Trail Laying Behaviour During Food Recruitment in the Ant *Lasius niger* (L.)

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Summary

The trail laying behaviour of foragers of the ant *Lasius niger* was observed in the laboratory on a 20cm bridge between the nest and the food source. We measured both the frequency of trail laying, as defined by the proportion of trips during which trail laying occurred, and its intensity, as defined by the number of marks laid during one bridge crossing.

Foragers do not exhibit trail laying behaviour until a food source is discovered. Trail laying then occurs more or less equally both to and from the nest, and both its frequency and intensity decrease as the recruitment proceeds. Foragers from very small colonies less than a year old appear to have quantitatively the same trail laying behaviour as those from older and much larger colonies.

Groups of recruiters and recruits were individually marked. Their trail laying intensity was similar, both for trips to and from the nest, and for an ant's first, second, third and fourth trip. The frequency diminished rapidly with the number of trips made by each individual, and was 2-3 times higher for recruiters than for recruits, for trips both to and from the nest. Even though foragers stop marking after a variable number of passages, they continue to move between the nest and the food source, and other ants start marking. Different foragers appear to have widely different levels of trail laying, although we cannot say whether these differences are stable between different recruitments.

Trail laying is strongly affected by the foragers' position on the bridge, especially for ants returning to the nest which lay up to five times more on the segment closest to the source than that closest to the nest. Foragers on a weakly marked trail appear to mark more than those on a well-marked trail. However this effect is weak and could partly be attributed to their lower speed.

Finally a model using the experimental data gathered on the individuals' trail laying behaviour reproduced satisfactorily the colony's global trail laying.

Introduction

Lasius niger is a very common palearctic species, characterised by its opportunism. In a recent paper (Beckers *et al.*, 1990) we described how chemically-mediated food recruitment allows a colony of this species to adjust its foraging behaviour to a changing environment. The colony is able, for example, to select the most rewarding of two or more food sources, to concentrate its activity on one source when two equal sources are presented, and to select the shorter of two paths (Beckers *et al.*, subm.).

Such decision making is a collective process that emerges from the foragers' trail laying and following behaviour. In this paper, our aim is to gather quantitative information on individual behaviour so as to understand more fully the link with the colony's global behaviour. We describe the dynamics of trail laying during food recruitment by *L. niger*, concentrating on the individual behaviour during a recruitment.

More specifically, we compare trail-laying when the foragers are moving from the food to the nest and from the nest to the food, and how this varies as a function of the number of trips made by an individual. We compare different individuals' trail laying, particularly recruiters versus recruits.

We examine the effect of passing from a marked to an unmarked section of the bridge on the amount of trail pheromone laid. This is to investigate the possibility of negative feed-back between trail laying and trail strength.

Finally we compare the colonys' global trail laying behaviour with that generated by a quantitative model that integrates the individual data collected, so as to test how far the individual behaviour can account for the collective behaviour.

Materials and Methods

Eight medium-sized colonies of 2-3000 individuals were collected in the neighbourhood of Brussels, reared in plaster nests (Janet type), and were used for each experimental series. Five foundation colonies less than a year old, reared in the laboratory from inseminated queens collected after summer swarming, and consisting of 12-23 individuals, were used in the global series (see below).

In each experiment. the colonies were starved for 4 days. On the third day the nest was connected by a cardboard bridge (horizontal section 20cm; access ramps 15 cm), to a 30 x 20cm foraging arena. On the fourth day, 3ml of 1M sucrose solution were placed at the foot of the bridge in the foraging arena. The ants rapidly discover the sugar and initiate a recruitment to it.

The foragers were observed laterally on the 20 cm horizontal section of the bridge using a video-camera. When depositing trail pheromone. a *L. niger* worker curves its gaster vertically to the ground (the normal position being horizontal), interrupts its walk for a fraction of a second and backs up to amplify the movement of its gaster (fig. 1). This behaviour was taken as the criteria for trail-laying, and defined a mark (see also Hölldobler and Traniello, 1980, Hölldobler, 1981, Van Vorhis Key and Baker, 1986, Aron *et al.*, 1989, and Detrain *et al.*, 1991 for similar techniques with other species), and was never observed in individuals that had not been in contact with the food.

A trailing passage was defined as a passage on the bridge during which the ant made at least one mark. The frequency of trail-laying was defined as the proportion of trailing passages, and the intensity of trail-laying was defined as the number of marks laid per trailing passage.

a. Global series

The global experiments consisted of an analysis of the colony's overall trail laying dynamics. A sample of passages on the bridge were analysed five minutes before the introduction of the food source (n=3 adult colonies, 30 passages) and all passages were analysed during the 30 minutes following its introduction (n=3 adult colonies, 2230 passages; n=5 foundation colonies, 188 passages). The time and number of trailing behaviours were recorded.

b. Individual series

In the individual series of experiments, divided into two sets, a sample of ants ingesting food at the source were individually marked with a colour spot on the gaster and observed over 60 minutes. The time and number of trailing behaviours were recorded.

In the first set (n=6 adult colonies), 5 to 7 recruiters per experiment were individually colour-marked, making 37 in all. A recruiter was defined as an ant that was in the foraging area at the introduction of the food source, found the source,

fed at it and then returned to the nest. The recruiters were marked while they were feeding, without appearing to be disturbed. To avoid possible confusion. all other ants in the foraging arena at the time were removed.

In the second set (n=5 adult colonies) the first 5 to 7 recruits that arrived at the source were individually colour-marked, making 37 in all. A recruit was defined as an ant that left the nest after the return of the first recruiters (which were marked differently so as to avoid confusion between the two categories), and whose behaviour was easily distinguishable from that of ants leaving the nest spontaneously (i.e. without "invitation" by a recruit or the trail).

c. Negative feed back between trail strength and trail laying

A final series of experiments examined the possible feed-back of trail strength on marking behaviour. The flat part of the bridge was split into two removable 10cm sections, A and B. The recruitment was allowed to run for either 20 minutes (n=4) or 40 minutes (n=4). Section B of the bridge, the one farthest from the nest, was then replaced by an unmarked section. The marking behaviour of all ants that passed on both sections of the bridge was analysed 10 minutes before and 5 minutes after this replacement. Trailing behaviour on the marked section A and the unmarked section B was then compared to see if the change of trail strength when passing from A to B (going to the source) or from B to A (returning to the nest) influenced the amount of marking. The ants' speed on each segment was measured in one experiment.

Results

a. Global series

The global experiments with the adult colonies showed that no trail laying behaviour occured before the introduction of the food source, even though a number of foragers were exploring the bridge and the foraging area. Trail laying started as soon as the source was discovered, being observed during 34% (363/1058) of passages analysed by ants returning from the food source to the nest, and 29% (343/1172) of those from the nest to the food source. This trail laying occured throughout the 30 minutes observation, supplementary observations showing that trail laying continues at least until 60 minutes after introduction of the source (the end of our observations).

The recruitment dynamics vary somewhat from experiment to experiment, but after 30 minutes as least as much trailing behaviour has occured when leaving the nest as returning to it, as measured by the total number of marks deposited, both for adult and foundation colonies (fig. 2c). Initially more trailing occurs returning to the nest whereas after 10-20 minutes this difference more or less disappears.

Both the frequency and the intensity of trailing decrease considerably as the recruitment proceeds (figs. 2a,b), but this is compensated by the increasing traffic (fig. 2c). Note that in one of the three experiments the trailing activity per individual was twice as much as in the others.

In the foundation colonies, trailing was observed in 20% (20/102) of analysed passages from the source to the nest, as with the adult colonies, and in 50% (43/86) of those from the nest to the food source. Overall their quantitative trailing behaviour (figs. 2d-f) is similar to that of adult colonies, excepting the very weak trailing by returning ants during the last period. Also, as there are less ants, the total number of marks is smaller than that of the adult colonies (fig. 2f vs. 2c).

In brief:

- No trail laying before the food was introduced.

- Overall equality of adult trail laying in the two directions.

- One adult ant passage in three includes trail laying.

- The frequency and intensity of trailing decrease with time.

- Foundation colonies have similar trail laying dynamics to adult ones.

b. Individual Series

The individual series of experiments on the adult colonies, in which a group of marked individuals were followed, confirmed that trail laying occured more or less equally in both directions. The intensity of trail laying was more or less the same for both recruits and recruiters, for trips to and from the nest, and for an ant's first, second, third and fourth trip (4-6 marks per trailing passage) (fig. 3a,b). This result shows that when an ant lays trail, it does so with a more or less constant intensity.

The frequency of trail laying diminished rapidly with the number of trips made by each individual, both for recruiters and recruits (fig 3c,d). The frequency

was 2-3 times higher for the recruiters than for the recruits (70/285 analysed passages vs 28/246), for trips both to and from the nest. Even though these ants stop marking after a variable number of passages, they continue to move between the nest and the food source (see number of passages in fig 3c,d).

The great majority (> 80 %) of trailing individuals started trailing during their first trip to or from the nest, and continued trailing until they stopped completely. Approximately half of the trailing ants did not exhibit trailing behaviour on their first return to the nest, and started trailing when they returned to the source.

Fig 4a shows that once a recruiter has started trailing it has a high probability of continuing to lay trail until the 6th trip, whereas a recruit's probability drops off more rapidly. They may continue, however, to go to the source and back, and make on average just as many trips as the recruiters ($\approx$ 7 in these experiments), and both recruiters and recruits can stop moving between the nest and the source before the end of the experiment.

Fig 4b shows that it was rare to observe an ant stop trailing and then start again during a later passage. Figs. 3c and 3d therefore are the result of the combined effect of the probabilities presented in fig 4. Note that no ant was seen to lay trail until it had been to the source, which accounts for the lower degree of trailing to the source observed during the first minutes of the global experiments (fig. 2).

Finally, the single most active, with respect to trail laying, of each group of 5-7 marked ants assured on average 60-70% of the group's trail laying, both for recruiters and recruits, without making more passages than the others. This proportion increases to 80-90% if we include the second most active ant (fig 5).

In brief:

- No ant marks until it has been to the source.

- The number of marks per trailing passage is relatively constant.

- Marking by any one ant decreases with the number of trips made.

- Recruiters mark 2-3 times as much as recruits.

- Recruits stop trailing sooner than recruiters.

- Once an ant has stopped marking it does not start again.

- Some ants mark a lot more than others.

c1. Positional, directional and temporal effects on trail laying

Table I presents the results of the experiments on feed back between trail strength and trail laying. An examination of the two five minute periods before the unmarked segment was placed (first 2 columns) shows a tendancy for returning ants to mark less than ants leaving the nest as the recruitment proceeds. This was also seen in the foundation colonies but not in the adult colonies, in the global experiments (fig. 2).

One can also observe a systematic difference between the trail laying on segment A (nearest to the nest) and on segment B (nearest to the source). Notably ants returning to the nest mark 2-3 times more on segment B than on segment A, and ants leaving the nest mark slightly more on segment A than on segment B. As segment B has not yet been replaced, there is no physical difference between the two segments, and this strong effect must be attributed to an influence of the ants' spatial position on its trail laying ("positional" effect).

Finally there is a small but systematic decrease in trail laying by ants in all categories between the period 10 minutes before the change and that five minutes before the change, as also seen in the global experiments (figs. 2a,b).

In brief:

- Returning ants mark less than ants leaving the nest, especially as the recruitment proceeds (directional effect).

- Ants leaving the nest mark slightly more on the segment nearest the nest.

- Ants returning to the nest mark 2-3 times more on the segment nearest the source (positional effect).

- There is a small but systematic decrease in trail laying between the two periods before the replacement (temporal effect).

c2. Feed-back between trail strength and trail laying

The third column in Table I shows the trail laying after segment B has been replaced by an unmarked one. To understand the effect of this change, in the light of the strong positional effect that already produces a difference between trailing on

segments A and B. one must compare the ratio of marking on segment B to segment A before the change with same ratio after the change.

For the experiment where segment B was replaced after 20 minutes. for ants returning to the nest the ratio B:A increases from 2.6 to 4.6, and for ants leaving the nest the ratio increases from 0.9 to 1.3 (Table IIa). Similarly for the experiments where segment B was replaced after 40 minutes the ratio B:A increases from 2.0 to 5.3 for returning ants and from 0.9 to 1.2 (Table IIb). There is thus a systematic increase in the trail laying on the unmarked segment B, albeit less pronounced for ants going to the source and quantitatively weaker than the positional effect (Table I).

Note that the very low degree of marking by returning ants on segment A (Table I) makes the B:A ratios highly sensitive to background variation, and they must therefore be treated with caution.

Table III shows the speed of the ants on segments A and B for the five minutes before and after the replacement of segment B ($n=60$ for each category). The ants leaving the nest have more or less the same speed as those returning, within each category. Significantly, the speed is lower on the unmarked replacement segment B (3 cm/sec) than on the marked segment A or segment B before replacement (4-4½ cm/sec). The ants thus spend some 50% more time on the unmarked segment B, which would account for a large part of the increase in marking on this segment. This however assumes that for any given moment during a recruitment, at any given position and for either given direction of travel, an ant marks a fixed amount per unit time. In other words the ants could mark more on segment B after the replacment than before simply because it spends more time crossing it ("speed" effect).

The same possible influence of speed can be seen for the other comparisons. Ants both leaving and returning mark slightly more on segment A before the replacement (0.6 vs 0.5 and 0.15 vs 0.09 marks/passage) and move correspondingly slower (4.4 vs 4.7 and 4.1 vs 4.9 cm /sec). Ants leaving the nest mark less on segment B before replacement (0.5 vs 0.6 marks/passage) and move correspondingly faster (4.1 vs 2.7 cm/sec), and those returning to the nest mark more (0.3 vs 0.5 marks/passage) and move slower (4.1 vs 3.1 cm/sec). Note that the estimates of marks per passage were made from a sample of 150-300 ants per category.

It is of course also possible that the weaker trail directly causes an increase of the ants' trail laying, independent of their speed ("direct feed-back" effect), implying that conversely a strong trail inhibits trail laying.

In brief:

- Ants returning to the nest already mark more on segment B than on segment A (positional effect). but this difference is doubled when segment B is replaced by an unmarked segment.

- Ants leaving the nest show the same tendancy to mark more on the unmarked segment B than before its replacement. but quantitatively to a lesser extent.

- The ants spend more time on the unmarked segment than before. This could account for most of the feed-back observed (speed effect), if trail laying ants mark a given amount per second rather than per cm.

- The feed back observed is quantitatively less important than the other effects, especially the positional one.

Model

We have constructed a model that reproduces the recruitment dynamics, incorporating as much as possible of the above data, to test how far the individual data gleaned above can generate the colony's global trailing behaviour.

The scenario is as follows. Of the 150 ants, only the 25% that are recruiters (experimental estimation) can leave the nest during the first 5 minutes. After this time the complement (the recruits) can also leave the nest (reproducing the experimental initial conditions).

The ants leave the nest, for the first time, both spontaneously and as a function of the trail strength according to a hypothetical function (see legend figs. 2g,h), calibrated to give experimentally observed traffic values. All the ants that leave the nest find the source 10 seconds later, feed for 50 seconds, return to the nest in 10 seconds and stay in the nest for 250 seconds before returning to the food source (average experimental values). The ants lay trail or not according to the number of trips they have made, and whether they laid trail or not in their preceding trip (as shown in fig. 4), making 4 marks per trailing passage (average experimental value).

The simulation's results are closely comparable to those of the adult colonies (figs. 2a,c vs figs 2 g,h), both as concerns the quantitative values and their temporal evolution. The temporal variation, seen for example in fig 2a, is thus seen to be a

consequence of the ants' probabilities of stopping trailing after a certain number of trips, rather than a direct consequence of time itself or the age of the recruitment. Note that the lower number of total marks during the first 10 minute period is largely due to the simulation's lower traffic.

In brief:

- The individual data gathered largely suffice to reproduce the colony's quantitative trail laying behaviour.

Discussion

Lasius niger is widely accepted to be an excellent mass recruiter, but little was known about individual trail-laying behaviour during a recruitment. It is striking, though not entirely unexpected, how many parameters influence the quantity of trail laid by an ant. In this series of experiments we have isolated the following influences on individual behaviour:

- Being a recruiter (one of the first ants at the source) or a recruited ant.

- The number of trips made.

- The quasi-irreversibility of stopping trailing.

- Strong individual variability, certain individuals marking more than others in single experiments.

- The position on the bridge, especially for returning ants.

- The concentration of the trail, possibly via the ant's speed.

The foraging areas used in these experiments are "known", or in other words have been explored for four days before the food source is introduced. *L.niger* workers explore independently and no trail trail laying is observed during the period of observation before the food is introduced. We have observed exploratory trails when a very large colony is given access to a large and unknown foraging area in

the absence of food (Beckers pers. comm.), suggesting that *L. niger* can behave like other species that explore collectively, such as *Iridomyrmex humilis* or *Pheidole pallidula* (Aron *et al.* 1989; Deneubourg *et al.*, 1990; Detrain *et al.*, in press). In our experience, however, *L. niger* generally explores individually, at least in laboratory conditions.

Once the food is discovered by *L. niger* workers, trail-laying (unrelated to exploration) occurs both to and from the source . This is contrary to a certain idea of mass recruitment, in which the ants are presumed to lay trail pheromone only when returning to the nest. Other ant species are also known to lay trail in both directions (e.g. *Myrmica sp.*, Cammaerts and Cammaerts, 1980; *Messor rufitarsus*, Hahn and Maschwitz, 1985; *I. humilis*, Van Vorhis Key and Baker, 1986,, Aron et al., 1989; *Ph. pallidula*, Detrain *et al.*, in press).

The individually marked foragers were seen to stop trail-laying after a few trips, even though they continued to move to and from the source. This is perhaps due to their spatial memory rendering trail following unnecessary, and therefore inhibiting their trail-laying, an idea which is supported by evidence showing that *L. niger* workers rapidly learn visual cues and orient towards them if they are placed in competition with a previously used chemical trail (Aron *et al.*, in prep.).

The recruiting trail, as well as rapidly mobilising a large number of individuals around a food source could therefore be just as important as a short-term guide for foragers while they learn the way to a rich source or area. This would be a shorter term equivalent of the establishment of a trunk trail. Even if the source that started the recruitment was rapidly consumed, some foragers could remain specialised to the area, at least for a while, and find new sources there especially if there is a certain spatial heterogeneity.

Competition between such types of signals (visual vs. chemical) have previously been analysed in a number of species (*Pogonomyrmex badius*, Hölldobler, 1971, 1976; *Pheidole militicida*, Hölldobler and Möglich, 1980; *Camponotus pennsylvanicus*, Traniello, 1977; *Lasius neoniger*, Traniello, 1989; *I. humilis*, Aron *et al.*, 1989; *Leptothorax unifasciatus*, Aron, 1990). One could perhaps divide ant species into two rough categories on the following basis. Some species "prefer" visual cues and use individual memory, and therefore explore and forage more individually (e.g. *L. niger*, *Leptothorax unifasciatus*). Other species "prefer" chemical cues, and therefore favour collective exploration and foraging (e.g. *I. humilis*, Deneubourg *et al.*, 1990). Our recent survey relating foraging strategy and colony size showed that species with smaller colony size fell more into the first category, while those with a larger colony size fell more into the second category (Beckers *et al.*, 1989).

Trail-laying in *L. niger* is not exhibited by all foragers. Recruiters trail more than recruits, and some individuals seem to do most of the work (similar results were described by Barata and Verhaeghe for *Myrmica rubra* - pers. comm.). However, it would be premature to interpret this as indicating a long-term specialisation amongst the foragers, as we do not know at this stage whether those individuals that trailed most in our experiments always do so, or whether the non-trailers we observed will exhibit trail-laying on other occasions.

One might imagine that a trail laying species would use a homeostatic trail system, with marking more frequent on weak trails than on strong ones so as to maintain trail strength within an "optimal" range. Our experiments, however, show that negative feed-back between the trail strength and the trail laying is not so clearly in evidence (see also Jaffe, 1980, Jaffe and Howse, 1979, 1982; and Van Vorhis Key, 1986).

The positional effect, however, is one of the strongest parameters that we found, especially for returning ants. Whether it acts with respect to the absolute distance from the nest or from the food source, or the distance along a straight stretch of trail or any other relative metric, cannot be established here. This positional effect is all the more surprising as each segment is only 10cm long, for ants that in nature can move at least five metres from the nest (although in these experiments the source was only some 30cm from the nest and the ants may have become "used" to the short distances experienced in laboratory conditions).

Generally speaking, food recruitment is an autocatalytic process by which a large number of foragers can be concentrated at one point in space and time. One may imagine that reinforcing the trail when leaving the nest speeds up its establishment, increasing the recruitment's precision and efficiency. Food recruitment can also, however, be a means of collective decision making whose nature depends on the individual trail laying dynamics (Beckers *et al.*, 1990). In the latter paper's model, individual experience was not however taken into consideration as in this paper's model, and the data gathered here will allow us to approach more closely our goal of understanding the link between individual behaviour and experience and the colony's collective behaviour.

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Fig. 1: A typical trail laying sequence. An ant is drawn at six different time intervals, the arrows indicating the point of reference on the bridge. Note the ant arching its gaster at 0.06 - 0.14s while backing up.

Fig. 2a: The average time evolution of the trailing frequency (i.e. the proportion of passages during which an ant laid at least one mark) on a 20cm stretch of cardboard bridge, by ants of the adult colonies (n=3) returning to the nest (dark columns) and going to the source (light columns). The food source was introduced at time zero. The numbers on top of each bar indicate the total number of ant passages. The frequency and intensity of trail laying decrease with time.

2b: idem for the trailing intensity (i.e. the number of marks per trailing passage). The numbers on top of each bar indicate the number of trailing passages.

2c: idem for the total number of marks.

2d-f: idem figs 2a-c, for the foundation colonies less than a year old (n=5). The results are similar to those of the adult colonies (figs 2a-c).

2g-h: idem figs 2a,c, for a simulation of the model (see later text). The probability of leaving the nest for the first time was given by the function: prob $= (k+Q)^2/((k+Q)^2+60^2)$, where $k= 2.5$ for the recruiters and 0 for the recruits and Q is the total number of marks laid. The marks' average life-time is 1000 seconds.

Fig. 3: Comparison of trail laying behaviour by recruiters and recruits.

a, b: The trailing intensity is presented as a function of the [1st], [2nd], [3rd] and 4th bridge-crossing made by individually marked ants. The values are stable between 4 and 6, even though the the number of passages during which trail-laying occurred decreases (see top of each column). The extreme values for the [3rd] and [4th] passage of recruits are probably due to the sample size of 1 or zero (see question mark). No major difference is seen in trail laying to and from the food source.

c, d: idem for the trailing frequency. The total number of passages (top of each column) shows that the ants continue to travel between nest and food

source even when they no longer lay trail. The frequency decreases with time, and is 2-3 times higher for recruiters than for recruits.

Fig. 4: The probability of continuing (++) trail laying and starting or re-starting (-+) and between successive passages for recruiters and recruits. The numbers at each point on the curves refer to the sample size (bold = recruits, plain = recruiters).

a: A transition ++ is counted when an ant that laid trail during its ith passage continues to lay trail during its $i+1^{th}$ passage. The first passage is always a return to the nest. Recruiters continue to lay trail longer than recruits.

b: A transition -+ is counted when an ant that did not lay trail during its ith passage laid trail during its $i+1^{th}$ passage. Note that the transition -+ between 0 and the 1st passage corresponds to the probability that the ant starts trail laying during its first passage. The probability of re-starting trail laying is very low.

Fig. 5: The % of the total marks laid by the group is ranked for each of the marked ants in the group of recruiters (fig. 5a) and recruits (fig. 5b). The values were obtained by ranking the individuals within each experiment (n=6 and 5 respectively) and then taking the average for each rank. In both groups, the most active individual assures 60-70% of the group's trail laying.

Table I: The number of marks per ant passage is presented for segments A (nearest the nest) and B (farthest from the nest), for ants returning to the nest and those leaving the nest, and for the two five minute periods before segment B is replaced by an unmarked segment and the five minute period afterwards. The last two lines give the total number of ant passages, summed over all experiments, during these periods, all of which were analysed. The replacement was made either 20 minutes (Ia, n=4) or 40 minutes (Ib, n=4) after the food source was introduced.

Table II: Idem table I for the ratio of the number of marks laid on segment B to that laid on segment A, calculated from the corresponding number of marks per passage from Table I.

Table III: The speed (cm/sec) of ants crossing segments A and B (n=60 for each category). Note the lower speeds on the replaced segment B (bottom right).
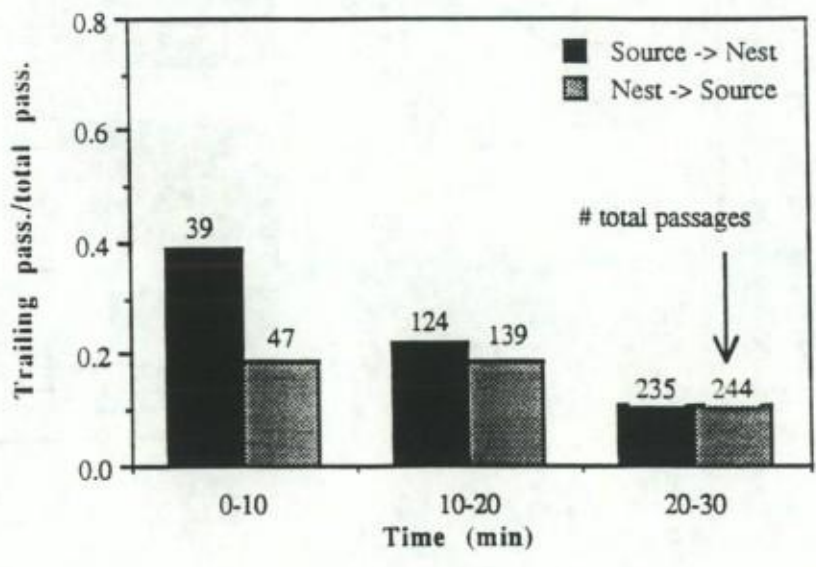
Fig 1

0.20   0.16   0.14   0.12   0.06   0.00

← Time (sec)

Figure 2a

Figure 2b

Figure 2c

Fig. 2d
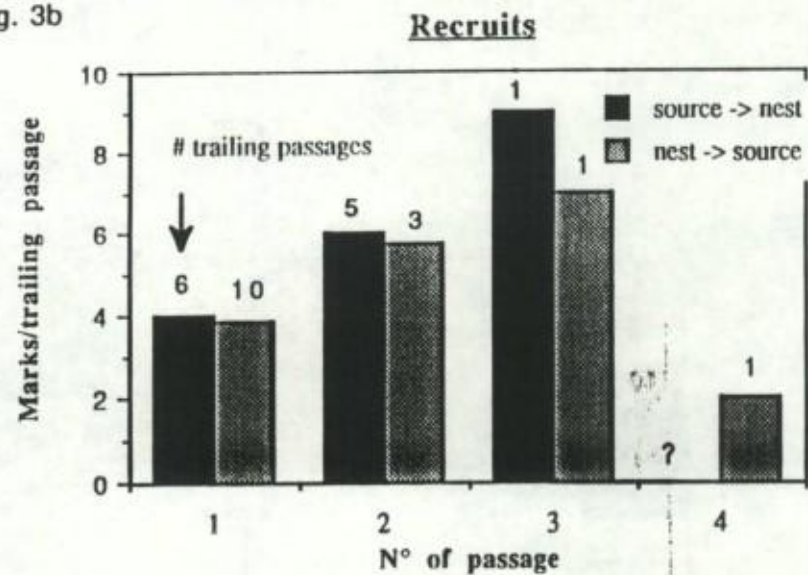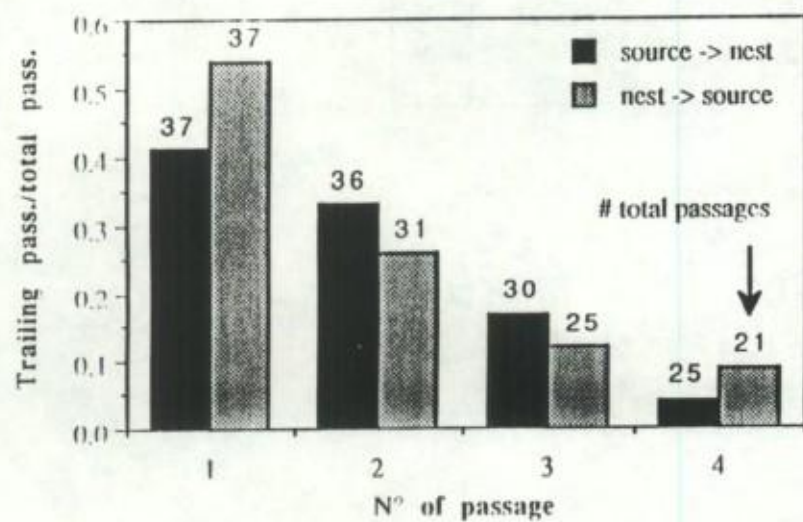

Fig. 2e

Fig. 2f

2 g

2 h

Fig. 3a — **Recruiters**

Fig. 3b — **Recruits**
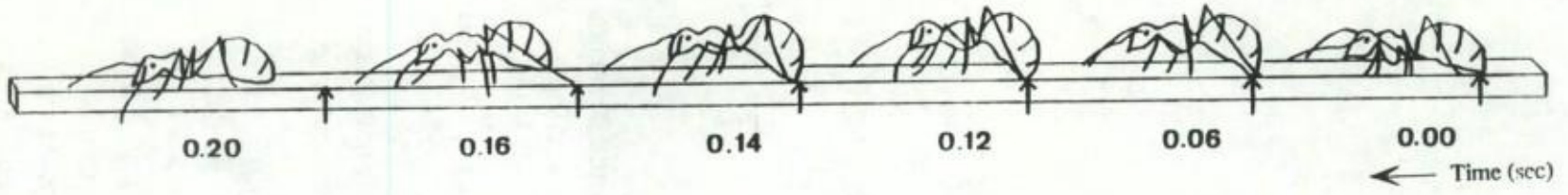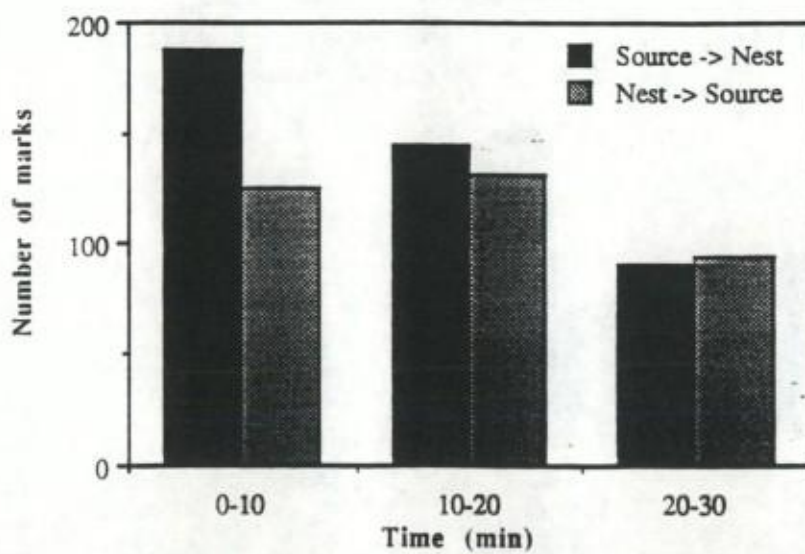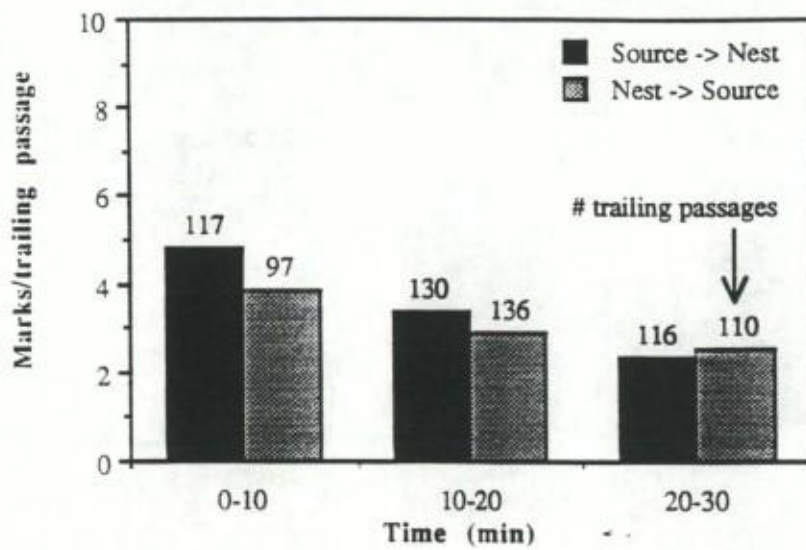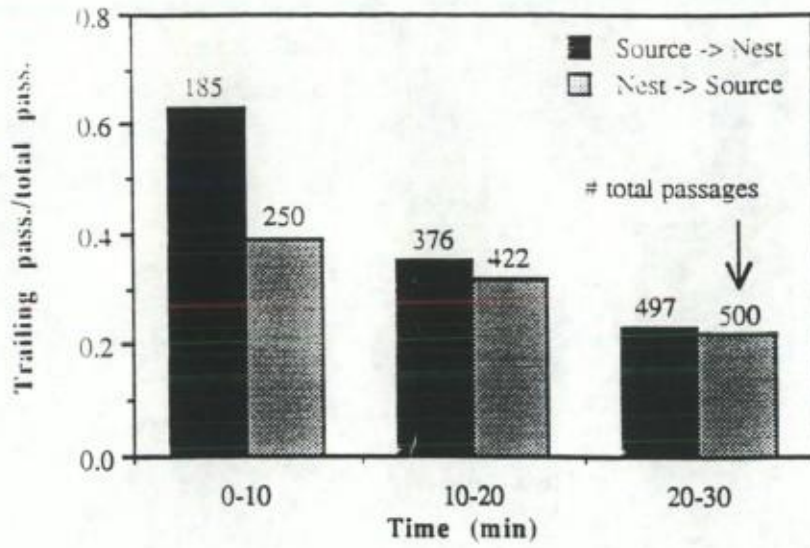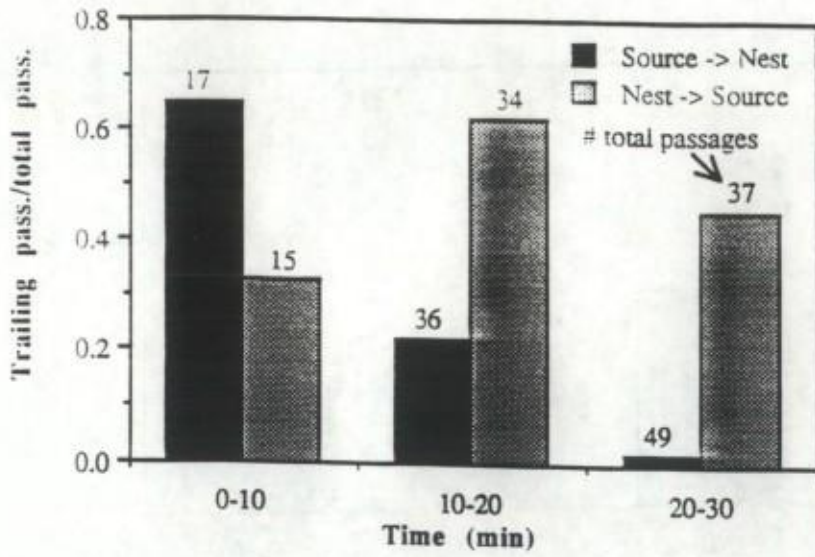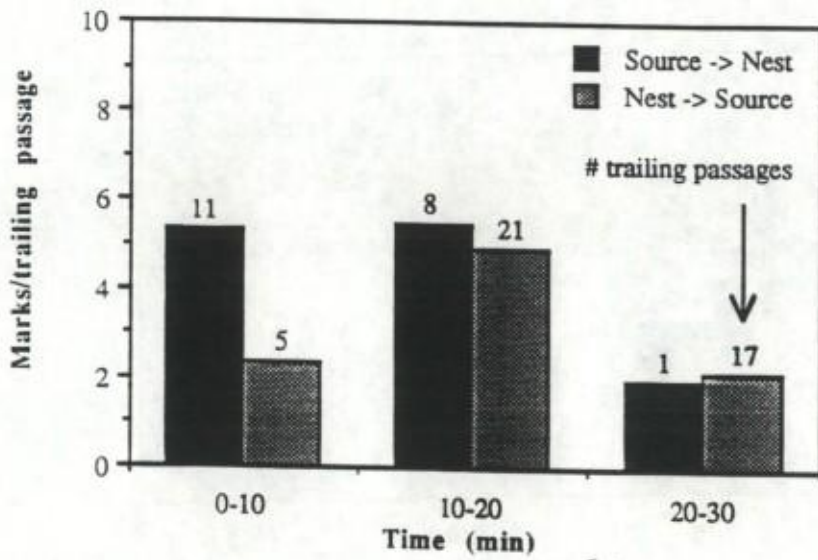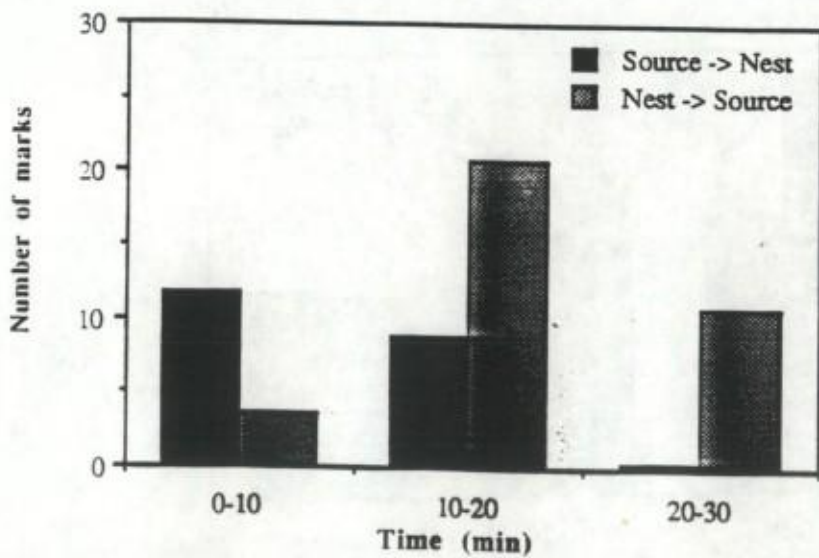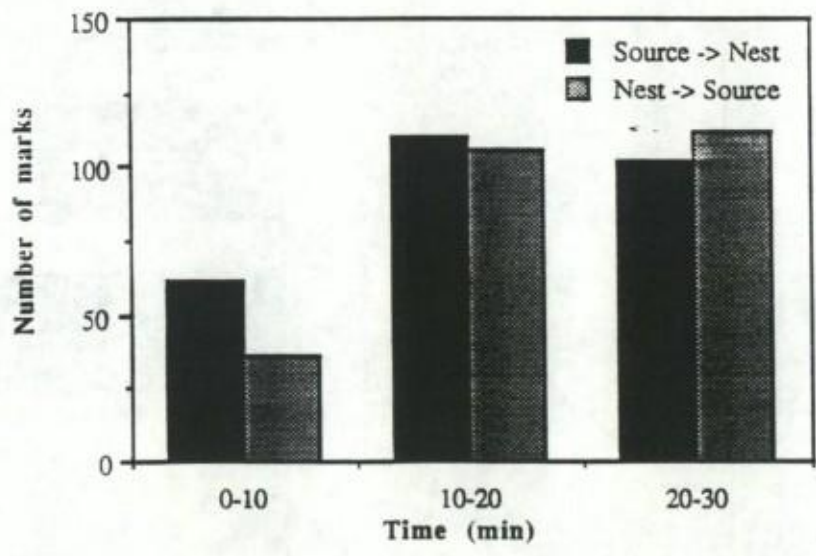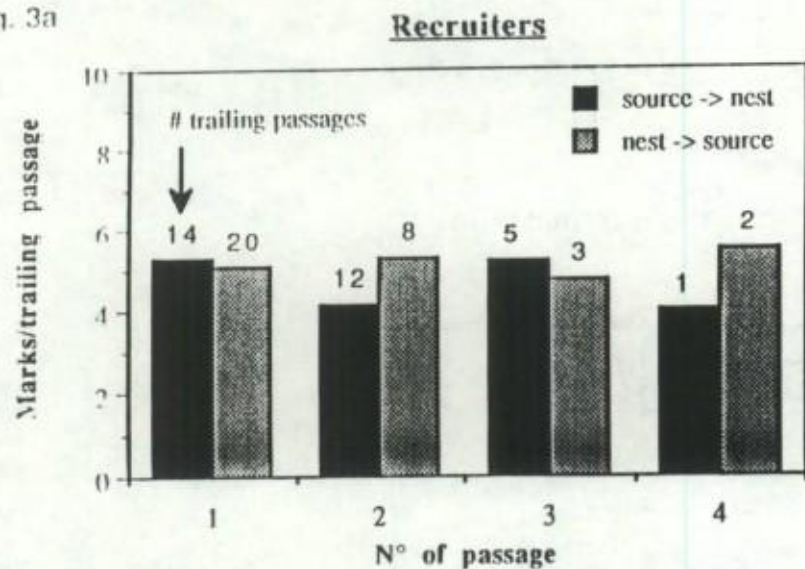
Fig. 3c

Fig. 3d

Fig. 4a

4b

Fig 5a

Recruiters

Fig. 5b

Recruits
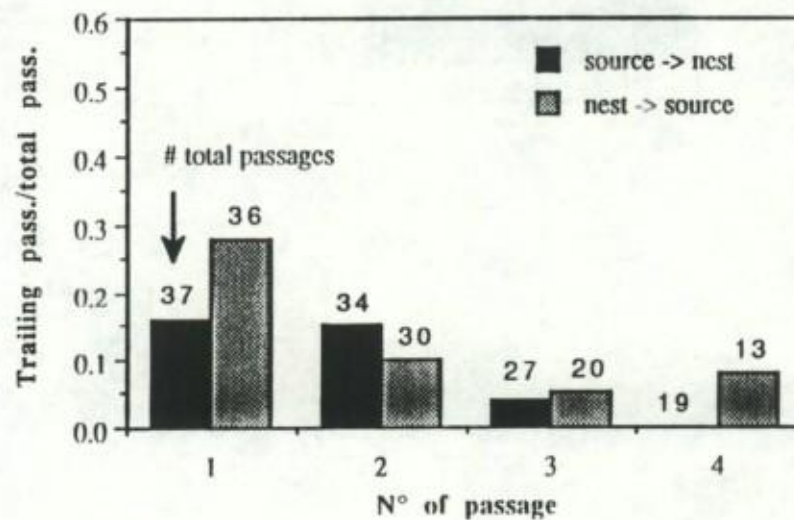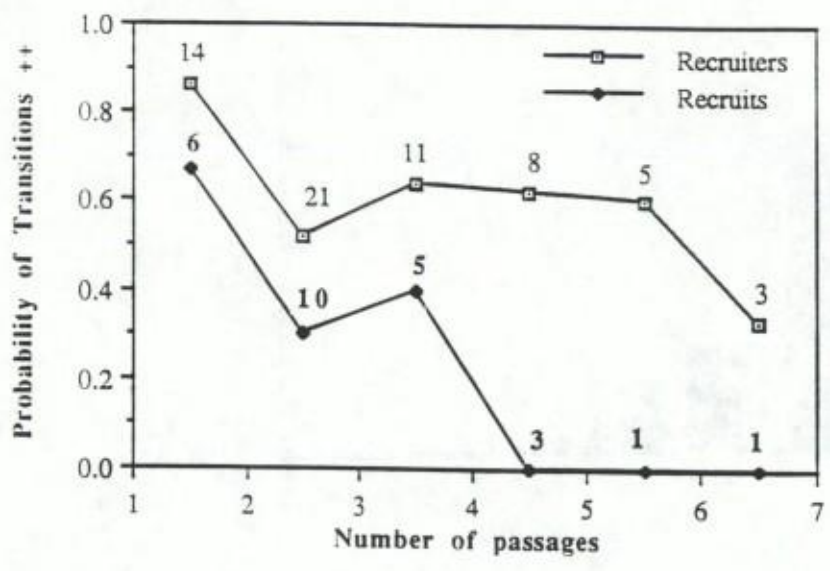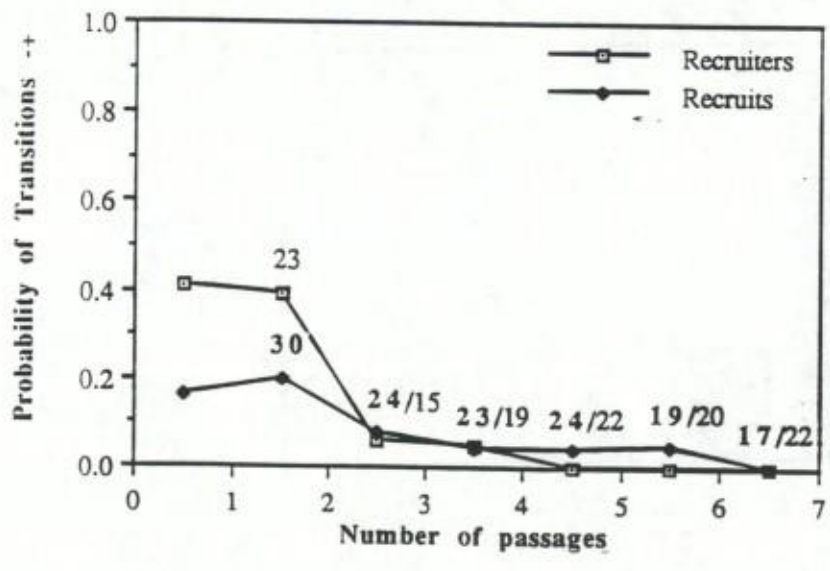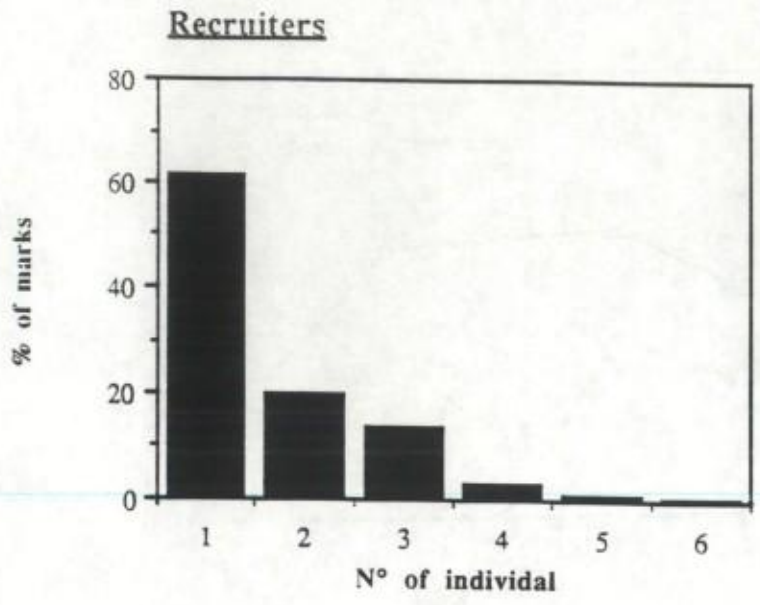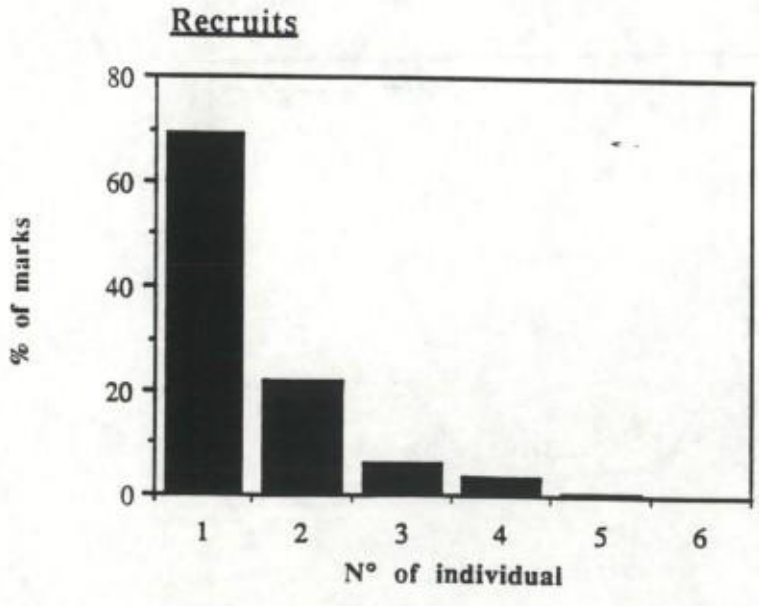
Table Ia

		10-15	15-20	20-25
Segment A	Nest to Source	0.8 ± 0.07	0.7 ± 0.09	0.4 ± 0.06
	Source to Nest	0.2 ± 0.03	0.2 ± 0.04	0.1 ± 0.03
Segment B	Nest to Source	0.6 ± 0.06	0.7 ± 0.09	0.6 ± 0.07
	Source to Nest	0.6 ± 0.06	0.4 ± 0.06	0.5 ± 0.06
# passages	Nest to Source	417	272	331
	Source to Nest	396	261	373

Ib

Replacement of Segment B
after 40 mins.

		30-35	35-40	40-45
Segment A	Nest to Source	0.9 ± 0.10	0.6 ± 0.10	0.5 ± 0.09
	Source to Nest	0.3 ± 0.05	0.2 ± 0.05	0.1 ± 0.02
Segment B	Nest to Source	0.8 ± 0.09	0.5 ± 0.09	0.6 ± 0.10
	Source to Nest	0.6 ± 0.08	0.3 ± 0.08	0.5 ± 0.08
# passages	Nest to Source	278	148	190
	Source to Nest	274	170	227

Table II a

		10-15	15-20	Replacement after 20 mins. 20-25
Ratio B/A	Nest to Source	0.69	0.93	1.34
	Source to Nest	3.07	2.60	4.63

II b

		30-35	35-40	Replacement after 40 mins. 40-45
Ratio B/A	Nest to Source	0.8	0.85	1.22
	Source to Nest	2.23	2.0	5.28

Table III

| | | | Replacement after 40 mins. | |
		35-40	40-45
Segment A	Nest to Source	4.4±0.1	4.7±0.1
	Source to Nest	4.1±0.1	4.9±0.1
Segment B	Nest to Source	4.1±0.1	2.7±0.2
	Source to Nest	4.1±0.1	3.1±0.2