine gland, which is associated with a characteristic cuticular structure. Since this gland seems to be a very distinct character trait of *N. cockerelli* and *N. albisetosus*, we suggested that it should be given considerable weight in the future taxonomic assessment of the species possessing it (Hölldobler et al., 1976).

Our field studies with *N. cockerelli* were conducted during the summer months of 1974, 1975, and 1977 in the Chihuahuan desert between Portal, Arizona, and Rodeo, New Mexico. *N. cockerelli* usually were active during the night, starting to leave the nests late in the afternoon and extending activity into the early morning (Wheeler and Creighton, 1934; Whitford and Ettershank, 1975). Foraging usually ceased by 8–9 a.m., but occasionally continued until 10–11 a.m., especially after heavy rainfalls or during overcast. Most field experiments were performed in the morning, late afternoon, and evening. Field observations with *N. albisetosus* were conducted at or near the Cave Creek Ranch (Portal) at the foot of the Chiricahua mountains. As Creighton (1950) pointed out, nests of *N. albisetosus* are found on the lower slopes of desert ranges, whereas *N. cockerelli* usually inhabits the flats of the deserts. Although populations of both species sometimes overlap, on most parts of their range they seem to be geographically well separated.

For our laboratory experiments, *Novomessor* colonies were excavated and housed in different types of artificial nests. We also raised colonies from single founding queens. The statistical evaluation of the experiments was based on the Student's *t*-test and χ^2 -test. The null hypothesis was

considered to be rejected when $P < 0.05$. Additional methodological details will be given with the description of the individual experiments.

Results

Although *Novomessor* is frequently considered to be a harvester ant, it is really omnivorous (Creighton, 1950; Whitford, 1978). Seeds and other plant material comprise only part of its diet; many *Novomessor* foragers return to their nest carrying termites, alates, and reproductives of other ant species captured during nuptial flight and colony-founding activities, and other insects or insect parts, some of which are of considerable size. Once we even observed *N. cockerelli* workers cutting large parts from a dead ground dove nestling, and retrieving these meat fragments in a coordinated group action very rapidly to their nest. Although *Novomessor* frequently forages individually, such group-retrieving behavior, where 2–10 or even more workers cooperate in transportation of large prey objects, seems to be an important part of their foraging strategy. Three to five *N. cockerelli* workers are easily able to carry a grasshopper with a dry weight of 200 mg. This equals the dry weight of approximately 240 termites. However, about 240 *Novomessor* foragers would be needed for the individual retrieval of such insects.

Three to five *Novomessor* workers, when jointly transporting a freshly killed grasshopper of ca. 750 mg (wet weight), need 5.3 ± 0.9 min ($n=10$) to move the prey over a distance of 7 m. An individual forager, carrying a termite (ca. 3 mg), needs for the same distance 1.3 ± 0.2 min ($n=10$) (soil temperature 27° C). Although the group-retrieving process is more time-consuming, it is obviously a much more economic way to gain energy, provided large prey objects are available. The existence of such well-developed cooperative food-carrying behavior suggests that *Novomessor* employs specific communication techniques that enable it to utilize large prey objects. The following sections describe how we tested this hypothesis.

I. Chemical Communication in N. cockerelli and N. albisetosus

1. Laboratory Experiments

For the first set of our laboratory experiments, colonies of *N. cockerelli* and *N. albisetosus* were housed in artificial nests similar to those described in Hölldobler (1976a, p. 5). Sand-filled terraria comprised the inner nest of the colony. Each nest terrarium was connected with a foraging arena (70 cm in diameter) by a 50 cm long bridge. Several thousands of workers, as well as abundant brood and queen, were successfully cultured in these nests.

In the center of the foraging arena of an *N. albisetosus* nest, a freshly killed cockroach (*Nauphoeta cinerea*) was pinned to the ground. When individual ants, which discovered this food source, were prevented from returning to the nest terrarium, no increase of foragers running over the bridge toward the arena

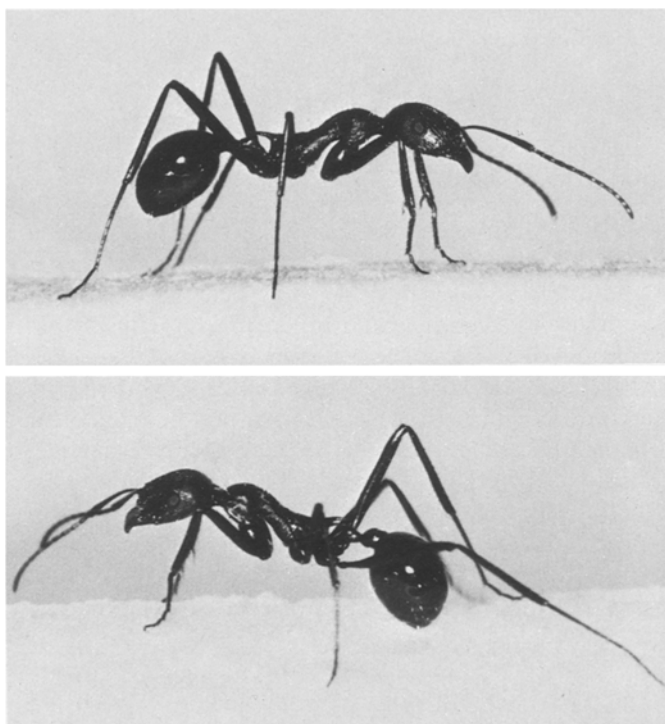
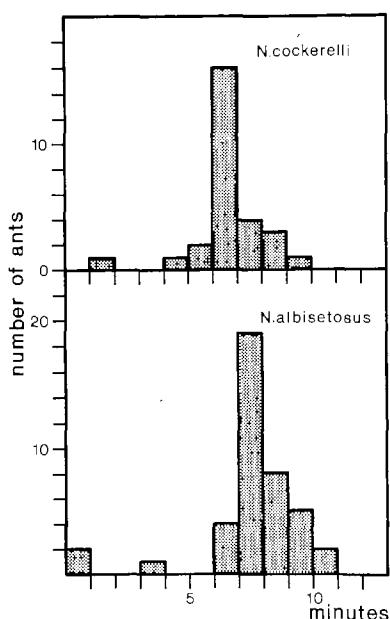


Fig. 1. Above: *N. albisetosus* worker with its abdomen in ordinary position moving over the nest bridge into the foraging arena. Below: After discovering a large prey object, the scouting ant returns to the nest, dragging the tip of its abdomen over the surface

was noted. In a typical experiment, the first ant to discover the prey was marked; all other scouting ants in the arena were removed. After several unsuccessful attempts to transport the cockroach, the scout ant typically ran excitedly in several loops around the bait, repeatedly touching it with its antennae and tapping the tip of its gaster on the substrate. Then the ant ran toward the arena exit and over the bridge to the nest. At this time, the change of its locomotory behavior was very obvious. Its gaster was bent downward and the tip dragged over the ground (Fig. 1). Almost invariably after the ant had entered the nest entrance, nestmates streamed out in a column over the bridge into the arena to the bait within seconds. Obviously the scout recruited nestmates to the newly discovered prey object, which seemed to be too heavy to carry home on her own. Similar results were obtained with *N. cockerelli*. Typical case histories for both species are illustrated in Figure 2. When the cockroach remained pinned down, workers repeatedly ran back to the nest and recruited additional foragers. However, when the needle was removed, several ants jointly lifted the roach and carried it in a well-coordinated fashion over the bridge into the nest (Fig. 3).

Further observations of the recruitment process were conducted inside the nest chambers of special observation nests, similar to those described by Hölldo-

Fig. 2. Number of ants running over the bridge leading from the nest to the foraging arena. Counts are reported for 5-min periods before and after a scout laying a chemical trail had crossed the bridge. As can be seen, the number of ants running toward the foraging arena increased dramatically during the second period



bler (1971a, p. 126). Queenright colonies consisting of 200–500 workers and various numbers of brood were kept for several weeks in these nests. The nest chambers were covered with a red glass plate through which the ants could be observed. When a recruiting scout entered the nest chamber, some nestmates were immediately attracted from as far away as 5 cm and subsequently left the nest, running in the direction from which the scout had come. Inside the nest, the recruiting ant rushed to several workers, staying less than a second at any single ant while swiftly antennating them. Then she usually stopped, groomed herself, and finally returned to the food source, often accompanied by another 5–10 ants that followed closely behind. In most instances, the recruiting ant spent less than a minute inside the nest chamber. No specific motor display (such as wagging or jerking) was observed.

These behavioral observations strongly suggested to us that *Novomessor* workers deposit a recruitment pheromone from gland openings at the abdominal tip. To localize the anatomical source of this pheromone, we dissected and prepared extracts from the following body parts, considered to be the most likely repositories of pheromones: the hindgut, Dufour's gland, poison gland, and tergal gland. The latter is a recently discovered bilateral glandular complex located under the third tergite (Hölldobler et al., 1976). For the following experiments, these organs were freshly dissected from single workers and smeared with the tips of hardwood applicator sticks over a cardboard floor of the arenas, to create artificial trails of 80 cm in length. The number of workers that followed each trail during the first minutes was then recorded. During the tests, two trails, a test trail and a control trail, were offered simultaneously, with both starting at the same spot at the nest entrance but then deviating

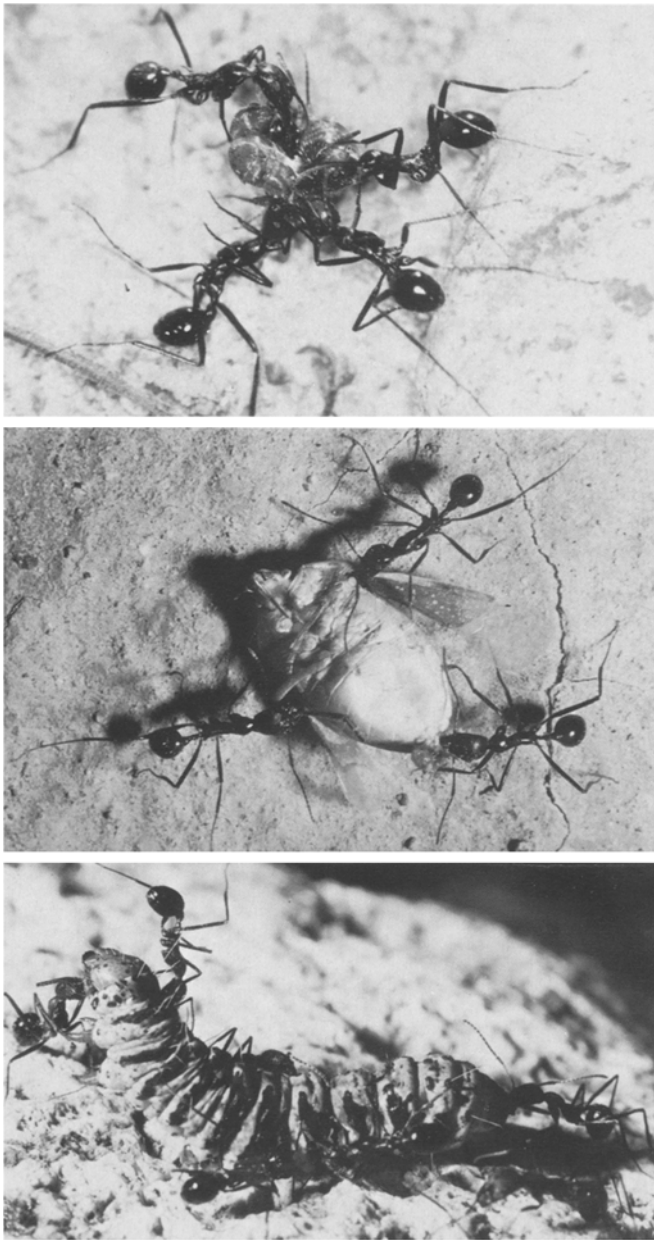


Fig. 3. Group retrieval of prey objects: *Above:* *N. cockerelli* workers have captured a freshly mated queen of *Pogonomyrmex*. *Middle:* *N. cockerelli* jointly retrieve a bug. *Below:* *N. albisetosus* have captured and jointly retrieve a lepidopteran caterpillar

so that the test trail was drawn along one side of the 15 cm wide cardboard and the control trail along the other side. Thus both trails ran 15 cm apart (Fig. 4). The sides of the trails were regularly alternated and for each test a new cardboard surface was used.

The results, presented in Table 1, were quite conclusive: Dufour's gland secretion elicited almost no noticeable behavioral response; hindgut material and, especially, tergal gland secretion induced an increase in random locomotory activity, while the latter substance also elicited some trail following. However, this response was very erratic and not at all as precise and dramatic as the one observed with poison gland secretion. Only material from the poison gland released the typical outrush of a group of workers that ran up to the ends of the artificial trails (Fig. 4). The poison gland of both *Novomessor* species is relatively large in comparison with the Dufour's gland. Its secretion has a distinctly sweet smell. The sting is reduced and certainly not functional as a weapon.

Our behavioral observations indicated that the recruitment pheromone is very short-lived. In fact, the poison gland secretion released no persistent trail-following behavior, but rather an outrush of a group of workers that moved in a phalanx-like formation along the trail. The persistence of the recruitment pheromone was tested in the following way: The secretion of one poison gland was smeared along a 30 cm long trail on a piece of cardboard; then periods of 1, 2, 3, 4, or 5 min elapsed before the cardboard was placed into the nest arena. The results clearly demonstrated that after 3 min the effectiveness of the pheromone was greatly reduced and after 4 min it was almost completely gone (Fig. 5). To avoid adaptation effects between each test, at least 30 min had to elapse before a colony was tested. In addition, the different samples were offered in a randomized manner.

Next, we undertook experiments to determine whether the poison gland secretion contains both a short-lived, stimulating and a longer-lasting, orienting component, similar to that found in *Atta texana* (Moser and Silverstein, 1967). A poison gland trail (30 cm long) was drawn along the side of a piece of cardboard; the trail extended from the middle to the end. As a control, a water trail was drawn on the opposite side and also extended from the middle to the end of the cardboard. After 5 min had elapsed, the board was placed into the nest arena, but just prior to this act the secretion of a freshly dissected poison gland was smeared along a trail 30 cm on both sides of the cardboard from the beginning to the middle where they were joined with the 5-min-old trails. Thus, the ants would be stimulated to follow a trail. But we ask: would they continue along the paths when reaching the midpoint? As can be seen from Table 2, the *N. albisetosus* workers did not continue to follow the old trails. The poison gland trail was as ineffective as the control (water) trail. Thus there seems to be no lasting orientation component in the poison gland secretion.

In *Pogonomyrmex badius*, which also employs poison gland secretion as a recruitment signal, circumstantial evidence suggested that Dufour's gland secretion can function as a long-lasting orientation cue (Hölldobler, 1971b; Hölldobler and Wilson, 1970). We therefore set out to determine whether this might

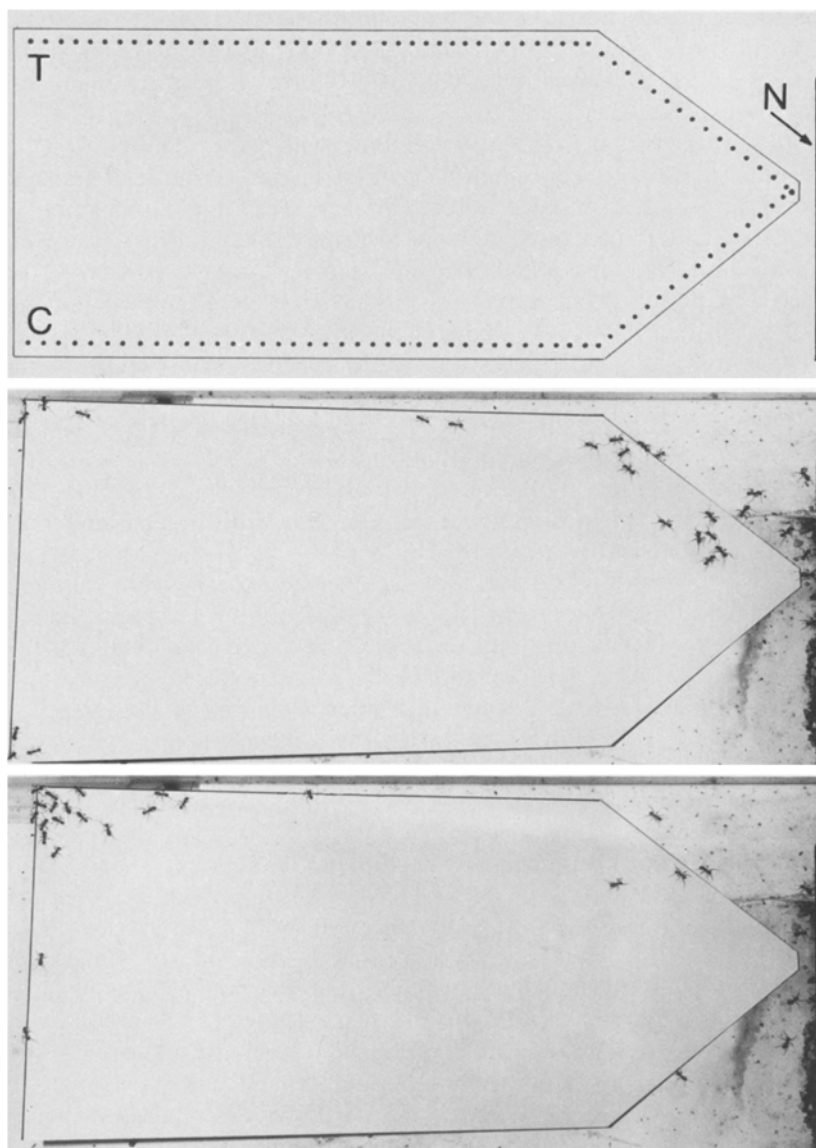
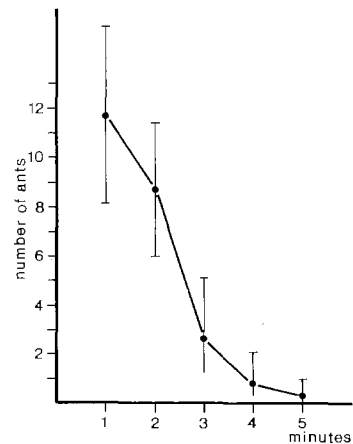


Fig. 4. Laboratory tests of the recruitment pheromone. *Above:* Schematic illustration of the test arrangement. Test trail (*T*) and control trail (*C*), both originating from the nest entrance (*N*), are drawn along either of both sides of a piece of cardboard. *Middle:* Seconds after the poison gland trail was offered, ants rushed out of the nest and followed the trail to its end. None or only very few ants followed the control trail. *Below:* Shortly afterward, the outrush of ants ceased, indicating that the pheromone is short-lived

Table 1. Artificial trails composed of secretions of different abdominal glands were drawn for distances of 80 cm from the nest entrance. During the next 5 min, all ants were counted that followed the trails to the end. Trails consisting of distilled water alone were used as controls. In one series, trails consisting of poison gland secretions and tergal gland secretions were offered simultaneously (last column). The mean (\bar{x}) with standard deviation (SD), range of the number of responding workers, and the number of replications (n) are given

	Poi- son gland	Control	Du- four's gland	Control	Hind- gut	Control	Ter- gal gland	Control	Poi- son gland	Ter- gal gland
<i>Novomessor cockerelli</i>										
\bar{x}	19.3	0	0.5	0.2	0.6	0	0.9	0	13.6	3.2
SD	6.6	0	0.5	0.4	0.9	0	1.1	0	5.7	2.5
Range	12-34	0	0-1	0-1	0-3	0	0-3	0	8-24	0-7
<i>n</i>	10		10		10		10		10	
	<i>P</i> < 0.001									
<i>Novomessor albigetosus</i>										
\bar{x}	19.7	1.0	0.4	0.5	0.1	0	3.0	0.2	19.4	2.9
SD	8.1	1.2	0.7	0.8	0.3	0	1.7	0.4	6.1	3.5
Range	8-36	0-3	0-2	0-2	0-1	0	1-6	0-1	10-26	0-9
<i>n</i>	10		10		10		10		10	
	<i>P</i> < 0.001									

Fig. 5. Persistency of the poison gland pheromone. Trails (30 cm long) were drawn with the secretion of one gland of an *N. albigesotus* worker. The trails were introduced into the test arena after periods of 1, 2, 3, 4, or 5 min elapsed. During the following minute, the number of ants following the trail were counted. The mean and standard deviations of ten replications for each period are given



also be the case for *Novomessor*. A fresh poison gland trail was drawn along both sides of a piece of cardboard to midpoint (30 cm); then on one side the trail was continued with the secretion of a crushed Dufour's gland and on the other side with water. The results were clear: all *N. albigesotus* workers became disoriented when they passed the midpoint on both sides (Table 2).

Table 2. Fresh artificial trails composed of poison gland secretions were drawn from the nest entrance of *N. albisetosus*, and after 30 cm were continued for another 30 cm by either a 5-min-old poison gland trail (test A) or a Dufour's gland trail (test B). In the control for both tests, the fresh poison gland trail was continued by a watery trail. The number of ants following the fresh trails and subsequently continuing on the second half of the trails was counted during a 2-min period

	Test		Control	
	Ants follow fresh poison gland trail	Ants continue on old poison gland trail	Ants follow fresh poison gland trail	Ants continue on watery trail
A	16.3 ± 6.9	0.4 ± 0.8	12.0 ± 3.6	0.7 ± 1.1
	n = 7		n = 7	
B	12.0 ± 5.2	0.2 ± 0.4	14.2 ± 3.1	0
	n = 7		n = 7	

The Dufour's gland secretion obviously does not function as a orientation cue. Similar results were obtained with *N. cockerelli*.

Up to this point we had used only relatively short artificial trails; we therefore conducted another series of experiments in which 4 m long trails were each drawn with the secretion of one poison gland on a cardboard platform starting from the nest entrance. The effectiveness of such trails lasted 4.7 ± 1.9 min. During this time, 25.0 ± 12.4 ants rushed out along the trails and 21.4 ± 12.2 followed them to their ends ($n=5$). This result demonstrates that the poison gland secretion is not only a powerful stimulating signal but also a sufficient guiding cue to a more distant target area.

Finally, we tested the specificity of the recruitment trail pheromone of *N. albisetosus* and *N. cockerelli*. When two trails, drawn with the secretion of one poison gland each, taken from *N. albisetosus* or *N. cockerelli*, respectively, were offered simultaneously to an *N. albisetosus* colony, workers responded to both pheromones by equally strong trail following. However, when the trails were presented simultaneously to *N. cockerelli*, workers of that species responded only to the trail pheromone of their own species. Thus we detected a partial specificity: *N. cockerelli* responds only to its conspecific recruitment pheromone, while *N. albisetosus* does not discriminate between its own trail substance and that of the second species. Neither species responded to poison gland trails of several *Pogonomyrmex* species.

In summary, we can say that the trail communication system in *Novomessor* is well designed for the rapid recruitment of a limited number of workers to a target area, but it is not designed to organize an outpouring of masses of foragers, as is the case in the typical chemical mass communication system of *Solenopsis* (Wilson, 1962) and *Pogonomyrmex* (Hölldobler, 1976 a). Further details of this recruitment system were analyzed in a series of field experiments.

2. Field Experiments

Most of the field experiments were carried out with *N. cockerelli*. Comparative studies with *N. albigulosus* did not reveal significant differences. We will therefore primarily report our results on *N. cockerelli*. During the activity periods, we observed *N. cockerelli* workers as they foraged in all directions around the nest, covering different distances up to ca. 35 m away from the nest. In most cases, individual foragers returned to the nest carrying plant material or insects. Occasionally, however, groups of *Novomessor* workers carried large prey objects in concert. This coordinated group action is an important part of the behavioral repertoire of *Novomessor*. Although it can also be observed in other ants, for example, in some species of *Myrmecocystus* and *Formica*, it is not at all a common feature of ant behavior. For example, we offered a water-soaked raisin, each 1 m from the entrance of a nest of *N. cockerelli*, *Pogonomyrmex barbatus*, *P. rugosus*, and *P. maricopa*. Often within seconds, 2–4 *Novomessor* workers discovered the bait and carried it jointly into the nest. In contrast, all *Pogonomyrmex* species usually could not manage to retrieve the raisin within an hour, although ten or even more workers would have gathered around the bait, trying to cut off little pieces, which they then carried away individually. As demonstrated previously in laboratory studies, the field experiments confirmed that this group retrieval of large prey is mediated with a specific recruitment technique.

In a typical experiment, we pinned a freshly killed grasshopper (ca. 4 cm long) to the ground 6 m from a nest of *N. cockerelli*. Soon afterward, one of the individual foragers discovered the prey, antennated it and then bit into it in an attempt to pull it away. During this first phase, lasting a minute or longer, the ant quite regularly produced one or a few stridulatory chirps (for a detailed analysis of the stridulatory signals, see part II of this study: Markl and Hölldobler, 1978). Often, but not always, this phase was interrupted by one or a few looping runs a few centimeters away from the bait and back to it. As in the laboratory experiments, the ant in the field frequently touched the ground with the tip of its gaster. Shortly thereafter, we observed that other workers which happened to come by were attracted from as far as 1–2 m to the prey, orienting preferentially against the wind. This part of the recruitment process we call *short-range recruitment*. When the prey could not be moved by its discoverer and the recruits, one of the ants headed straight home to the nest, touching its abdominal tip to the ground. After this individual arrived at the nest, several other workers soon departed and oriented along the track where the nestmate came from. This process we call *long-range recruitment*. In most cases, long-range recruitment was employed only when workers attracted by short-range recruitment could not retrieve the food by themselves. A typical case history of these two phases of the recruitment system is given in Figure 6.

a) Short-Range Recruitment. As standardized bait for analyses of recruitment mechanisms, we used a water-soaked raisin, which proved to be an attractive food object for *Novomessor*. The raisin was fixed on the ground with a pin or to the screw-top of a glass vial with a thin strip of masking tape. This

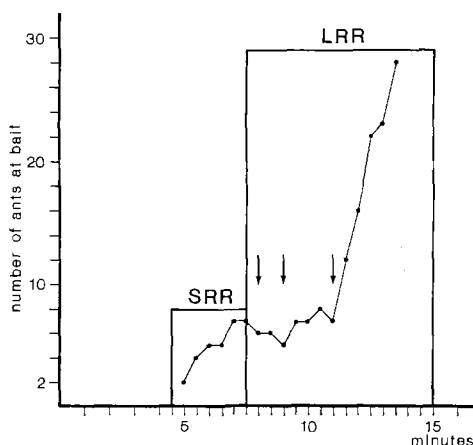


Fig. 6. Short-range recruitment (SRR) and long-range recruitment (LRR). A freshly killed grasshopper was pinned to the ground 6 m from the nest of *N. cockerelli*. Soon after the first *Novomessor* worker discovered the prey, others were attracted too (SRR). When the first scouts returned to the nest, laying a trail (arrows), the number of recruits at the bait increased dramatically (LRR)

prevented the ants from carrying off the raisin; even as many as a dozen workers could not move it unless they cut it to pieces, a process taking well over 15 min.

The first series of experiments were designed to test how much the efficiency of short-range recruitment varies with the distance of the bait from the nest, so as to determine the possible effects of prevailing wind currents and wind directions. Since the quantitative data are reported in Markl and Hölldobler (1978) (part II of this study), we will only summarize the results here. Short-range recruitment is significantly more efficient in the close vicinity (up to a few meters) of the nest and when the wind blows over the bait toward the nest. Even if no wind is blowing, the efficiency is still better than when the wind blows in the opposite direction, that is, over the nest toward the bait. This result, together with our observations that recruited workers tend to approach the bait upwind, strongly suggested to us that short-range recruitment is mediated by a pheromone.

We next attempted to localize the glandular source of the chemical signal of short-range recruitment. The major exocrine glands, i.e., mandibular glands, metapleural gland, tergal gland, Dufour's gland, poison gland, and hindgut, were dissected out of workers of *N. cockerelli*. For replication, the organs of a kind from five workers were crushed in 0.2 ml ether. Aliquots of 5 μ l of ether solution of the glandular secretions were then applied on pieces of filter paper (25 mm²), which were exposed at 2 m and 6 m distance from the nest entrance of an *N. cockerelli* colony in upwind direction (wind blowing over paper toward nest; wind speed 0.1–0.5 m/s, measured with a Datametrics airflow meter). All ants crossing a circle of 10 cm in diameter around the test paper were caught and counted during a 2-min period. The ants were trapped with a glass vial that was carefully placed over them, in order to prevent them from being disturbed and releasing alarm or defensive secretions. As can be seen from Table 3, the poison gland secretion elicited by far the strongest attraction response. Most ants approached the paper by moving upwind. Ants as far away as 2 m responded to the chemical signal by suddenly changing their

Table 3. Ether solutions of different glandular secretions of *N. cockerelli* were applied on pieces of filter paper and exposed at 2 m and 6 m from the nest entrance of *N. cockerelli* in upwind direction. All ants crossing a circle of 10 cm in diameter around the test paper were caught and counted during a 2-min period. For each test, the mean and standard deviation of eight replications are given

Distance from nest	Number of ants attracted by secretions from					
	Poison gland	Dufour's gland	Hindgut	Tergal gland	Mandibular gland (heads)	Metapleural gland (thoraces)
2 m	17.7±9.9	0.6±0.9	1.5±1.7	2.4±2.5	0.5±0.8	0.3±0.5
6 m	5.1±3.3	0.1±0.3	0	0.4±1.1	0	0

course, then moving through a pattern of zig-zag loops toward the odor source, their antennae vigorously waving. Secretions from the metapleural gland (thoraces), Dufour's gland, mandibular gland (heads), and hindgut released almost no response, except that the latter three substances elicited some aggressive attraction (gaping of mandibles) when ants passed within 10–15 cm of the odor source. Although tergal gland secretion did not release an oriented attraction response, it apparently was sensed as far as 1 m away and elicited a frantic, seemingly erratic running behavior, especially when offered near the nest entrance. We suspect that the tergal gland secretion functions as a 'panic alarm releaser' particularly designed to organize defensive actions against army ants' raids (Hölldobler, in preparation).

From these results we conclude that the chemical short-range recruitment signal originates from the poison gland. Obviously, scout ants that first discover the prey release the recruitment pheromone while next to the prey and/or during the circling runs around the prey.

b) Long-Range Recruitment. The results of our laboratory experiments and field observations suggested that long-range recruitment is also mediated by the discharge of the poison gland pheromone. Recruiting ants deposit the substance along a trail and in this form stimulate and guide nestmates to the target area. Experiments in the field confirmed this: 3 m long artificial trails drawn with poison gland extracts from the nest entrance outward elicited a strong following response, with many of the ants running along the trail to its end. No comparable responses could be obtained with trails drawn with other glandular secretions.

Once a certain number of ants has gathered around the bait, long-range recruitment ceases. Most of the ants attempt to move the prey, others swarm around it and chase away possible competitors, such as *Pogonomyrmex* or *Myrmecocystus*. In order to find out whether there is a regulatory feedback involved, we removed ants from the bait after long-range recruitment had ceased. One typical case history out of ten is given in Figure 7. During these experiments, water-soaked raisins were pinned to the ground at 6 m distance from the nest. Every 60 s, a count was taken of the number of ants at the bait and of the ants returning to the nest laying a trail during this time. As documented in

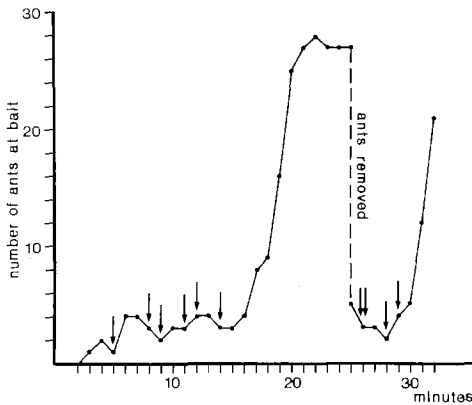


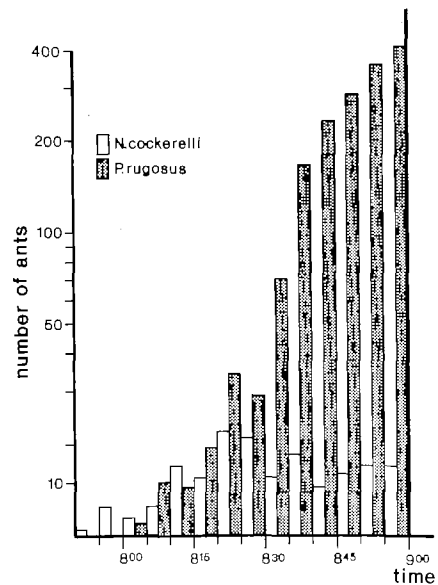
Fig. 7. Regulatory feedback between number of ants at bait and long-range recruitment activity. Bait (water-soaked raisin) was pinned to the ground at 6 m distance from an *N. cockerelli* nest, and the number of *Novomessor* workers assembled at the bait were continuously counted. Arrows indicate when one worker returns to the nest, trailing. Trailing stopped when ca. 25 ants had gathered around the bait. After we removed 20 workers, trailing recurred

Figure 7, long-range recruitment stopped when ca. 20–25 workers had gathered around the bait. But when we removed ca. 20 of these ants, long-range recruitment recurred and, shortly afterward, newcomers arrived at the bait. Some additional pilot experiments indicated that this response depends on the size of the prey. More workers assembled at a larger bait (six raisins) before long-range recruitment ceased. Of course, when the raisin was not tethered to the ground, short-range recruitment was ordinarily sufficient to summon enough foragers for the quick retrieval of the bait. However, there is considerable variability in the conditions under which long-range recruitment is initiated. In 33 experiments, where a fixed raisin was offered 6 m away from the nest entrance, *N. cockerelli* foragers started with long-range recruitment after 3.5 ± 1.7 nestmates (range 1–8) had gathered at the bait. Only in three cases did we observe that the original discoverer left the bait for long-range recruitment even before an additional nestmate had been attracted. Thus, a newly discovered prey was rarely left without a guard.

II. Ecological Significance of Food Recruitment in *Novomessor*

A mature nest of *N. cockerelli* often consists of various (2–4) nest mounds separated by up to several meters (0.5–5 m). Each mound has an independent exit, but workers regularly commute between them. In our study area, the mean distance between adjacent *N. cockerelli* colonies was 22.9 m (SD=6.1 m; $n=20$). Many *N. cockerelli* mounds were relatively close to *Pogonomyrmex* nests, sometimes less than 2 m away. The mean distance to the nearest *Pogonomyrmex* neighbor (*P. barbatus*, *P. maricopa*, *P. rugosus*) was 6.7 m (SD=3.0 m; $n=20$). Although the foraging activity rhythm of *N. cockerelli* is generally different from that of most of the *Pogonomyrmex* species (Whitford and Ettershank, 1975), there exist broad overlapping time periods in the morning and late afternoon. In a total of 14 experiments, we offered densely packed seeds (millet) on patches (20 × 20 cm) 6 m away from an *N. cockerelli* nest; a relatively weak recruitment response was noted each time (a representative example is given

Fig. 8. Recruitment of *N. cockerelli* and *P. rugosus* to a patch of densely packed seeds. Distance of *N. cockerelli* nest to seed site 10 m; *P. rugosus* 20 m. This is one representative example of a total of 11 similar tests with approximately the same results (7 *P. rugosus* / *N. cockerelli*; 4 *P. barbatus* / *N. cockerelli*). The number of workers arriving at the seed site were counted during successive 5-min-intervals



in Fig. 8). When *Novomessor* had to compete with *P. barbatus* or *P. rugosus* for the same seed source, both *Pogonomyrmex* species invariably recruited more efficiently and thus exploited the seed patch considerably faster than *Novomessor*, even though their nests were often further away (Fig. 8). The picture was quite different, however, when we offered a raisin, a freshly killed cockroach or grasshopper, or any other large food object rather than seeds. Although *Pogonomyrmex* foragers were attracted to these baits, they were unable to retrieve them in cooperative action. *Novomessor*, on the other hand, very effectively recruited nestmates to the food items, displaced *Pogonomyrmex* workers by overt aggression and quickly carried away the prey. But *Pogonomyrmex* is not the main competitor of *Novomessor* for these large prey items. Considerably more important are several of the small mass-recruiting species, such as *Forelius foetidus*, *Iridomyrmex pruinosus*, *Solenopsis xyloni*, and *Monomorium minimum*. Although the workers of these species do not carry large food items into their nest, but instead dissect them at the spot into little pieces and retrieve on an individual basis, they are nevertheless fierce competitors of *Novomessor*. All these species are able to displace *Novomessor* from the prey object with the aid of a powerful repellent secretion. In *F. foetidus* and *I. pruinosus* the repellent substance originates from the anal gland, in *M. minimum* and *S. xyloni* from the poison gland (Hölldobler, in preparation). As soon as an individual forager of one of these species discovers the prey object, it immediately returns to the nest, laying a highly effective mass-recruitment trail. Within seconds, a huge number of nestmates rushes along this trail toward the newly discovered food source. Having arrived there, they discharge the repellent secretion as soon as they come in contact with *Novomessor*. This obviously irritates *Novomessor* intensely, because they literally jump back and wipe their mouthparts

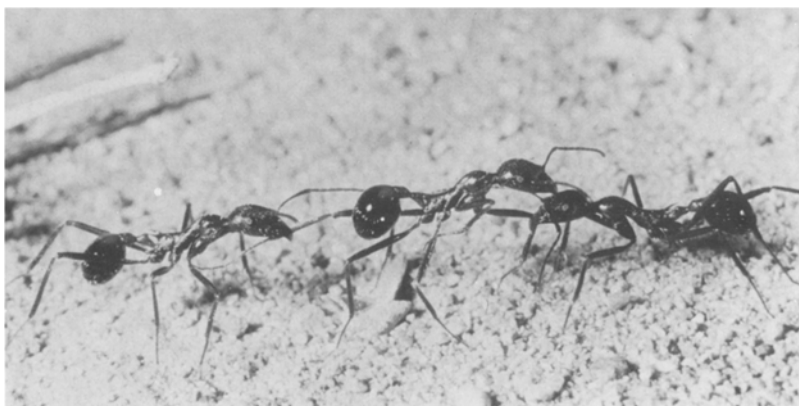


Fig. 9. During an antagonistic encounter between members of two neighboring *N. cockerelli* colonies, two ants hold one foreigner, preventing it from having access to a prey object

and antennae on the ground. Thus, once *Forelius* or any of the other 'repellent strategists' (Hölldobler, 1973) have occupied the prey, *Novomessor* has permanently lost its access to the food source. The only chance *Novomessor* has is to move the prey from the spot quickly before it can be occupied by the repelling competitors. Even if *Novomessor* succeeds in moving the food item over short distances, this may prevent its loss to the mass-recruiting species. For example, when *Novomessor* and *Forelius* scouts simultaneously discover the prey, the latter have to return to the nest in order to recruit nestmates along the trail to the food source. *Novomessor*, on the other hand, can often attract nestmates more quickly by short-range recruitment, enabling it to move the prey away before its competitors arrive. Thus the trail of mass-recruiting species may lead to an empty spot. In a total of 46 experiments when the bait was pinned to the ground, the *Novomessor* lost it in 19 cases to one of the competitors (*I. pruinosus*, *F. foetidus*, *S. xyloni*, *M. minimum*) within 30 min (mean 12.1 ± 5.4 min).

The recruitment system of *Novomessor* also plays a role in intraspecific competition. Although few aggressive interactions between *N. cockerelli* workers can be observed in the field, these ants clearly discriminate against members of neighboring conspecific colonies, and they show agonistic displacement behavior when workers of neighboring nests meet at the same bait. We observed this kind of interaction in a series of experiments in which large bait (cellulose soaked in honeywater) together with the attending foragers from the home range of one colony was picked up and placed into the home range of a neighboring colony. Soon scouts of the second colony discovered the bait and foreign ants and ran back to their own nest, initiating long-range recruitment. Each scout returned to the bait with 15–20 nestmates following closely behind. Once the group arrived, they immediately pulled the foreign ants from the food, dragging them 1 m or more away and holding them in place. Usually two to three workers held one foreign ant (Fig. 9). Meanwhile, other scouts recruited reinforcements, so that foragers of the second colony were soon able

to take over the bait completely. Most intraspecific aggressive interactions on the bait consisted of owners restraining foreign ants from getting to the food. In this way, competitors were obviously prevented from retrieving the prey and from recruiting additional sister workers. Once the prey was removed, these agonistic actions declined and the foragers returned to their respective colonies. In a series of experiments in which baits were placed between neighboring colonies, we were able to demonstrate that the closer colony was the one that usually succeeded in taking over the bait. Even if a forager of a more remote colony discovered the bait first, its short-range recruitment signal attracted workers mostly belonging to the closer colony. These ants quickly displaced the original discoverer and carried the bait to their own nest. Thus, although the foraging ranges of neighboring colonies often overlap, colonies closer to the larger prey objects are usually the ones that retrieve them.

Discussion

Although *N. cockerelli* and *N. albigetosus* frequently forage individually, they employ short-range and long-range recruitment techniques when large prey objects are encountered. Chemical recruitment signals discharged from the poison gland function in both recruitment systems as powerful attractants. During short-range recruitment, they are released on or next to the prey into the air, whereupon nestmates approach upwind from as far away as 2 m. During long-range recruitment, a recruiting ant lays an odor trail with poison gland secretion from the prey to the nest. Nestmates are stimulated by the recruitment pheromone to follow the trail to the prey and require no further stimulus. The recruitment pheromone is very short-lived and trail laying does not lead to mass-recruitment communication. This is an additional example demonstrating that attempts to discover recruitment trail pheromones in ants can fail, if only one routine laboratory method is applied. Blum (1974) exposed *N. cockerelli* to circular trails (15 cm in diameter) drawn with extracts of their sting glands or hindguts. When groups of ten workers were subsequently introduced into the center of the circle, no trail following could be observed. We noted frequently that *Novomessor* workers react too sensitively to any mechanical disturbance to permit reliable assays of the trail pheromone on small groups of workers separated from their colony. For this reason, we designed tests to utilize the undisturbed colony. Furthermore, we have shown that the recruitment pheromone is very volatile. Therefore, a circle that is only 15 cm in diameter may simply be too small to allow precise trail following.

Instead of dissecting the prey into small pieces that could be carried home by individual ants, several *Novomessor* workers usually transported the whole prey in a highly cooperative action to their nest. This is a very efficient foraging method, by which large food objects are retrieved with a minimum of energy investment, ensuring that valuable food is quickly sequestered away from competitors. When abundant large prey items were available in the field, for example, during nuptial flight activities at the mating leks of *Pogonomyrmex* (Hölldobler, 1976b), *Novomessor* employed this cooperative foraging technique almost exclusively.

Oster and Wilson (1978) recently reviewed the foraging techniques used by social insects. They distinguished five basic foraging types. It is difficult to assign *Novomessor* to any single type; in fact, *Novomessor* possesses a very broad behavioral foraging repertoire, and their foraging strategy varies according to food availability. They can forage as solitary harvesters or huntresses, or add large food items to their resource spectrum through recruitment and cooperative retrieval, or subdue exceptionally difficult and resistant prey by recruitment and group attack. *Novomessor* can be considered a monomorphic rather than a polymorphic species. As Oster and Wilson have pointed out, that should make them less versatile at harvesting single items, unless they keep open the option of exploiting larger items by the use of recruitment. Indeed, due to their special short-range and long-range recruitment techniques and highly coordinated group-carrying behavior, *Novomessor* is not only able to exploit a broad spectrum of resources but also to compete successfully with ant species that have evolved highly sophisticated forms of mass recruitment and powerful chemical repellent strategies.

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