Ann. Zool. Fennici 24:137–146. 1987

Trail communication and directional recruitment to food in red wood ants (*Formica*)

Rainer Rosengren & Wilhelm Fortelius

Rosengren, R. & Fortelius, W. 1987: Trail communication and directional recruitment to food in red wood ants (*Formica*). — Ann. Zool. Fennici 24:137–146.

Laboratory experiments confirm that protein-starved red wood ants of the *Formica rufa* group and *Formica truncorum* Fabr. react to the presence of protein baits in the foraging area with alerting and orienting signals resulting in directional recruitment. Evidence is presented that the cause of directional recruitment in *F. rufa* group ants is a scent trail laid from the bait toward the nest, while "centripetal" recruitment, due to orienting signals provided by scouts returning to the bait from the nest, is of negligible importance. An interesting complication was detected in *F. truncorum*, which showed adequate communication of direction to a food source in the light, but not in the dark. Alternative explanations for the latter phenomenon are discussed. The laboratory results are related to field observations of red wood ant colonies, which indicate a rather limited use of directional recruitment, because of the stable distribution of resources. It is pointed out, however, that temporary shortages of resources, especially in spring, may have favoured evolution of mechanisms for directional recruitment.

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1. Introduction

Foragers of many, perhaps most, social insects inform their nest mates about the presence of food in the habitat. The message, transmitted from scouts to recruits, may stimulate recruits to forage without indicating the location of the food source or it may also provide spatial information. The alerting and directing components of the message may consist of different signals, separable in carefully designed experiments (Hölldobler 1971, 1974, Möglich & Hölldobler 1975, Traniello 1977, 1982), but this is not always the case. Here, we use the term "directional recruitment" as a joint name for the alerting and orienting components of the message.

Do the mound-building species of red wood ants of the subgenus *Formica* have directional recruitment to food? Do foragers of that species group convey spatial information to nest mates by pheromone trails or other means? Directional recruitment is obviously adaptive and often easy to confirm in opportunistic ant species utilizing ephemeral sources of clumped food. Red wood ants do not belong to that ecological category, however. They show permanent defence of climax habitats that provide spatially stable point sources of honeydew in the form of aphid colonies in forest trees, and in addition, they collect insect booty scattered throughout the territory. As pointed out long ago, this resource structure is likely to favour foraging tactics based on individual searching and partitioning of the foraging area among workers, rather than tactics based on concentration of efforts through mass recruitment and conveyance of directional information (Dobrzanska 1958). Recently this view appeared to be confirmed by a study expressing doubts concerning the existence of directional recruitment in red wood ants (Cosens & Toussaint 1985).

Old, veteran red wood ant foragers do indeed maintain a surprisingly persistent site allegiance based on a hierarchy of individually remembered topographic cues (Rosengren & Fortelius 1986a). But this system combining territorial traditions with dispersal of foraging and guarding efforts (Rosengren & Sundström 1987) does not preclude and may actually be complementary to recruitment of young, novice foragers to rewarding sites, a hypothesis consistent with field experiments (Rosengren 1971, Rosengren 1977a). It has, furthermore, been shown that during both foraging and migration red wood ant workers have the habit of laying scent trails emanating from the hind gut (Horstmann 1976, Elgert & Rosengren 1977, Elgert 1980, Bhatkar 1982, Horstmann & Bitter 1984). In *Formica polyctena,* at least, these chemical trails can be used for directing conspecific recruits to a source of food (Horstmann 1976, Horstmann & Bitter 1984). Horstmann suggests that, in this case, the only source of directional information is the scent trail laid by replete foragers returning from the food source to the nest. Such "centrifugal" trail laying cannot be denied, but it is at present difficult to exclude the possibility that a scout returning from the nest to a recently visited food source could provide orienting signals to alerted recruits. In some species such a "centripetal" recruitment mechanism is known to be based on pheromones and/or tactile stimuli, binding scouts and recruits in tandem pairs (Hölldobler 1974, Möglich et al. 1974). Tandem running does not occur in red wood ants, but a scout could direct recruits through a centripetally laid trail or a "leading"-pheromone (Verhaeghe 1982) or it could, as discussed previously (Wilson 1971, Rosengren 1977a), even provide directing visual stimuli based on the kinopsis or optomoter principle. The present experiments were designed, not to indentify the signals, but to find out whether centripetal recruitment occurs in red wood ants.

2. Material and methods

2.1. The ant material

Ants of the *Formica rufa* group, virtually identical to *F. polyctena* Förster with respect to worker morphology but similar to *F. aquilonia* Yarrow in queen characters, were used in most experiments. The species or subspecies, common in southern Finland and adjacent Baltic areas, has recently been described and figured under the preliminary name *F. grankullensis* (Collingwood & Agosti 1986). Proper species identification is often pointed out as crucial for behavioural work, but there are two reasons why we do not consider the unclear status of *F. grankullensis* particularly disturbing. Firstly, it is still unclear whether the genetically tight cluster of apparent sibling species, constituting the European *F. rufa* group, consists of reproductively isolated units or whether it is a plexus of differentiated local populations forming a partly interbreeding multispecies (Pamilo et al. 1979). Secondly, it is far from clear whether a typological concept is really a good predictor of behaviour and ecology in this case; conspecific populations living in different parts of the distribution area may show behavioural differences as large as those found between morphologically differentiated species of the group (Rosengren & Cherix 1981). Clearly, the local or regional population is the safest taxon in this case. The *F. grankullensis* material used in this study was collected from a moundnest in a patch of coniferous forest, in Kilo, 10 km west of Helsinki.

Formica truncorum Fabr., although belonging to sg. *Formica* L. (Kutter 1977) and obviously a "red wood ant" (actually more brightly red-coloured than other European red wood ants) is, as discussed previously (Rosengren et al. 1985), morphologically, biochemically and ethologically sharply separated from the complex discussed above and should, following Collingwood (1979), not be included in the *F. rufa* group. The material of this species was from an islet (Haraholm) situated 40 km west of Helsinki in the Ingå archipelago (habitat descriptions in Rosengren et al. 1985, 1986).

2.2. Experimental procedure

Ant groups of natural composition, comprising several thousand workers, the brood and some queens, were housed with natural nest material in spacious laboratory nests, as described previously (Rosengren 1977b, Rosengren & Fortelius 1986b). A 12 : 12 h light: dark regime was maintained in the laboratory (temperature, light intensity and humidity according to Rosengren & Fortelius 1986b). The light regime lead to an activity rhythm with maxima occuring at artificial dawn (Rosengren & Fortelius 1986b), but the short-term recordings, reported here, were made during the middle of the light period and were hence not influenced by diel variations.

The basic design of the device allowing automatic recording of ants departing from the nest along one-way bridges is given in Fig. 1 (for technical details see Rosengren 1977b and Rosengren & Fortelius 1986b). The ants entering the bridges were recorded by transistors coupled to a printing counter adding impulses through 5 min periods. Traffic on each given bridge could only occur in a given direction (to a foraging field *or* from a foraging field, Fig. 1). The one-way traffic was obtained by leaving a 0.5 mm gap between the terminal point of each bridge and the floor of the arena (Fig. 1) implicating that ants entering a foraging field (or returning to the nest field) had to "jump down" from the thin and slippery glass tip in which each bridge terminated. The gap made it easy to capture all ants crossing a given bridge by placing a Fluon^R -treated container under the glass tip.

The machine recordings contained a considerable amount of random-type noise and many ants entering a recording bridge (Fig. 1) turned back before reaching the foraging field, thus crossing the infrared beam and transistor more than once. This will not lead to systematic bias (Rosengren & Fortelius 1986b), but means that more ants are recorded by the apparatus than actually reach the foraging field. We do not, however, consider the correlation (Fig. 2) between manual counts (click counters and a stop watch) and machine counts too poor for the present purpose. A more serious source of bias is that signifi-

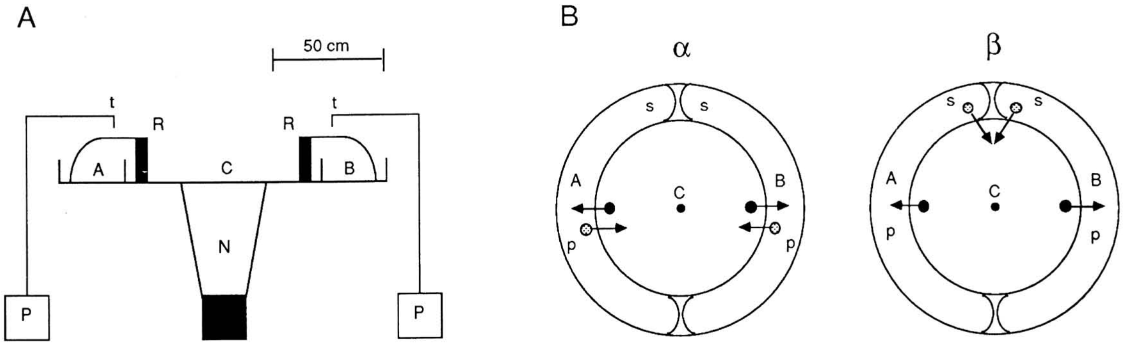


Fig. 1. Laboratory nest, foraging fields and recording method used for the experiments. — A. Device seen from the side: N = nest. R = one-way recording,bridges leading from the central field C, surrounding the nest entrance, to foraging fields A and B. The traffic activity on both the bridges was recorded by transistors (t) coupled to printing counters P, which summed impulses at 5-min intervals. — B. Device seen from above with return bridges in two different positions, α and β. Points connected to arrows symbolizes the four one-way bridges and their traffic directions (the tip of the arrow marks the terminal point of a bridge while the black point indicate the black pillar from which the ants enter a given bridge). The two bridges entering each of the foraging fields A and B (the separations isolating the fields from each others are indicated) are marked with arrows pointing toward the foraging fields while bridges for ants returning to the nest (small point in the centre of field C) are marked with arrows pointing toward the nest. The terminal points of the latter bridges are in the case of the α -position situated so that trails made by workers returning to the nest will coincide with the direction from the nest to the bridges entering A and B. The two bridges for return traffic to the nest are in the β -position situated so that trails made by workers returning on either bridge will coincide. The ants were fed with two identical and continuous sources of honey-water indicated by S (in A and B) while baits of protein food (P) was provided occasionally in either A or B.

cant but arbitrary activity maxima, occurring in some of our recordings, reduced the signal-to-noise ratio to a point where interpretations became difficult. Such "stochastic" peaks (e.g. in Fig. 7) suggest positive feed-back, perhaps based on some kind of diffuse social facilitation.

The ants were continuously satiated with sugar from a stable source of honey-water (Fig. 1). The protein food, offered only during the experiments, consisted of about 100 g of fresh beef, cut into pieces, (experiments 2–7) or a large amount of minced mealworms (experiment 8). The mealworms and some of the pieces of beef were sufficiently small to be carried by the ants to the nest but this was not a prerequisite for recruitment. The strong recruitment responses reported here could be found only if the ants had been deprived of protein for 1–2 weeks before the experiment. Some colonies showed a weak or no response, however, after even longer starvation periods, which suggested that additional variables were involved (e.g. the stage of the season, the size of the brood within the nest). Colonies reacting weakly to the baits were discarded. Recruitment could be observed in autumn, as well, but the reaction of the ants during this season proved difficult to predict (probably because of incipient hibernation) and we therefore preferred to carry out experiments in early spring to midsummer.

The ants could use the black-painted wooden pillars of the bridges (R in Fig. 1) as signposts for checking their course, but the visual panorama surrounding the nest entrance was symmetric with respect to the alternative foraging fields (A and B in Fig. 1). Visual differences between side A and B were further minimized by keeping the device within a large centrally lighted cylindrical drum, painted matt white on the inside. The ants in the marking experiment, in Fig. 5, had been marked with two colours, one for each foraging field. Indirect proof that we succeeded in excluding visual cues by these measures is that no site allegiance could be seen in the marked ants, although site allegiance has been demonstrated in laboratory arenas equipped with a "forest" of landmark cues (Rosengren 1971, Cosens & Toussaint 1985). Idiothetic orientation (Schöne 1984) is more difficult to eliminate, although we alternated baiting between side A and side B in different experiments. Elimination of visual or idiothetic cues is not, however, a prerequisite for the interpretation of our main results.

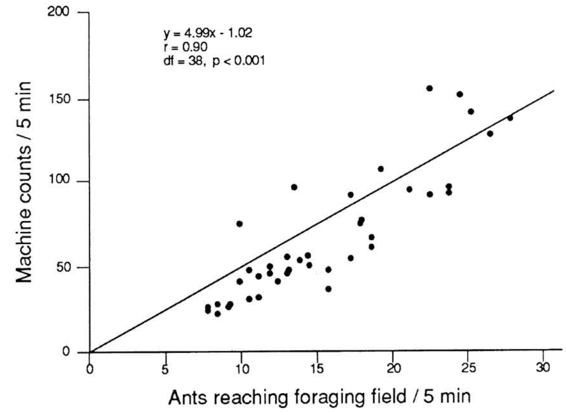


Fig. 2. Correlation in *F. grankullensis* between manual counts (per 5 min) of workers reaching a foraging field (X-axis) and machine counts on the corresponding bridge (Fig. 1). 81 % of the variation along the Y-axis is explicable by variation along the X-axis.

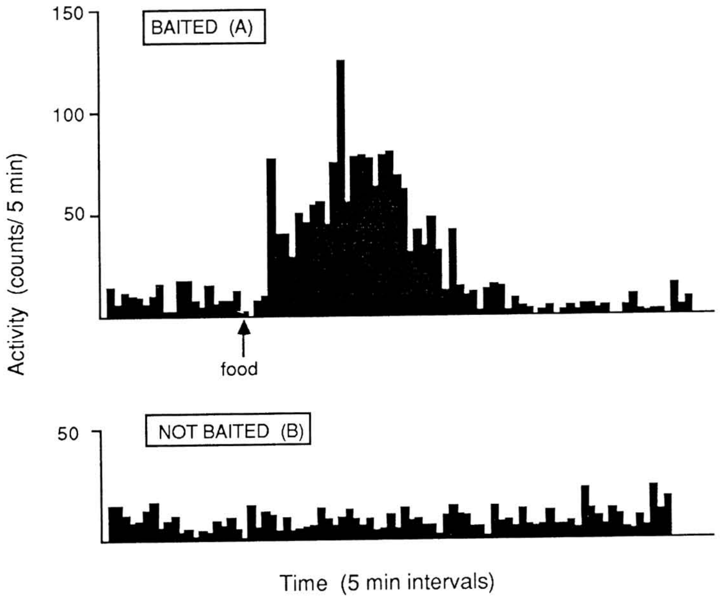


Fig. 3. Activity of *F. grankullensis* workers (machine counts/5 min) on bridges leading to a baited (side A) and an unbaited (side B) foraging field. The bridges for returning ants were in the α position (Fig. 1). Exhaustion of the bait (pieces of beef) and/or satiation of the ants lead to gradual decline of activity on the baited side. Note that no regular activity changes can be observed on side B. The introduction of the bait on side A is marked. Bars represent 5 minutes of recording.

3. Results

3.1. *Formica grankullensis*

The traffic intensity on the baited side increased dramatically, while neither an increase nor a decrease was detectable on the unbaited side, provided the bridges were in the α position (Fig. 3). Replete foragers of *F. aquilonia* returning from the food source are characterized by increased running speed (Cosens & Toussaint 1985) and speed can be assumed to affect the mean journey time of foragers (the time elapsing before the foragers are observed again at the same point). The mean journey time consists of the time spent by foragers within the foraging field, the time spent within the nest and the time used for the journey from the foraging field to the nest and back again. The result shown in Fig. 3 cannot be explained, however, by a decrease in the mean journey time of a fixed number of foragers assumed to cross the bridge more frequently when protein was provided. Firstly, even a modest increase in traffic intensity (the parameter measured in Fig. 3) resulted in a rapid accumulation of foragers within the baited field (Fig. 4), which showed that the bait increased the absolute number of participating foragers. Secondly, both the data presented in Fig. 4 and other observations suggest that at the beginning of recruitment many foragers actually prolong the time spent in the foraging field because they "investigate" the bait, while foragers visiting an unbaited field usually return to the nest after only a short "inspection". This behaviour is likely to compensate for the effect on the mean journey time of the increased running speed of ants travelling between the foraging field and the nest. That the absolute number of ants visiting a baited foraging field will increase is also clear from the following experiment. Slightly more than 30 % of the foragers visiting each of the foraging fields in the absence of bait (low traffic intensity, no protein on either side)

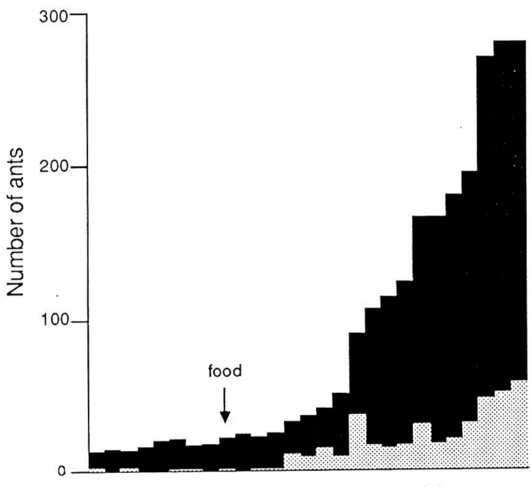


Fig. 4. Manual counts of *F. grankullensis* workers reaching a baited foraging field within 5-min periods (black area) and total number of ants counted in the foraging field at 5-min intervals (grey area). The introduction of the bait is indicated.

had been colourmarked. When one side was baited the percentage of marked ants on that side decreased to about 6 %, while remaining unchanged on the unbaited side (Fig. 5). This is a further argument to show that true directional recruitment is involved because the result, supporting a previous field experiment (Rosengren 1971), suggests that a group of ants that forages less regularly is enticed to the baited but not to the unbaited field.

Capture of all ants returning from the baited side (bridges in α position) resulted in a rapid reduction of the recruitment peaks (= traffic of ants departing from the nest) but did not affect traffic to the unbaited field (Fig. 6). When released in the centre of the arena, the captured ants immediately ran back to the baited side, although the return traffic was blocked (see the narrow activity peak in Fig. 6). A corresponding peak was not seen on the unbaited side, which indicates that the captured ants running back (and possible recruiting others) to the bait were well-oriented. This orientation was probably due to scent trails marking out the baited side (also functioning in the absence of continuous return traffic) because the device was visually symmetrical, although allowing use of visual cues for course checking (see Materials and Methods and Discussion). Removal of the trap blocking the return traffic again resulted in a strong activity maximum, which suggests directional recruitment (Fig. 6).

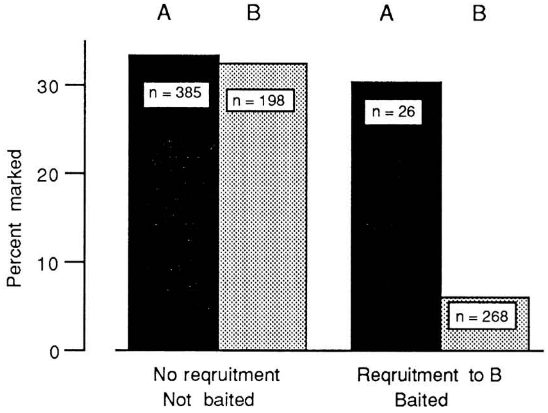
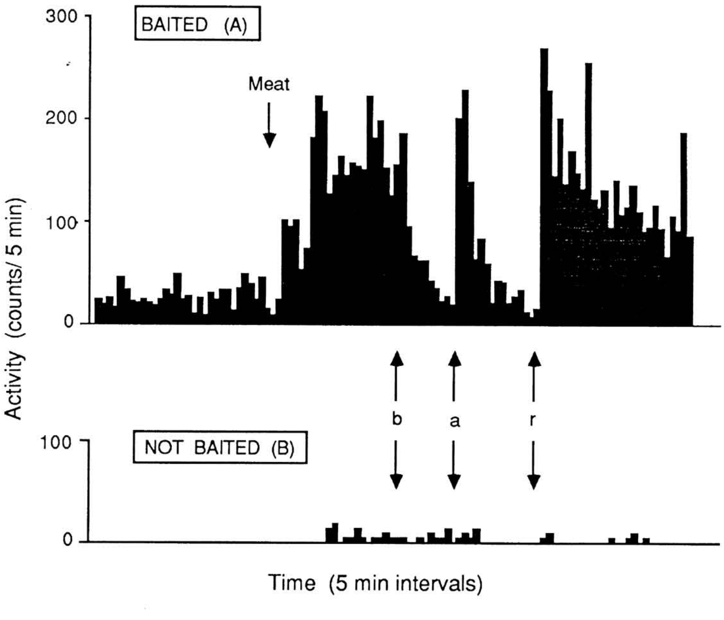


Fig. 5. Proportion of colour-marked *F. grankullensis* workers in samples of ants captured on the foraging fields A and B (Fig. 1). The ants had been marked in the foraging fields when no bait was present on either side. They were later sampled in A and B either in the absence of any bait on either side and hence no recruitment (left histogram) or during peak recruitment to B when a bait had been placed in foraging field B (right histogram). The values for non-recruitment (left histogram) were obtained by pooling several spotsamples (each consisting of all ants found at a given moment in the foraging fields A and B), while the values for baited conditions (right histogram) represent a single spotsample of ants captured in A and B respectively. The proportion of colour-marked ants differ significantly (χ^2 = 11.0, 1 *df*, $P<0.001$) when comparing the two histograms.

Fig. 6. — Upper figure: Machine recordings of *F. grankullensis* workers crossing the bridge to the baited foraging field A in 5-min periods. Return bridges in the α -position. A bait of meat placed on side A. b = the return traffic from side A blocked by placing the terminal point of the return bridge in a Fluon^R–treated trap. a = the trapped ants put back into the arena centre (return traffic still blocked). r = trap removed from return bridge. — Lower figure: Part of the traffic to the unbaited side B counted manually because of technical troubles with the recorder (manual counts transformed to machine counts with the aid of the regression equation in Fig. 2). The letter symbols refer to the measures taken on side A (above). Bars represent 5 minutes of recording.



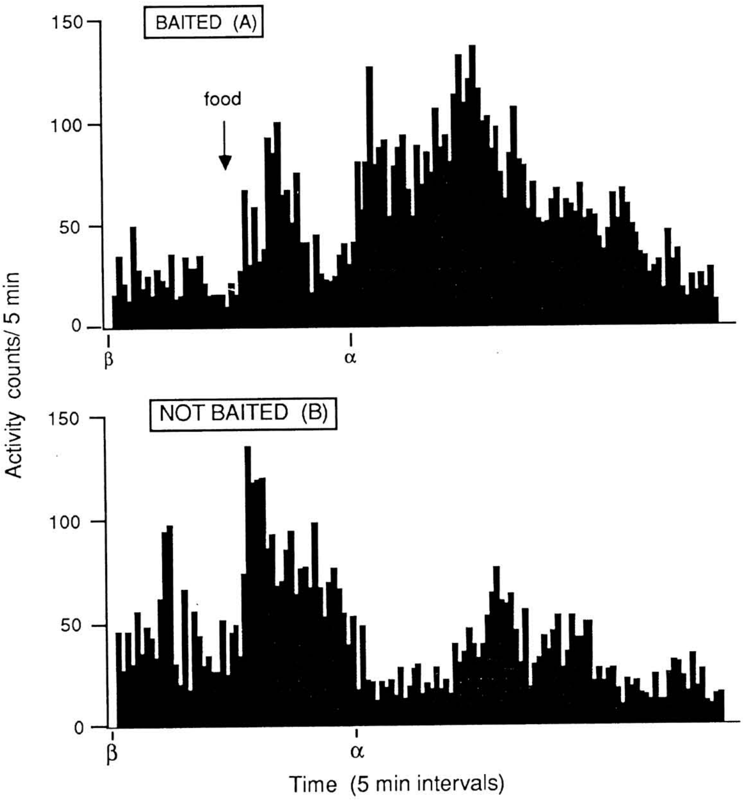


Fig. 7. Activity of *F. grankullensis* workers (machine counts/5 min) on bridges leading to the baited side A and the unbaited side B. The bridges for returning ants were in the β position (Fig. 1, cf. Fig. 3) in the first part of the experiment (β in the Fig.) but were later moved to the α position (α in Fig.). The introduction of the bait on side A is indicated. The cause of the extra "stochastic" peaks is unknown, but the result strongly suggest that recruits cannot decide the position of the bait when the return bridges are in the β position. Bars represent 5 minutes of recording.

The situation was very different when the bridges were in the β position. In this case, food on side A evoked strong recruitment response on both side A and side B, which indicates that the ants were unable to locate the direction of the bait (Fig. 7). Directional recruitment was restored, however, when the bridges were changed during the experiment from the β position to the α position (Fig. 7). The result is understandable if we assume that foragers, returning from the baited field to the nest, mark the path with scent (either a continuous streak or trail or discrete patches of pheromones). If laid from a return bridge in the α position, such scent marks will direct recruits to the food source. A scent trail laid from a bridge in the β position, however, will not allow the recruits to decide about the direction of the baited field and will thus not communicate relevant directional information (cf. Fig. 1).

3.2. *Formica truncorum*

With the bridges in the α position, directional recruitment was evident in this species, too (Fig. 8, upper graphs), but repetition of the experiment in the dark (light source switched off shortly before the experiment) revealed an unexpected complication (Fig. 8, lower graphs). Recruitment response in the dark was not only very slow but the recruits proved, at least initially, unable to distinguish between the baited and the unbaited field (Fig. 8). Directional recruitment was restored as soon as the light was switched on (Fig. 8).

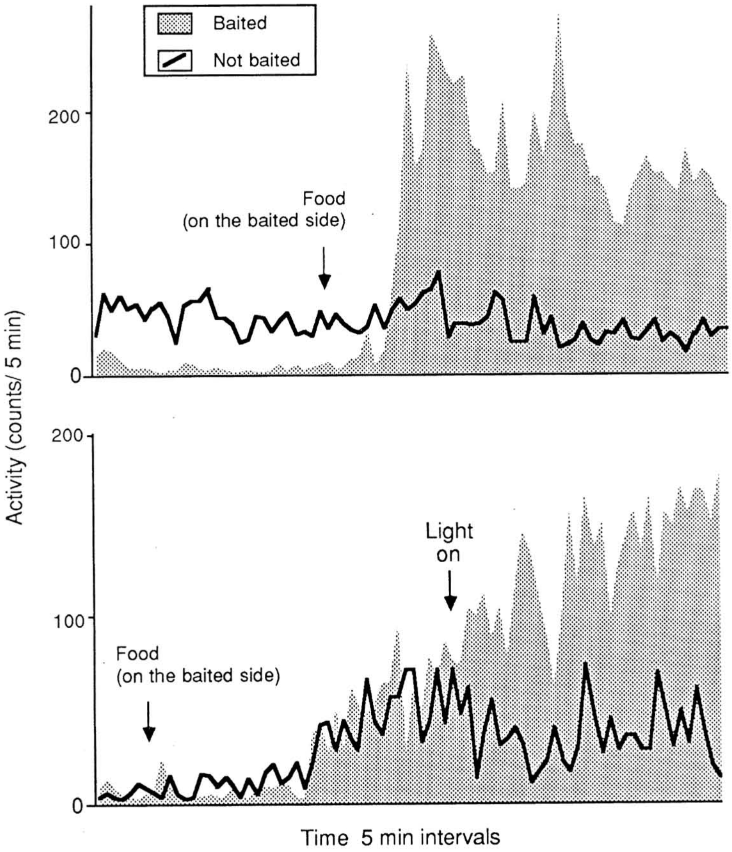
4. Discussion and conclusions

4.1. Experimental results

We intended to test recruitment in the dark in *F. grankullensis* and the effect of the bridge position (α, β) in *F. truncorum,* but a technical accident destroyed one of our printing counters before we had completed the test series. Our results, consequently, leave some of the questions unanswered but provide information on the following points:

1. Protein-starved laboratory colonies of the species tested show a very strong and rapid recruitment response to freshly introduced protein food, as

Fig. 8. Activity of *F. truncorum* workers (machine counts/5 min) on the baited and unbaited sides figured in the same graphs. Unbaited side = line. Baited side = hatched area. Upper graphs: continuous light throughout the experiment. Lower graphs: darkness in the first part of the experiment, light on indicated. Introduction of bait indicated on both graphs.



also observed previously (Rosengren 1977b). Red wood ant colonies can be deprived of proteins but not of sugar for a long time and we, therefore, used protein starvation in sugarsatiated colonies as the basis for our routine procedure. Recruitment to sugar baits after mild sugar starvation (a few days) is also possible (unpubl.), as noted by other authors (Horstmann 1976, Horstmann et al. 1982, Cosens & Toussaint 1985), but we found it easier to demonstrate recruitment with protein baits (note that a *large* amount of freshly minced insects or first-class beef has to be used). The latter observation is clearly at variance with the results of Horstmann et al. (1982) and Horstmann & Bitter (1984), which show that the recruitment response is much slower and weaker to insect booty than to sugar. This discrepancy indicates that account must be taken of a number of variables related to the experimental procedure, which was very different in the experiments by Horstmann & Bitter (1984).

2. Working with *F. aquilonia,* Cosens & Toussaint (1985) found recruitment of the same rapid type observed by us, but concluded that replete ants returning to the nest from food may stimulate nest mates to revisit previously remembered sites. We agree that the latter proposition could explain the present results as well, but disagree with the implication that this does not represent a case of directional recruitment. Whether the recruits revisit previously remembered sites or not, recruitment without conveyance of directional information would imply that the traffic to the unbaited side would also increase (note that the baiting in the different experiments was alternated between side A and side B and that when no bait was used the traffic intensities on the two sides were similar, see Fig. 3). A further argument for transfer of directional information is that, as observed in baiting experiments in the field as well (Rosengren 1971, 1977a), the recruits represented a different population (probably containing a high fraction of ants in the stage of transition from intranidal to extranidal work) from the workers frequenting the extranidal space in the absence of bait (Fig. 5). It is not important here whether those "novices" had some

experience of the foraging field they were visiting. The essential point is that the "novices" (whether strictly inexperienced or not) visited only the foraging field in which the bait was offered. The absolute increase in the number of workers present in the baited foraging field (Fig. 4) demonstrated that directional recruitment was taking place.

3. The failure of *directional* recruitment in *F. grankullensis* when the bridges were in the β position (Fig. 7) is consistent with the view that the main source of directional information may be scent trails laid from the food source toward the nest, as previously concluded by Horstmann (1976) for *F. polyctena*. An alternative possibility is that scouts may calculate the outward direction wrongly during the preceeding inward journey and communicate this direction in centripetal recruitment, thus making it impossible for recruits to decide whether the bait is in field A or B. Individual red wood ant workers are, however, able to use separate routes for the inward and outward journeys (Rosengren, unpubl.), which makes the latter interpretation appear less likely.

4. Red wood ant scent trails persist for a long time (Horstmann 1976, Elgert 1980, Horstmann & Bitter 1984). An alerting signal identical with the scent trail is not likely to lose its effect as soon as ants returning to the nest are captured — namely, in such a case the inward and outward traffic flow would not be strictly correlated. It was observed, however (Fig. 6), that the outward traffic decreased markedly as soon as the return traffic was blocked but increased immediately when returning workers were allowed to reach the nest (see also a laboratory experiment with *F. rufa* L. in Rosengren 1971). This could indicate the presence of alerting invitation signals (including offering of food) provided by returning workers inside or at the nest and separate from the orienting signals represented by the trail. Jerking motor displays shown by "excited" workers returning to the nest have been observed in red wood ants (Rosengren 1971) and the recruitment process in ants of the subgenus *Serviformica* consists of both alerting motor signals and a pure orienting component represented by the trail (Möglich & Hölldobler 1975). The significance of alerting motor signals of the jerking or wagging type (Hölldobler 1974) has been questioned in the case of red wood ants (Horstmann et al. 1982) and there is reason to believe that, for example, the jerking response frequently observed in red wood ants is not a context-bound but a modulatory social signal (see Markl 1985) with an array of different functions (Rosengren 1971). We consider it likely, however, that recruitment in *Serviformica* and *Formica* s.str. is similar in some basic respects and that alerting motor signals, whether having a limited function or not, may play a decisive role in red wood ant recruitment too.

5. Our finding that *F. truncorum,* although showing clear directional recruitment in the light, was unable to communicate direction adequately in the dark (Fig. 8) should, for reasons mentioned above (see Material and Methods), not be generalized to other species of the subgenus. *F. truncorum,* a xerothermic species inhabiting rocky habitats with sparse pine forest and frequently foraging on barren cliffs (Rosengren et al. 1985), has a diel activity pattern with stronger concentration of activity to the light period than in other tested *Formica* s. str. species (Rosengren & Fortelius 1986b). Ants usually forage in areas covered by a carpet of vegetation and this may have prevented evolution of recruitment systems based on visual signals, favouring the use of chemical trails. It is of some interest to note that the habitat is more favourable to the use of visual signals in the case of *F. truncorum,* but visual recruiting signals, although a constituent of the waggle dance of *Apis florea* bees (Gould et al. 1985), still remain a very remote possibility in the context of ant foraging. Red wood ant foragers returning from a rich food source have increased running speed (Cosens & Toussaint 1985) and there are indications that excited workers departing from the nest may have a different running pattern (Rosengren 1977a), but we have no evidence that such excited runners could act as guides for other workers. There is in fact another, more plausible interpretation of our finding (Fig. 8). Our device was symmetric with respect to external visual cues and this reduces the plausibility of a hypothesis based on visual communication or other centripetal mechanisms. A scout returning from food to the nest would afterwards have difficulty in separating the baited from the unbaited side of the device because the alternatives were visually equivalent (Fig. 1). It seems therefore more parsimonious to assume that, in this case too, the baited side was marked with a scent trail laid by scouts returning to the nest from the bait. But why should the ants be unable to extract directional information from a chemical trail in the dark while being able to interpret the message correctly during the period of light?

Orientation based on olfaction is often contrasted with visual orientation, as if those sensory modalities were mutually exclusive. Red wood ants appear to use a hierarchy of orientation cues, in which visual cues dominate over pheromonal cues when the cues are spatially separated by the experimental procedure (Rosengren & Fortelius 1986a). Such a conflict between visual and olfactory cues is certainly rare in nature, where the spatial information received through the different senses usually coincides and thus may be used as a double check in direction finding and homing. Closely related species adapted to different types of habitat differ in the relative importance attached to visual and olfactory orienting cues or they may have developed orienting mechanisms in which one type of cue can be utilized only in the presence of another type. The pheromone trail of *F. truncorum* may be too fragmentary to be used without a visual reference, a situation observed in recruiting *Trigona* bees using the sun compass for following a path marked by social chemical signals (Lindauer & Kerr 1960). Thus, pheromone trails could constitute the basis of directional recruitment even in species unable to use the information from the trail as the sole means of direction finding.

4.2. The ecological function of directional recruitment in red wood ants

Communication in social insects is sometimes interpreted according to a classical evolutionary ladder, in which "higher" species are figured as possessing more "advanced" means of social communication. This view overlooks the fact that the communication system, e.g. the mechanisms of recruitment, is likely to mirror the ecology of a species (see also discussion in Horstmann 1976). The desert ant *Cataglyphis bicolor,* relying on highly scattered, individually carried insect carrion, appears to lack food recruitment completely (Wehner et al. 1983), although the species is classed among "higher" ants. Red wood ants appear at first glance to represent a similar case (see Introduction) and this impression is strengthened by the observation that both their system of trunk routes and the distribution of traffic among the routes may remain virtually unchanged for a long time (Rosengren 1971). Directional recruitment to food may indeed, as concluded by Horstmann et al. (1982), be of limited significance during most of the summer season and field experiments with baits of beef (or mealworms) or sugar usually fail to give any evidence of recruitment to food during that period (Rosengren, unpubl.). It may be that artificial baits cannot compete with natural food in the summer (Horstmann 1975, Sudd & Sudd 1985) or are simply masked by the large amount of naturally occurring food brought to the moundnest from all parts of the habitat. Why should the ants react with mass recruitment to some mealworms presented by the observer, when hundreds of naturally occurring items of booty are brought by the ants each hour to their nest?

In early spring, before the maturation of aphids, red wood ants have to rely on ephemeral sugar sources of low quality, in southern Finland mainly sap leaking from birches (Rosengren & Sundström 1986), and during that period they can be enticed in large numbers to artificial sugar baits (Rosengren 1971, 1977a, Horstmann 1975). Shortages of insect booty seem to be rarer in the spring period in southern Finland (but see Driessen et al. 1984), but are sometimes observed in autumn (Rosengren 1977a). Baits of meat, although usually without a clear effect in spring, were found to release intense mass recruitment during a period of prolonged warm weather in autumn (Rosengren 1971), though protein baits do not have this effect every autumn (unpubl.). It has also occasionally been observed that red wood ants (probably due to shortages of insect booty) may visit vertebrate carrion in large numbers (Rosengren, unpubl.). Even if rare, seasonal shortages of resources could exert strong selection pressure in favour of directional mass recruitment during periods of starvation. Moreover, it should be noted that the lack of field evidence of directional recruitment in summer is not proof that no directional information is transmitted during that period. Maintenance of the forager population in a steady state implies that dead foragers are continuously replaced by novices, and novices departing from the nest for the first time are likely to be guided by scent trails along the permanent trunk routes of the colony (Rosengren 1977a). The only observable result of this process would be a gradual shift in the distribution of traffic among the routes, in response to the relative profitability of these routes, and even this effect could be too slow to be observed in the most stable habitats. The slowness of change during most of the summer period need not result from resource stability alone, however, but could also be due to high site allegiance in the majority of the foragers and a scarcity of potential recruits. The spring situation, by contrast, may be characterized not only by stronger temporal and spatial variation in resources but also by a much higher frequency of novices (advanced from intranidal to extranidal tasks during winter) with a versatile reaction to recruiting signals.

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Received 5.XI.1986 Printed 14.VIII.1987