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SOCIAL ORGANIZATION OF NEST EMIGRATION IN *LEPTOTHORAX* (HYM., FORM.)

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SUMMARY

The investigated species of the genus *Leptothorax* have small colonies and nest in fragile nest sites. Thus they depend on frequent nest emigrations, if the ecological conditions are no longer favorable. Field observations of nest sites of *L. rugatulus* are reported and experiments show that even slight physical disturbances easily release nest emigrations. Six species (*L. muscorum, L. rugatulus, L. longispinosus, L. curvispinosus, L. acervorum* and *L. crassipilis*) use both tandem running and carrying behavior during nest emigration. Tandem running is strictly limited to the first phase of nest emigration, whereas carrying behavior is the predominant technique (84 %). This is the first case discovered in ants where two different recruitment techniques are employed for different purposes during one recruitment task. Workers which are recruited by tandem running inspect the new nest site. If they accept it, they join the scout force and lead or carry nestmates to the new nest by themselves. Thus the recruitment of workers by tandem running serves to increase the number of active scouts and « movers » (« recruitment of recruiters »). The efficiency is considerably higher in the species which use this combined technique than in *L. nylanderi,* a species in which tandem in only the opposite direction could be recorded. These reverse tandems do not increase the number of scouts. It is not yet proven which workers « decide » whether or not still more new recruiters are to be recruited. A hypothesis is discussed that the severity of the ecological conditions inside the old nest affects the behavioral threshold of workers to respond to the signals of a tandem calling nestmate.

ZUSAMMENFASSUNG

Soziale Organisation des Nestumzuges bei *Leptothorax* (Hym., Form.)

Die untersuchten Arten der Gattung *Leptothorax* bilden kleine Kolonien an Nestplätzen, deren ökologische Bedingungen sich leicht verändern können. Aus diesem Grund müssen sie häufig einen neuen Nestplatz suchen und die gesamte Kolonie dorthin verlagern. Freilandbeobachtungen haben gezeigt, daß schon geringe, von uns am Nest induzierte Störungen Nestumzüge auslösen. 6 von 7 untersuchten Arten (*L. muscorum, L. rugatulus, L. longispinosus, L. curvispinosus, L. acervorum* und *L. crassipilis*) verwenden beim Nestumzug sowohl den Tandemlauf als auch Trageverhalten, um Nestgenossinnen in das neue Nest zu bringen. Tandemrekrutierung ist ausschließlich auf die erste Phase der Nestemigration beschränkt, während die meisten Arbeiterinnen zum neuen Nest getragen werden (84 %). Es konnte erstmals für Ameisen nachgewiesen werden, daß zwei verschiedene Rekrutierungsweisen zur Organisation einer Rekrutierungsaufgabe verschiedene Funktionen besitzen. Arbeiterinnen, die im Tandem rekrutiert werden, untersuchen den Nestplatz in gleicher Weise wie die ersten Kundschafterinnen. Wird der Nestplatz akzeptiert, dann beteiligen sie sich aktiv am Umzug, indem sie selbst Nestgenossinnen zum neuen Nest führen oder tragen. Die Tandemrekrutierung zu Beginn eines Nestumzuges erhöht somit die Zahl der Kundschafterinnen sowie der Träger (»recruitment of recruiters«). Dadurch wird eine schnellere Verlagerung der Kolonie ermöglicht. Bei *L. nylanderi* wurden nur Tandempaare entgegen der Umzugsrichtung beobachtet, wodurch die Zahl von Rekruteuren nicht erhöht wird. Wir konnten noch nicht klären, durch welche Arbeiterinnen es »entschieden« wird, ob immer noch neue Nestgenossinnen als Rekruteure geworben werden sollen. Wir nehmen an, daß die ökologischen Bedingungen im alten Nest die Antwortschwelle der Arbeiterinnen herabsetzen, den Signalen sterzelnder Nestgenossinnen zu folgen.

INTRODUCTION

Nest emigrations are common among the social insects and serve several different purposes (see review in Wilson, 1971). In many social Hymenoptera and in some of the higher termites colony multiplication is achieved by a partial nest emigration. For example when a honey bee colony reaches a certain degree of congestion in the spring, the old queen and a portion of workers depart and move to a new nest site. This mode of colony multiplication is also employed by several ant species which form large polygynous societies.

A second major type of nest emigration involves the whole colony and is independent from reproduction. Social insect colonies which are no longer able to cope with changes of their environment are forced to move to other nest sites. A considerable decrease in food supply, a drastic change in temperature or humidity or an increase in pressure by enemies and competitors can force a colony to move to a new nest site. Especially those species which form small societies and are therefore less able to regulate temperature and humidity by their own means and which often occupy relatively unstable nesting sites are occasionally required to emigrate to other localities.

The ant genus *Leptothorax* belongs to this group (Gösswald, 1932; Talbot, 1957). *Leptothorax* colonies can frequently be observed in the field moving from one site to another, yet very little has been learned about the social organization of nest emigration in this ant genus.

MATERIALS AND METHODS

Seven species of *Leptothorax* which were collected from several localities in West-Germany and USA (table I) were included in this study. Entire colonies were housed in artificial nest chambers made with plaster of Paris or in little cardboard chambers (2 × 6 × 0.2 cm). The latter nest type was ideal for observing the behavior of the

TABLE I. — Species of *Leptothorax* investigated in this study; nest site and locality are indicated.

TABELLE I. — Nestplätze und Fundorte der untersuchten *Leptothorax*-Arten.

Species	Nest site	Locality
L. nylanderi (Foerster)	Hollow twigs.	Oak forest near Frankfurt, West-Germany.
L. acervorum (Fabr.)	Hollow twigs.	Nürnberger Reichswald, West-Germany.
L. muscorum (Nyl.)	Hollow twigs.	Nürnberger Reichswald, West-Germany.
L. longispinosus (Roger)	Acorns.	Estabrook Woods, Oak forest near Concord, Mass., U.S.A.
L. curvispinosus (Mayr)	Acorns.	Estabrook Woods, Oak forest near Concord, Mass., U.S.A.
L. rugatulus (Emery)	Under rocks.	Chiricahua Mountains, Portal, Arizona, U.S.A.
L. crassipilis (Wheeler)	Under rocks.	Chiricahua Mountains, Portal, Arizona, U.S.A.

ants inside the nest and it also allowed the easy transfer of whole colonies during experiments without any disturbance. The colonies were fed with honeywater and insect prey (cockroaches) and had access to a water supply located in the surrounding foraging arena.

In order to release nest emigrations I removed the covering red glass lids and exposed the colonies to a bright light source. Thus I changed ecological factors like light, humidity and temperature within the nest chambers. Simultaneously I offered one or more new nest chambers in an adjacent arena with optimal conditions. Both arenas were connected by wooden bridges over which the ants could move to the new nest sites. The ethograms were taken either by tape recording of verbal descriptions or by a 10-channel event recorder (Miniscript Z, BBC Metrawatt, Nürnberg, West-Germany). In order to get data concerning division of labor, behavioral specialization and participation of individual workers during different stages of the nest emigration, I tried several marking techniques. Unfortunately all attempts failed due to the small size and the considerable sensitivity of the *Leptothorax* workers to paint. When I succeeded in applying tiny paint spots, nestmates removed the marks by intensive grooming. I also applied microscopic fluorescent dust by blowing it dry through capillary tubes onto the ants. However, this method also failed because I could not prevent other workers from being contaminated. For some observations I marked a few ants by clipping one or both epinotal spines in addition to just one spot of paint. The behavior then had to be observed through a movable microscope to determine the identity of a single ant. This method was limited, however, to very small colonies. Thus, because all attempted marking techniques were unsatisfactory, I was forced to determine the participation of individual workers by watching a single worker during the whole experiment. This method was extremely time consuming especially since very often sight contact could not be maintained throughout the experiment.

The field work was conducted in the Chiricahua Mountains near the Southwestern Research Station in Portal, Arizona.

EXPERIMENTS AND RESULTS

1. Field observations on nest sites and nest moving in Leptothorax rugatulus

L. rugatulus can be found nesting under rocks or in crevices of splitted rocks. Our study area was located in a mixed oak-juniper forest in the Chiricahua Mountains at an elevation of about 2100 m. A plot 42.67 × 36.58 m was subdivided by a removable string grid into squares of 9.3 m^2. The area was moderately steeply sloped, and numerous possible nest stones were scattered around.

FIG. 1. — Colony of *Leptothorax rugatulus* at natural nest site after stone was turned over. Black arrows : Base of the nest chamber; white arrows : Remaining fragments of the chamber walls.

ABB. 1. — Kolonie von *Leptothorax regatulus* an natürlichem Nestplatz nach Umdrehen des Steines. Schwarze Pfeile : Boden der Nestkammer; Weiße Pfeile : Reste der begrenzenden Seitenwand der Nestkammer.

The whole population was first checked on one day by turning over every stone on the plot for a time of about 1 minute or less for identification or sampling of single workers. By checking 2091 turnable nest stones we found 228 colonies of *Leptothorax*. A random subsample of 51 colonies was examined more closely, which required a somewhat longer exposure, but usually did not exceed the time of 5 min. Since all collected samples consisted entirely of *L. rugatulus* it is very likely that there were no other species of *Leptothorax* present in this area.

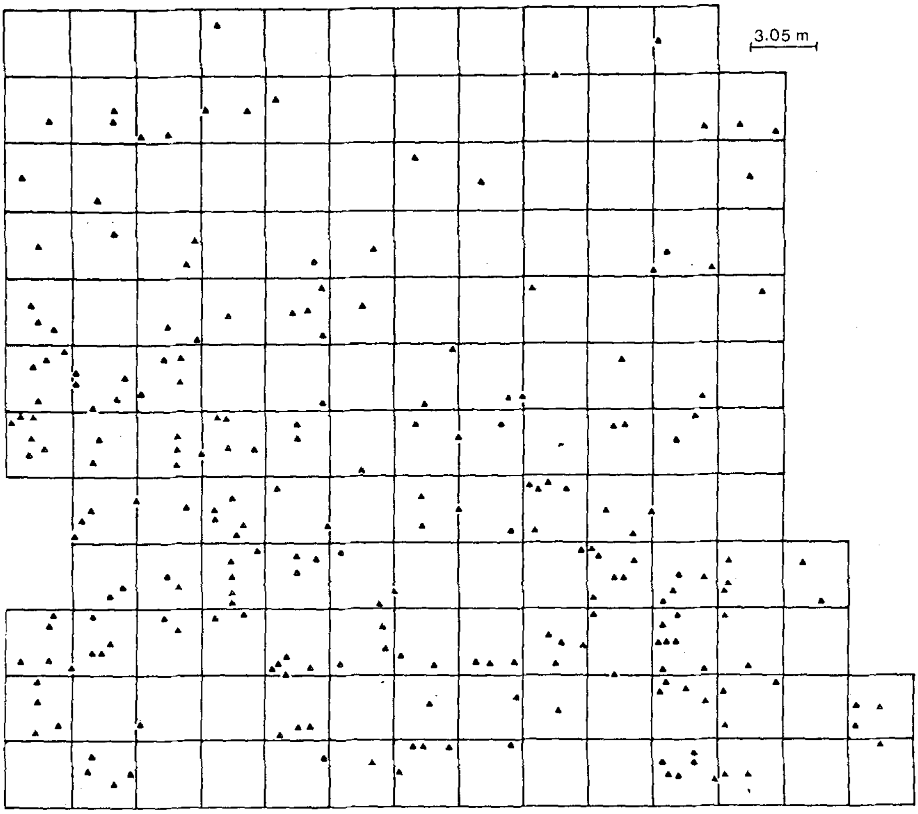


FIG. 2. — Distribution of colonies of *Leptothorax rugatulus* in a mixed oak-juniper forest at Chiricahua Mountains near Portal, Arizona; elevation : 2100 m. Each triangle represents one colony.

ABB. 2. — Karte der Kolonieverteilung von *Leptothorax rugatulus* in einem Eichen-Juniperus Wald in den Chiricahua Mountains (Portal, Arizona). Höhe : 2100 m ü.M. Jede Kolonie wird durch ein schwarzes Dreieck symbolisiert.

The colonies contained usually one queen, an average of 109 workers (range 30 to over 200) and an unestimated amount of brood. Dry brown oak leaves, juniper needles, little twigs and a diversity of other plant materials formed the bases of the nest chambers, which showed flat, often unbroken surfaces. Thus the whole colony was exposed after the stone was turned (fig. 1).

The ants were crowded together either on the top of the material or upside down on the stone ceiling. Sometimes, however, a few small chambers were built into the base of the nest. Although the space covered by the rock measured 219 ± 292 cm^2 (range 32-1 800 cm^2) the nest chambers were considerably smaller (24 ± 17 cm^2; range 2.4-63 cm^2). The walls confining the nest chambers were constructed out of fine material like soil and small vegetation particles.

As the map of the distribution of *Leptothorax* colonies shows (fig. 2), we found a maximum density of 7 colonies per grid square but most of the squares held fewer colonies (mean density 1.5 ± 0.9 per 9.3 m^2). The distribution seems to depend on the height of the slope, whereas neither the number of available nest sites nor the pressure by other ant species seem to set limitations on the distribution of the population (MÖGLICH, in prep.).

As we pointed out, ant species with small colonies and fragile nest sites should be expected to conduct nest emigrations relatively often. What do we consider fragile nest sites and what are the parameters that cause the ants to move in the field ? As HÖLLDOBLER (1976) showed, there can be intra- and interspecific competition. When colonies of *Pogonomyrmex barbatus, P. maricopa* and *P. rugosus* establish their foraging territories too close to each other, increases in aggressive interactions can force weaker colonies to emigrate.

Although the field studies of *L. rugatulus* are not yet completed, there is no evidence for any intra- or interspecific competition leading directly to spacing by means of nest emigrations. Sometimes we found more than one *L. rugatulus* colony under one stone, or we found *L. rugatulus* sharing the space under stones with the nest entrances and the upper nest chambers of other ant species. We have no information about predators and there is no known slave raiding parasite. A possible cause of nest emigrations, however, are physical disturbances, i.e. turning over of stones by erosion or larger animals.

In order to test whether such disturbances can lead to emigration, we turned occupied nest stones several times. We thereby broke up the enclosure and exposed the colony to light for a short period without changing other parameters too much. Of 207 colonies checked, 30 % had already moved after one turn of their nest stone. After we disturbed them three times, 58 % of the colonies had absconded their nest site.

To test the effect of different periods of disturbance we set up two test groups. One was opened only less than 10 sec, the other about 5 min. The percentage of nest emigrations did not differ significantly. We recorded 37 % (N = 162) in the first case and 41 % (N = 31) in the second one. Thus a longer exposure to light does not increase the number of moving colonies. Laboratory observations confirm that species of *Leptothorax* tolerate exposure to light as long as they are still enclosed (e.g. inside a narrow glass tube; *L. rugatulus*, own observations; *L. duloticus*, WILSON, 1975).

Because the applied disturbance and the checking procedure are identical, we were not able to set up a control group to check how many undisturbed colonies emigrated during the test period. Nevertheless, we have indirect evidence that our disturbance provided the major cause of nest emigration. If we look at test groups where the second check occured after different time periods (6 [30], 10 [16], 11 [14], 12 [162] days; N in [ ]), we find that for all four cases the portion of emigrated nests do not differ significantly. The data are 30, 37, 28 and 36 % (mean 33 ± 4 %). If there had been a large portion of nest emigrations due to other factors, we should have observed more nest emigrations in the test groups where the second check occured later than when it occurred earlier (1).

These few experiments clearly demonstrate that physical disturbance easily affects the very fragile nests of *L. rugatulus* and it is therefore obvious that nest emigrations play an important role in the ecology of the species. Furthermore, if we consider how easily other *Leptothorax* species' nest sites, such as acorns or hollow twigs on the ground, can be dislocated or destroyed, it becomes clear how important it is for such small colonies to move quickly to a new nest site.

In the following laboratory study I investigated the social organization and the communication techniques which enable *Leptothorax* to effectively emigrate with the entire colony.

2. Behavior during nest emigration

If one changes the light, temperature and humidity conditions of a laboratory colony of various *Leptothorax* species and provides a new enclosure with optimal conditions, soon scouts will start searching for new nest possibilities. Newly discovered nest sites are inspected by the scout inside and outside, then she moves out and back to her colony. Sometimes she returns again to the new nest site repeatedly, before she finally starts to recruit nest mates. Recently we have analysed the communication behavior involved in recruitment in *Leptothorax* (Möglich *et al.*, 1974). We discovered a new kind of signal in ant communication, which we called chemical tandem calling. A returning scout rapidly antennates several nestmates which it encounters inside the nest. Thereafter she turns around, slants her gaster upwards and with the sting extruded she discharges poison gland secretion. Nestmates are attracted by this substance (tandem calling pheromone) and as soon as one worker touches the calling ant, tandem running starts. The nestmate is then led to the new nest

(1) We were not able to check, if previously absconded stones had been occupied by colonies. If this occured, then the actual percentage of nest emigrations could be larger than observed for one or more of the test groups. Out of 2091 suitable stones 228 (11 %) were occupied. After the test period, an average of 33 % of the occupied stones were found evacuated. If we assume that a previously occupied stone has the same probability of being moved to as a « new » stone, then the total probability for reoccupation calculates as 3.63 % (product of percentage of occupied stones being absconded (33 %) times the percentage of occupied stones (11 %). Thus the percentage of nest emigrations could be at most 36.63 % (33 % + 3.63 %).

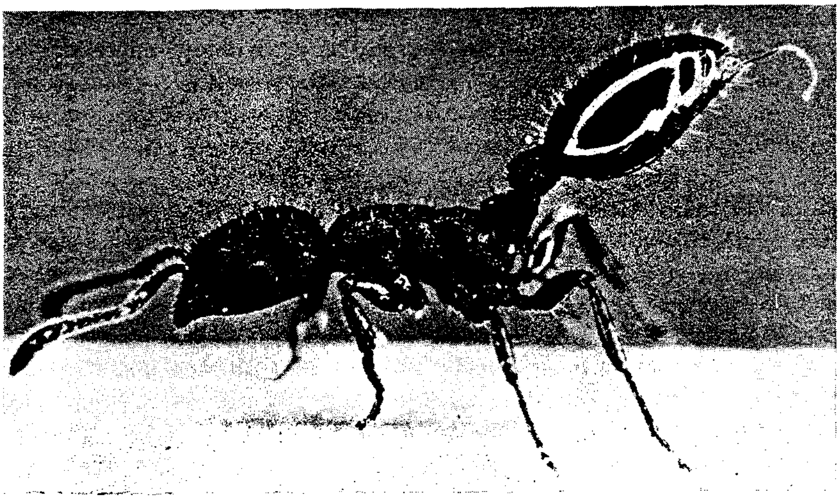


FIG. 3. — Chemical tandem calling behavior of a worker of *Leptothorax acervorum*. The gaster is raised upwards into a slanting position. Simultaneously the sting is extruded and poison gland secretion is discharged.

ABB. 3. — Tandemsterzeln einer Arbeiterin von *Leptothorax acervorum*. Während die Gaster schräg nach oben angewinkelt ist, wird der Stachel ausgestreckt und Giftdrüsensekret abgegeben.

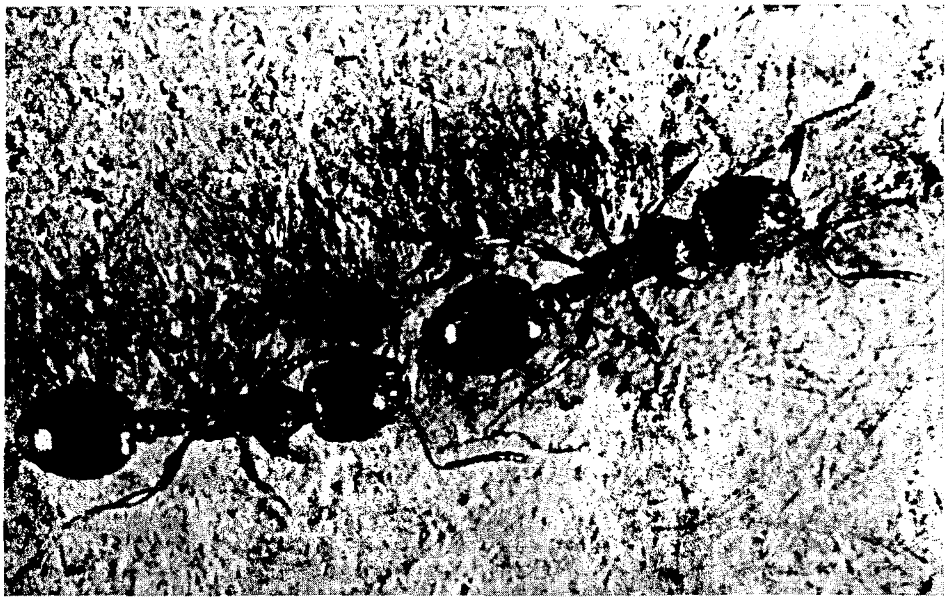


FIG. 4. — Tandem running in *Leptothorax rugatulus*. A nestmate is led into the new nest.

ABB. 4. — Tandemlauf bei *Leptothorax rugatulus*. Eine Nestgenossin wird in das neue Nest geführt.

site. During tandem running, mechanical and chemical signals are involved to keep or to restore contact (fig. 3 and 4).

In addition to recruitment by the tandem running technique, even more frequently scouts can be observed carrying nestmates to the new nest. The carrying posture is typical to that of most species of the subfamily Myrmicinae (see MÖGLICH and HÖLLDOBLER, 1974). The transported ant is either seized at the mandibles, the « neck » or the « cheeks » and is curled over the head of the transporting worker (fig. 5 *a* and *b*).

Tables II and III summarize the data of several nest moving experiments conducted with seven species of *Leptothorax*. For example, during 5 nest emigrations performed by 3 different colonies of *L. muscorum* the average portion of workers recruited by tandem running is 14 % (11-17 %). Thus carrying behavior can be considered the major recruitment technique being used during nest moving, and as tables II and III show, the same pattern was obtained in most of the other *Leptothorax* species.

FIG. 5. — Carrying behavior in *Leptothorax rugatulus*. A worker *(a)* and a female *(b)* are carried into the new nest in the typical carrying posture of the Myrmicinae.

ABB. 5. — Trageverhalten bei *Leptothorax rugatulus*. Eine Arbeiterin *(a)* und ein Weibchen *(b)* werden in der für Myrmicinen typischen Tragehaltung in das neue Nest transportiert.

3. The sociogram of nest emigration

To obtain more detailed information on the temporal organization of nest emigrations, all data concerning tandem running and carrying behavior were recorded as ethograms over time. The results of 5 nest emigrations of *L. muscorum* are given in figure 6. The number of ants recruited by tandem running or carrying behavior are plotted over time. For better distinction, the curves for both behavior patterns are graphed separately (C, T). In addition, figure 7 (a-d), shows the sociogram of 4 single nest emigrations in detail. Each

TABLE II. — Comparison of the organization of some nest emigrations of 7 species of *Leptothorax*.

Many more nest emigrations were conducted but were recorded in a different way. Thus some of the conclusions, like the consideration of *L. curvispinosus* and *L. crassipilis* as species which generally use tandem running during the first stage of nest emigration are based on more observations than are given in this table.

* Recording uncompleted.

TABELLE II. — Organisation des Nestumzuges. Zusammenfassende Daten für einige Nestumzüge von 7 *Leptothorax*-Arten werden verglichen.

Es wurden zahlreiche weitere Nestumzüge durchgeführt, die aber in anderer Weise aufgezeichnet wurden. Zuordnungen einzelner Arten zu der Gruppe von *Leptothorax*, die zu Beginn von Nestumzügen häufig im Tandem rekrutieren, basieren deshald auf weit mehr Beobachtungen als in dieser Tabelle aufgeführt sind (z.B. *L. curvispinosus*, *L. crassipilis*).

* Beobachtung abgebrochen.

Species	Number of colony	Time until start of recruitment (min.)	Number of workers carrying workers	Tandem to new nest site		Number of tandem pairs to old nest site	Number of workers carrying brood
				#	% of total recruitment		
L. muscorum	1	35	135	18	12	0	242
	2	20	142	21	13	0	248
	3	30	230	48	17	2	237
	2	30	129	23	15	0	234
	3	30	193	23	11	0	197
L. rugatulus	1	48	48	12	20	0	29
	1	58	59	5	8	3	30
	1	118	61	9	13	0	32
	1	42	59	9	13	2	29
L. longispinosus	1	85	24	7	23	0	?
	1	70	22	8	27	0	?
	2	85	25	5	17	0	?
	1	77	28	3	10	0	96
	1	71	23	5	18	0	85
	1	43	23	1	4	0	90
L. curvispinosus	1	55	42	2	6	5	136
	1	78	38	0	0	10	147
L. acervorum	1	70	27 *	12	? *	0	?
	2	30	179	1	1	0	239
	3	15	60	0	0	0	120
	4	40	108	0	0	0	59
	4	42	93	0	0	0	176
	3	30	79	0	0	0	78
L. crassipilis	1	115	127	1	1	?	116
	1	235	71	9	13	14	?
L. nylanderi	1	158	54	1	2	29	?
	2	290	116	0	0	16	233
	3	40	21	2	9	1	90
	2	505	115	0	0	22	118
	4	154	71	0	0	6	63
	1	93	23	0	0	0	28
	5	375	18	1	5	1	57
	2	423	52	0	0	1	94

TABLE III. — Comparison of period of time and portion of tandem and carrying recruitment during nest emigration of 7 species of *Leptothorax*.

TABELLE III. — Prozentualer Anteil und Zeitverlauf von Tandemlauf und Trageverhalten bei Nestumzügen von 7 *Leptothorax*-Arten.

Species	Number of nest emigrations	Time between first tandem and first carrying behavior (min.)	Time between first carrying behavior and termination of tandem (min.)	Portion of nest emigrations completed at the end of tandem recruitment (%)	Portion of total recruitment accomplished by tandem (%)
L. muscorum	5	21 ± 14	29 ± 6.5	33 ± 6.7	14 ± 2.4
L. rugatulus	5	32 ± 23.5	51 ± 37.9	41 ± 21.6	14 ± 5.0
L. longispinosus ...	6 (3)	43 ± 16.5	0.8 ± 2.0	11 ± 6.8 (3)	17 ± 8.4
L. curvispinosus ...	2	32 ± 45.3	0	3.0 ± 4.2	3.0 ± 4.2
L. acervorum	1	5	0	1	1
L. crassipilis	1	25	20	23	7.0 ± 8.5
L. nylanderi	8	—	—	—	2 ± 3.3

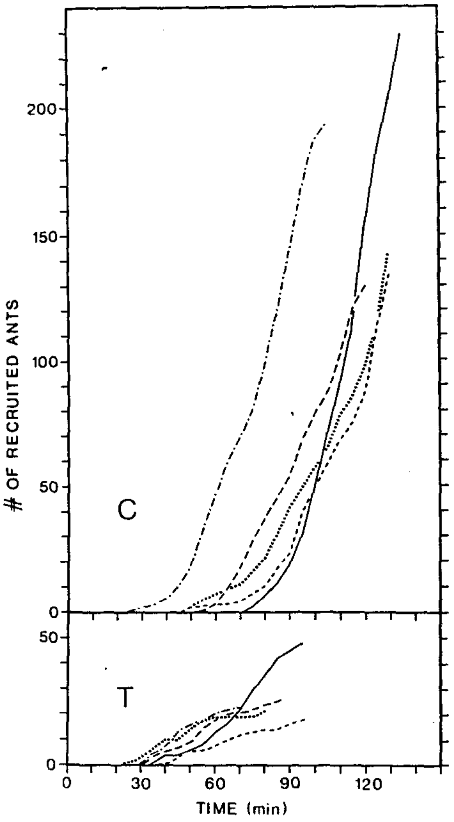


FIG. 6.

Recruitment by carrying behavior *(C)* and tandem running *(T)* during 5 nest emigrations of 3 different colonies of *Leptothorax muscorum* (total number of ants over time).

ABB. 6.

Rekrutierung durch Trageverhalten *(C)* und Tandemlauf *(T)* bei 5 Nestumzügen von drei verschiedenen Kolonien von *Leptothorax muscorum* (Gesamtanzahl von Ameisen gegen die Zeit).

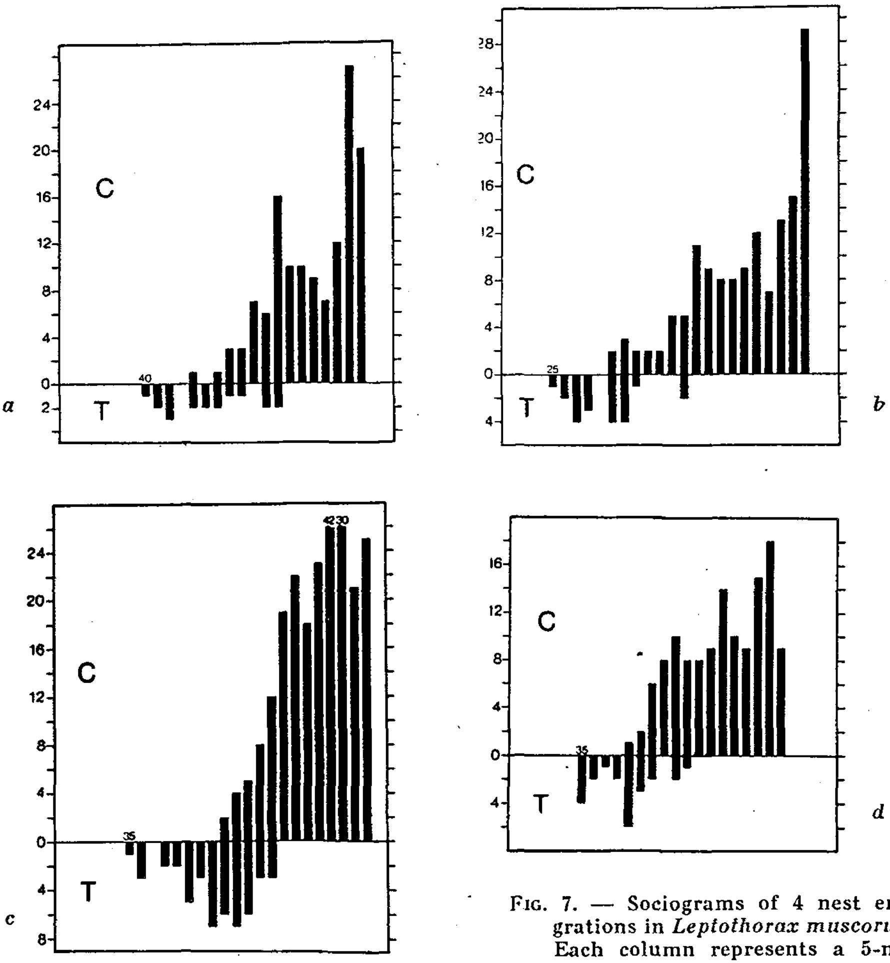


FIG. 7. — Sociograms of 4 nest emigrations in *Leptothorax muscorum*. Each column represents a 5-min count of the number of carrying acts (C, above O-line) and tandem pairs (T, below O-line). The time of the first recruitment is indicated in min above the first column.

ABB. 7. — Soziogramme von 4 Nestumzügen bei *Leptothorax muscorum*. Die Säulen geben die Anzahl von Trageakten (C, oberhalb der O-linie) sowie der Tandempaare (T, unterhalb der O-Linie) für 5-min Intervalle an. Die Zeit vom Beginn des Experimentes bis zur ersten Rekrutierung ist in min über der ersten Säule angegeben.

column represents a 5-min count; columns below the O-line show the tandem running (T) and those above show the carrying recruitment (C).

The data of experiments with *L. muscorum* as presented in fig. 6 and 7 uncover the following patterns : 1. Nest emigrations start with tandem running. In four cases we observed tandems during 20-40 min before the first worker was carried. 2. Never does tandem recruitment continue through the end of the nest emigration. It stops at an average time of 29 min (20-35 min) after carrying behavior started. Thus tandem recruitment is terminated at a time when an average of 33 % (26-40 %) of the total recruitment task is completed. 3. The frequency of tandem pairs remains relative constant, whereas the number of carrying ants per time interval increases considerably during the first stage of recruitment. There are two possible explanations : Either the same number of carriers work faster over time or the number of carriers increases. Since a recruiting interval (picking up a nestmate — running to the new nest — dropping the nestmate — running back to the old nest and recruiting again) does not decline significantly during the nest emigration, more and more workers must start to carry nestmates. This suggests that the pool of recruiters is enlarged by the first workers being recruited, which are the tandem followers. The comparison of the four sociograms in figure 7 demonstrates quite clearly the consistency of the temporal organization of nest emigration. Similar patterns were observed in the other species of *Leptothorax,* which will now be discussed briefly.

Leptothorax rugatulus

We conducted 21 nest emigration experiments with this species. Figure 8 gives one representative example and shows that the general characteristics of the recruitment procedure are basically the same as in *L. muscorum,* although the time periods of exclusive tandem recruitment and tandem termination are not so consistent in *L. rugatulus* (table III).

Leptothorax longispinosus

Three representative cases out of 13 experiments are shown in figure 9 (a-c). Because we only had small colonies of this species to work with, the frequencies of both recruitment techniques were much lower. Nevertheless, the overall pattern of nest emigration is similar to that of the two species discussed above. An interesting difference seems to be the temporal separation of tandem and carrying, which is indicated by a very short time in which recruitment is terminated after carrying started (table III).

Leptothorax curvispinosus

Colonies of *L. curvispinosus* organize their nest emigration basically in the same way as described, although 5 conducted experiments showed a considerable number of tandems going in the opposite direction.

Leptothorax acervorum

In *L. acervorum* the organization patterns differ among nest emigrations. The start by tandem was only observed twice out of 6 nest emigrations. During the experiment shown in figure 10 only one tandem pair was recorded before

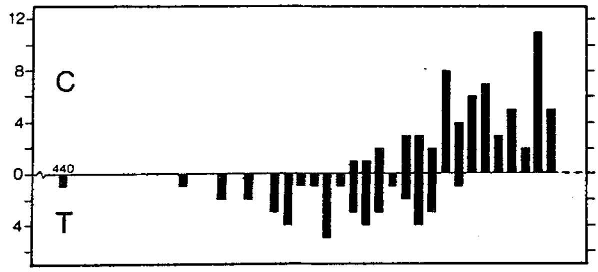


FIG. 8. — Sociogram of a nest emigration of *Leptothorax rugatulus*. (for details see Fig. 7 and text).

ABB. 8. — Soziogramm eines Nestumzuges bei *Leptothorax rugatulus*. (Einzelheiten siehe Abb. 7 und Text).

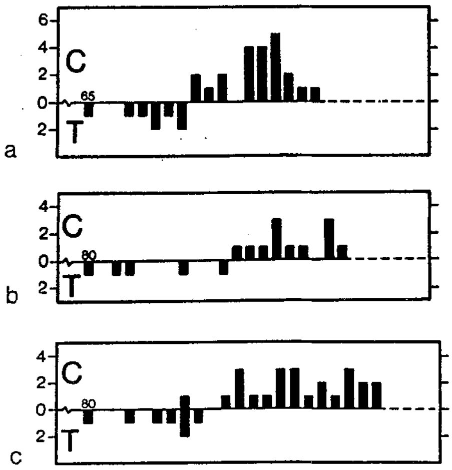


FIG. 9.

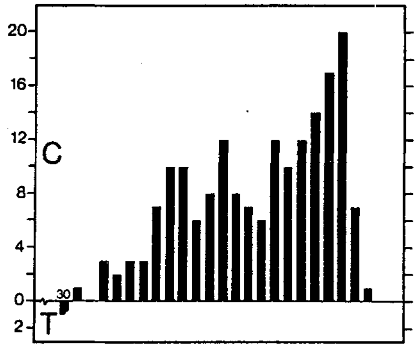


FIG. 10.

FIG. 9. — Sociograms of 3 nest emigrations of *Leptothorax longispinosus*. (for details see Fig. 7 and text).

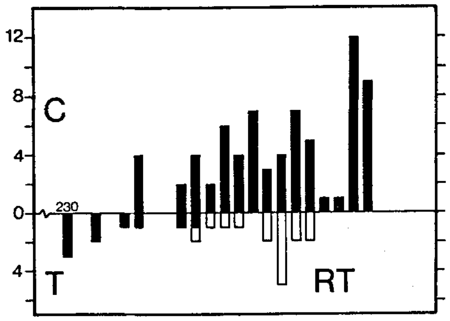
ABB. 9. — Soziogramme von 3 Nestumzügen bei *Leptothorax longispinosus*. (Einzelheiten siehe Abb. 7 und Text).

FIG. 10. — Sociogram of a nest emigration of *Leptothorax acervorum*. (for details see Fig. 7 and text).

ABB. 10. — Soziogram eines Nestumzuges bei *Leptothorax acervorum*. (Einzelheiten siehe Abb. 7 und Text).

FIG. 11. — Sociogram of a nest emigration of *Leptothorax crassipilis*. The white columns represent the number of reverse tandems (RT) per 5-min time interval. (for details see Fig. 7 and text).

ABB. 11. — Soziogramm eines Nestumzuges bei *Leptothorax crassipilis*. Die weißen Säulen geben die Anzahl von Tandempaaren in entgegengesetzter Richtung zum Nestumzug an (reverse tandems, RT). (Einzelheiten siehe Abb. 7 und Text).



the carrying technique took over completely. However, during another experiment 12 tandems were observed at the beginning. Since in additional 4 experiments no recruitment by tandem running was recorded, one can conclude that *L. acervorum* frequently organizes nest emigrations by the carrying recruitment technique alone (table II).

Leptothorax crassipilis

This species also shows the typical temporal pattern of recruitment procedures during nest emigration (8 experiments). However, I recorded here an unusual large number of tandem recruitments in the opposite direction, i.e. from the new nest back to the old one (white columns in fig. 11, RT). These reverse tandems tend to begin towards the end of the normal tandem recruitment activity (old nest to new nest).

Reverse tandems also occurred very sporadically in *L. muscorum, L. rugatulus, L. curvispinosus* and *L. longispinosus,* whereas in *L. acervorum* I have not yet observed them. The irregularity of their occurrence suggests that they may not play an important role in nest emigration.

Leptothorax nylanderi

During 8 nest emigrations I observed reverse tandems even more frequently in *L. nylanderi.* The case graphed in figure 12 starts with carrying behavior and does not show a single worker recruited by tandem to the new nest. On the contrary I recorded 16 reverse tandems, which seem to follow no regular time characteristics. It is a general result that reverse tandems — when they occur — were mostly distributed throughout the nest emigration. Table II summarizes the results for all 8 nest emigrations. I only saw a few regular tandems in three nest emigrations, but recorded reverse tandems in almost all experiments.

In order to compare the efficiency of the recruitment to the new nest sites in *L. nylanderi* with one of the other species, (e.g. *L. muscorum*) I plotted the carrying and tandem frequencies of a nest emigration of each species over time (fig. 13). This shows clearly that the number of carrying acts per time interval (solid line) does not increase in *L. nylanderi,* whereas *L. muscorum* shows an exponential increase of carrying runs during the first phase of the emigration process (dashed line b). It can also be seen that this increase coincides with the period of heavy tandem recruitment (dotted line a). This result suggests that *L. muscorum* first recruits new secondary recruiters by the tandem technique (recruitment of recruiters), and increases thereby the carrying worker force during the initial phase of nest emigration. It also indicates that the « reverse tandems », recorded in *L. nylanderi* do not have the same effect.

Thus the system employed by *L. muscorum* is considerably more efficient (with a mean carrying rate of 3.8 workers/min) than that of *L. nylanderi* (0.9 worker/min). With these different efficiencies the same portion of both

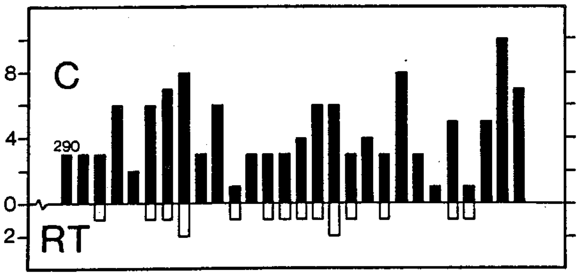


Fig. 12.

Sociogram of a nest emigration of *Leptothorax nylanderi*. (for details see Fig. 7 and 11, and text).

Abb. 12.

Soziogramm eines Nestumzuges bei *Leptothorax nylanderi*. (Einzelheiten siehe Abb. 7 und 11 sowie Text).

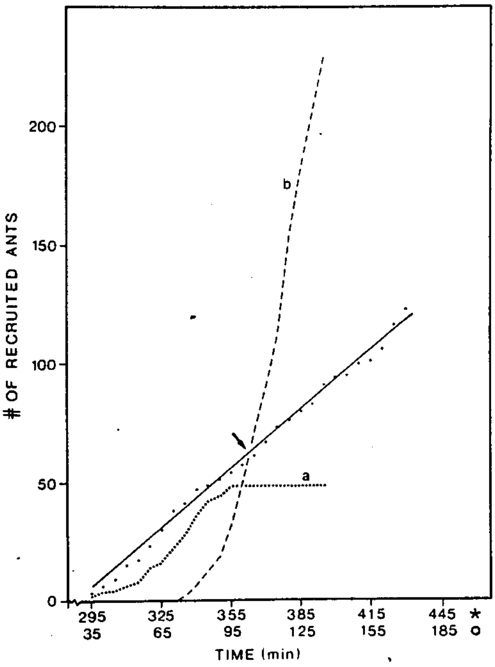


Fig. 13. — Comparison of recruitment efficiency (in number of ants recruited) during a nest emigration of *Leptothorax muscorum* (dotted line a = tandem recruitment; dashed line b = carrying recruitment) and *Leptothorax nylanderi* (solid line = carrying recruitment). The period of time from the start of carrying differs in both species : time axis * = *L. nylanderi*; time axis 0 = *L. muscorum*. The arrow indicates the point, where the carrying recruitment of *L. muscorum* exceeds that of *L. nylanderi*.

Abb. 13. — Vergleich von Rekrutierungseffektivität (Anzahl von Ameisen, die rekrutiert werden) zwischen einem Nestumzug von *Leptothorax muscorum* (gepunktete Linie a = Tandemläufe; gestrichelte Linie b = Trageakte) und *Leptothorax nylanderi* (durchgezogene Linie = Trageakte). Für beide Arten gelten verschiedene Zeitachsen : Zeitachse * = *L. nylanderi*; Zeitachse 0 = *L. muscorum*. Der Pfeil markiert den Zeitpunkt, an dem die Zahl der getragenen Arbeiterinnen von *L. muscorum* die von *L. nylanderi* übersteigt.

colonies is moved 32 min *(L. muscorum)* or 72 min *(L. nylanderi)* after carrying recruitment started (see arrow in figure 13).

The results so far demonstrate that except for *L. nylanderi* all other *Leptothorax* species studied show basically the same temporal pattern of recruitment during nest emigrations : During the first phase scouts recruit nestmates by the tandem running technique, whereas during the second phase the colony is moved by the carrying method. Strong circumstantial evidence suggests that during the first phase additional potential carriers are recruited by tandem running. After inspecting the new nest site they in turn may also recruit additional recruiters before finally the whole colony is moved by the carrying technique.

4. Behavior of individual workers

I attempted to test this hypothesis by gathering complete ethograms of individual ants. Since I did not succeed in marking individual ants, I continuously observed single ants which were being led in tandem during the first part of the nest emigration. Because the ants were not marked, many were lost from sight during the experiment. If there was the slightest doubt of the identity, the experiment was stopped and started again on another day. Those ants we have been able to follow through the major part of the nest emigration (*L. rugatulus,* $N = 6$) showed exactly the behavior predicted. Three typical ethograms are given in figure 14 (a-c). The graphs show the time intervals individual workers spent within the old nest (A), at the bridge and connected arenas (B), and within the inner chamber of the new nest (C). Different hatchings distinguish the recruiting behavior of carrying and tandem running.

After the workers were recruited by a tandem leader, it took them some time to assess the situation themselves (28 ± 3 min). This phase between an individual's arrival, passively led by a nestmate, and the start as an active recruiter is characterized by frequent locality changes between the inner nest chamber of the new nest and its outer arena and the bridge. The three workers left the new nest 4 — 6 times and spent roughly equal amounts of time inside (43 ± 11 %) and outside the inner chamber of the new nest (51 ± 14 %). Once they entered the old nest, they started to recruit almost at once ($t_{\text{old nest}} = 2 \pm 2$ min). Worker (a) (fig. 14, *a*) carried brood twice and nestmates 4 times into the new nest. She was very fast compared to the other two workers, as indicated by an average total time for one recruiting run of 2.0 ± 0.5 min ($N = 6$). After the last carrying run the worker came back to the old nest twice, but met only other scouts there, because the nest emigration was completed. The scouts refused being picked up by her and she finally returned to the new nest.

Worker (b) (fig. 14, *b*) recruited 5 nestmates by tandem before she started carrying. Total recruitment time was 10.0 ± 2.3 min per run ($N = 4$; two recruitment runs were not completed, because the follower was lost on the way to the new nest) no matter if the tandem or the carrying technique was used.

The third ethogram (fig. 14, *c*) demonstrates the behavior of a worker which led one tandem and then switched to carrying behavior (recruitment time 7.5 ± 1.3 min per run; $N = 3$; one worker was picked up at the bridge). I included this example because this worker seemed to need many reassurances even after she started recruiting. This is shown by the frequent switch between inner chamber and arena or bridge after the first active tandem and after the first carrying recruitment as well.

To summarize the demonstrated ethograms and other additional single-worker-observations, we found that in all cases the worker which was recruited by tandem became an active recruiter herself, leading and/or carrying other nestmates to the new nest site throughout the whole nest emigration.

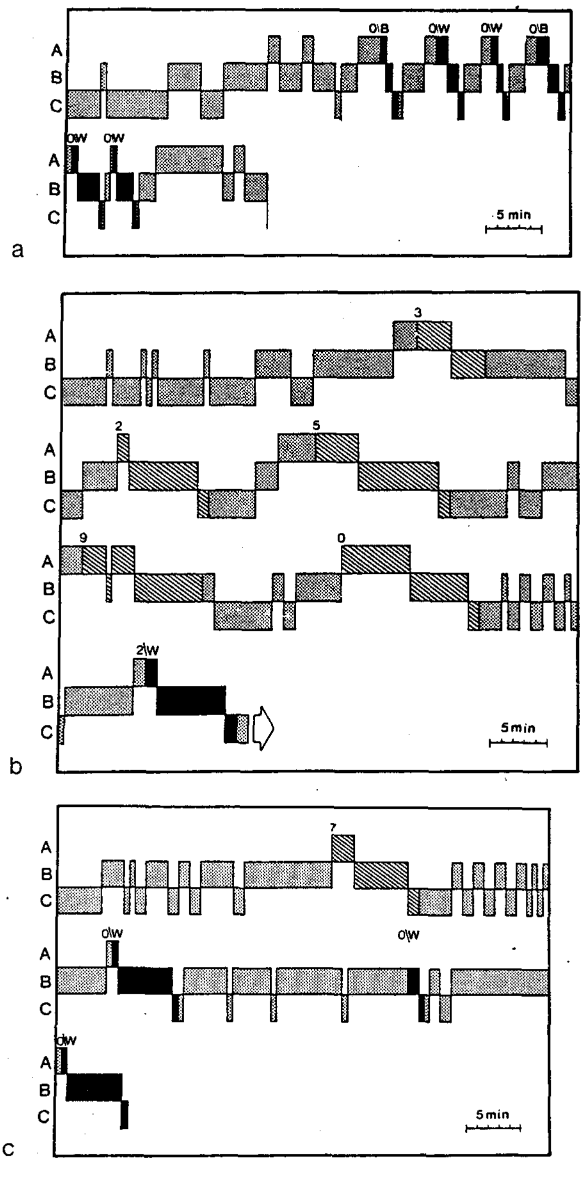


FIG. 14. — Ethogram of single tandem followers of *Leptothorax rugatulus.* The graphs show the times (horizontal axis) spent by three different workers *(a, b, c)* at three different localities : A : The old nest with unfavorable conditions; B : Arena of the new nest and bridge which connects both nests; C : Inner chamber of the new nest. The hatchings represent three different categories of behavior : Black : Carrying behavior; Striped : Tandem running; Dotted : All other activities which are performed by the ant without contact to other ants (which includes in these observations : Walking, resting, self-grooming). The recording starts at the moment when the worker loses tandem contact to her leader ant inside the inner chamber of the new nest. In a and c the worker was observed through the whole experiment; worker b was lost out of sight shortly before the nest emigration was completed. The number of workers encountered with invitation behavior (antennating) before tandem or carrying started is indicated at the beginning of each recruitment run. In the case of carrying behavior, it is distinguished whether a worker (W) or brood (B) was carried.

ABB. 14. — Ethogramm von individuellen Tandemfolgerinnen von *Leptothorax rugatulus.* Die Diagramme zeigen die Zeiten (horizontale Achse), die von drei verschiedenen Arbeiterinnen *(a, b, c)* an drei Orten der Versuchsanlage verbracht wurden. A : Altes Nest mit schlechten ökologischen Bedigungen ; B : Arena des neuen Nestes und Brücke, die beide Nester verbindet; C : Innere Kammer des neuen Nestes. Folgende Symbole sollen die an den entsprechenden Orten gezeigten Verhaltensweisen wiedergeben. Schwarz : Tragen von Nestgenossinnen, Weibchen oder Brut; Schraffiert : Tandemführen von Nestgenossinnen; Raster : Alle anderen Verhaltensweisen ohne direkten Kontakt zu Nestgenossinnen (hier : Laufen, am Ort verharren, Putzen von Antennen und Beinen). Die Registrierung beginnt jeweils dann, wenn die Arbeiterin in der inneren Kammer des neuen Nestes den Kontakt zu ihrer Tandemführerin verliert. In den Experimenten a und c konnte die Arbeiterin jeweils über den gesamten Nestumzug hinweg beobachtet werden, während die Arbeiterin in Experiment b nach dem Trageakt aus der Kontrolle verloren wurde. Die Zahl der Nestgenossinnen, die vor dem jeweiligen Rekrutierungsakt durch Antennenbetrillern aufgefordert wurden, ist zu Beginn jedes Rekrutierungslaufes angegeben. An gleicher Stelle wurde zwischen Tragen einer Arbeiterin (W) oder Brut (B) unterschieden.

These results lead necessarily to the question : What is the behavior of those workers which are carried into the new nest ? Again we induced nest emigrations in *L. rugatulus* and observed 6 single workers which had been carried. It turned out that they did not go back to the old nest to recruit by themselves (see fig. 15). Although the first workers carried in a nest emigration briefly left the new nest several times, they never went back to the old nest to recruit nestmates. Workers carried later in the experiment did not even leave the inner chamber after they had been dropped down, but sat mostly together with other nestmates close to the brood.

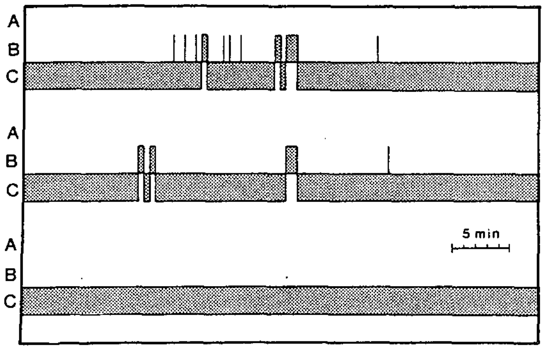


FIG. 15.

Ethogram of a single worker after being carried to the new nest (for details see Fig. 14).

ABB. 15.

Ethogramm einer einzelnen arbeiterin, nachdem sie in das neue Nest getragen worden war. (Einzelheiten siehe Abb. 14).

DISCUSSION

Species of the ant genus *Leptothorax* recruit nestmates to new food sources exclusively by the tandem running technique, but nest emigrations are organized by a recruitment system in which tandem running and carrying behavior interact.

Six of the seven investigated species of *Leptothorax (L. muscorum, L. rugatulus, L. longispinosus, L. curvispinosus, L. acervorum, L. crassipilis)* start a nest emigration with several tandem recruitment acts, before the entire colony is moved by carrying behavior in which brood, queens and workers are carried by a few « movers » to the new nest site. Continuous observations of individual workers *(L. rugatulus)* which had just been led by tandem to the new nest site revealed that they became recruiters themselves; I call this phenomenon « recruitment of recruiters ». This process occurs exclusively in the initial phase of the nest emigration, and it probably serves to increase the number of scouts inspecting the new nest site before a « decision » is made whether to move. In addition, « recruitment of recruiters » also increases the number of active « movers », and thereby facilitates an efficient nest emigration.

As I pointed out, the workers recruited by the tandem running technique apparently decide by themselves about the nest quality and whether or not to recruit nestmates. To be able to do so, they need the same information the first scouts have acquired, concerning the location, distance, direction, difficulty of terrain and conditions of the new nest site. Being led in tandem is far more likely to provide all this information then being passively carried. In fact, I never observed a worker which was carried to the new nest return to the old nest site and become a recruiter.

While 6 investigated species of *Leptothorax* proved extensively similar in the organization of their nest emigrations, *L. nylanderi* showed a different pattern. This species used almost exclusively carrying behavior. Tandem pairs, however, were frequently observed in the opposite direction of recruitment. Sometimes these reverse tandems appeared to be less stable than a tandem in the recruiting direction. Often neither the leader ant waited nor the follower searched for the recruiting ant if the tandem contact was interrupted. I demonstrated that reverse tandems in *L. nylanderi* do not affect the efficiency of recruitment because they do not increase the number of recruiting ants.

It has recently been reported that some ant species use distinct recruitment techniques for food recruitment and nest emigration (HÖLLDOBLER, 1971; MÖGLICH and HÖLLDOBLER, 1975). It is also known that in some cases more than one recruitment technique can be employed during nest moving, as described for *Leptothorax* in this report. In this genus however, I was able to demonstrate that both recruitment techniques have different functions.

It remains a question which workers « decide » whether or not more active « movers » are still needed. If the « decision » is made by the tandem calling scouts, by inviting still more nestmates to follow in tandem instead of carrying them, it is difficult to understand which parameter can provide information about the needed size of the moving force. It is more likely that the severity of the ecological conditions inside the old nest could affect the behavioral threshold of workers to respond to the signal of a tandem calling nestmate. Thus the worse the conditions inside the old nest, the more easily « movers » would be recruited and the faster the colony could be moved.

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