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Research article

How does food distance influence foraging in the ant *Lasius niger:* the importance of home-range marking

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Abstract. We study the influence of food distance on the individual foraging behaviour of *Lasius niger* scouts and we investigate which cue they use to assess their distance from the nest and accordingly tune their recruiting behaviour.

Globally, the number of U-turns made by scouts increases with distance resulting in longer travel times and duration of the foraging cycle. However, over familiar areas, home-range marking reduces the frequency and thereby the impact of U-turns on foraging times leading to a quicker exploitation of food sources than over unmarked set-ups. Regarding information transfer, the intensity of the recruitment trail reaching the nest decreases with increasing food distance for all set-ups and is even more reduced in the absence of home-range marking. Hence, the probability of a scout continuing to lay a trail changes along the homeward journey but in a different way according to home-range marking. Over unexplored setups, at a given distance from the food source, the percentage of returning trail-laying ants remains unchanged for all tested nest-feeder distances. Hence, the tuning of the trail recruiting signal by scouts was not influenced by an odometric estimate of the distance already travelled by the ants during their outward journey to the food. By contrast, over previously explored set-ups, a distance-related factor – that is the intensity of home-range marking – strongly influences their recruiting behaviour. In fact, over a home-range marked bridge, the probability of returning ants maintaining their trail-laying behaviour increases with decreasing food distance while the gradient of home-range marks even induces ants which have stopped laying a trail to resume this behaviour in the nest vicinity.

We suggest that home-range marking laid passively by walking ants is a relevant cue for scouts to indirectly assess distance from the nest but also local activity level or foraging risks in order to adaptively tune trail recruitment and colony foraging dynamics.

Introduction

In order to make adapted individual decisions, foragers have to assess information about characteristics of food sources and the environment. Instead of making a complex assessment of all factors, they can utilize cues with a highly reliable and functional informative content (Detrain and Deneubourg, 1997, 2002). Several studies investigated how mass-recruiting ants tune their foraging and trail-laying behaviour mainly according to food characteristics (in *Lasius niger*, food quality: Beckers et al., 1993; food volume: Mailleux et al., 2000; food type: Portha et al., 2002; Le Breton and Fourcassié, 2004 or food weight in *Lasius neoniger,* Traniello, 1983; for a review see also Detrain et al., 1999a) but to a less extent according to environmental factors such as food distance. Concerning food distance, most authors who aimed at testing optimal foraging predictions, have examined how distance influences foraging strategies in terms of time/energy costs and gains for ant colonies. Relationships between increasing food distance and larger forager body sizes or heavier food loads were reported in fungus-growing (Roces, 1990; Wetterer, 1991; Roschard and Roces, 2003a), harvester (Nonacs, 2002) or honeydew collecting ant species (McIver and Loomis, 1993; Wright et al., 2000; Nonacs, 2002). There is also evidence that distance of food patches determines task partitioning, sequential load transport (Anderson et al., 2002; Roschard and Roces, 2003b) and size-matching (Ferster and Traniello, 1995; Roschard and Roces, 2003b). As regards food exploitation dynamics, distance acts upon the timing and/or intensity of nestmates recruitment to a foraging place (e.g. in *Paraponera clavata* (Fewell et al.,

1992), in fire ants (Hangartner, 1969; Horton et al., 1975; Taylor, 1977) and in harvester ants (Hölldobler, 1976; Taylor, 1977). Food distance also determines patterns of carbohydrates, lipids and protein flows in ant colonies (in *Solenopsis*, Weeks et al., 2004). While the ultimate causes of these foraging strategies have been extensively discussed, surprisingly less is known about how distance is assessed by scouts and influences foraging behaviour and recruitment decision-making at the individual level (see reviews by Hölldobler and Wilson, 1990; Detrain et al., 1999b). In this respect, *Lasius niger* foragers can monitor spatial information through the combined use of chemical and visual landmarks (Aron et al., 1993) but we do not know how they assess distance to discovered food sources (even in the absence of visual cues) and accordingly tune colony foraging dynamics.

Therefore, the two questions we have to answer are: 1) how distance influences the individual behaviour of scouts as well as their laying of a recruitment trail and 2) how it is assessed by ants either by a direct odometric measure of distance per se or by the use of a distance-related cue. We examined whether home-range marking could indirectly provide *Lasius niger* scouts with such cue since the local concentration of home-range marks that are laid passively by walking workers (Yamaoka and Akino, 1994; Devigne and Detrain, 2002; Depickère et al., 2004) is directly related to ants' density and thus decreases with distance from the nest.

Materials and methods

Rearing of ant colonies

Ten queenless *Lasius niger* colonies of about 800 individuals were reared in the laboratory within plaster nests (20 x 20 cm). Nests were placed in plastic trays (48 x 34 x 7.5 cm) the side of which had been coated with Fluon to prevent the ants' escape. Room temperature was kept at 23 ± 2C. Colonies were fed with dead cockroaches (*Periplaneta americana*) once a week and had permanent access to sugar solution (1 M) and water.

Experimental procedure

Before the experiment, colonies were starved for four days and were connected by a cardboard bridge (1 cm width) to a foraging platform (13 x 13 cm). A food source (1.5 ml of 1 M sucrose solution) was then placed in the middle of the foraging platform. A drawbridge system was used so that only one scout was given access to the bridge. Since we investigate the influence of distance and exploratory marking over the recruiting behaviour of scouts, we observed only the first ants that discovered the food source without the help of a previously laid trail to follow. We observed each scout during its whole foraging cycle from its arrival at the bridge until its departure from the bridge after having drunk at the food source. In order to prevent recruitment of nestmates and to ensure that only scouts were observed, we removed the observed ant just before it reached the nest, and kept it apart from the nest for the rest of the day. At most six ants were observed within the same experiment.

The whole experimental set-up was surrounded with a 50 cm high opaque enclosure to prevent scouts from using visual cues.

Since trail marks laid by a returning scout could influence the behaviour of next coming ants, around 25 min elapsed, on average, between two successive observations of scouts. This period was a reason-

able compromise between limiting a possible decrease of exploratory home range marks between the first and the last scout observed and allowing the evaporation of trail pheromone between successive scouts. We checked for the potential influence of one scout and its trail laying on the behaviour of following ones by comparing, with the Friedman's test (Zar, 1996), time parameters and number of trail marks of the first, second, third, fourth, fifth and sixth observed scout. We did not find any significant differences for any of these parameters over each set-up (all values of F_r with associated probabilities p > 0.15 and p > 0.1 for time parameters and trail-laying parameters, respectively).This confirmed that with this 25 min time interval, there was no influence of a previous scout on the behaviour of the following one (see Devigne et al., 2004).

To investigate how distance can influence foraging behaviour, scouts were tested over bridges differing in length, with a flat section of 30, 60 or 120 cm. For each of these lengths, we compared ant responses on bridges that differed in their exploratory marking as follows:

– Unmarked set-up (US). Ants were not allowed to explore and chemically mark either the bridge or the foraging platform before food introduction. Moreover, while the scout was drinking at the discovered food source, the bridge – which might have been marked during its outgoing trip – was replaced by a virgin one. Between successive observations of scouts, both the bridge and the platform were removed and replaced by new ones. This set-up allowed us to isolate the influence of distance alone on the behaviour of scouts.

– Marked set-up (MS). On the third day of starvation, the foraging platform was placed "in situ" and connected to the nest by the bridge. Ants were allowed to explore and mark the experimental set-up for 20 h before the introduction of the food source. In an earlier paper (Devigne and Detrain, 2002), we found that *Lasius niger* exploratory marking is rather a home-range than a true territorial marking since it does not give an edge for the residents during competitive interactions with intruders.

As *Lasius niger* scouts never lay their gaster tip over the substrate during their exploratory trips (pers. obs.), home range marks most probably originate from foot print hydrocarbons laid passively by walking ants (Yamaoka and Akino, 1994). The intensity of home-range marking is thus directly related to the density of workers and to the local activity level.

Hence, this second set-up is expected to have a gradient of home-range marks decreasing with the distance from the nest. In preliminary tests (n = 15), we allowed 38 scouts to explore an unmarked 120 cm bridge put "in situ" till they reached the platform area and we measured the number of passages over each section of this bridge. We found that the number of passages and thereby the amount of home-range marking decreased linearly with the distance from the nest (y = –0.11 x +2.64 (r² = 0.94)) confirming that a gradient of home-range marking actually occurs along the bridge. By using such a previously explored set-up, we examined the concurrent influence of home-range marking and distance on the foraging behaviour of scouts.

– "Homogeneously" marked set-up (HS). On the third day of starvation, the foraging platform and the bridge were not placed "in situ" but were positioned over the plastic trays at around 10 cm from the nest, parallel to its front edge. As a result, the set-up was home-range marked but was neutral with regard to directional information. Due to this lack of directionality, this set-up was referred to as being homogenously marked even though differences in home-range marks' concentration may occur locally. After 20 h of exploration, the bridge and the foraging platform were placed "in situ" and connected to the nest before the introduction of the food source. Comparisons between the results obtained on the HS and those on the MS point out the possible influence of a gradient of home-range marks on scouts foraging responses.

For each scout, we measured the following times:

– the time it took to discover the foraging platform, beginning when the scout climbed upon the bridge and ending when it reached the foraging platform.

– the time to discover the food source, beginning when the scout reached the foraging platform and ending when it began to drink.

– the total drinking time. As an ant could spontaneously interrupt food ingestion, successive drinking times were added up.

– the first time to leave the area beginning when the ant stopped drinking
and ending at its first departure from the platform. As scouts could
make U-turns over the bridge and return to the foraging platform, we
also noted the time until the last departure from the foraging platform
– the return time, beginning at the ant's last departure from the platform
and ending when it reached the end of the bridge.
– the duration of the foraging cycle of one scout is the sum of the above
time parameters.

To assess the influence of food distance on trail recruitment, we meas-
ured, for each scout, the intensity of its active laying of a chemical trail
by counting the number of marks deposited on the foraging platform as
well as on each bridge section. The flat part of the bridge was divided
into 10 cm sections, section A being the nearest to the platform. We
judged a forager to be laying a trail if its gaster curved to touch the
bridge and we assume that the number of marks and the actual quantity
of pheromone on a trail were closely related (as experimentally sup-
ported by Beckers et al., 1993).

To investigate how trail laying behaviour was tuned by scouts on
their way back to the nest, we compared for different distances and types
of marking how the proportion of trail-laying ants changed between suc-
cessive sections of the bridge.

In order to determine the influence of distance and home-range
marking on ants' orientation, we also measured the number of U-turns
during their outbound and inbound trips over the bridge. An ant is con-
sidered as making a U-turn as soon as it turned on the bridge and walked
at least 1 cm in the opposite direction.

Data analysis

In most cases, data were compared statistically using non-parametric
tests because the conditions of normality (checked with Kolmogorov-
Smirnov's test) and/or homoscedasticity (checked with Levene's test)
were not met. Time data as well as the number of trail marks laid by
scouts, were compared between set-ups by the Kruskal-Wallis' test and,
when significantly different, by Dunn's test for multiple comparisons.
The percentage of trail-laying ants were compared across different dis-
tances or marking set-ups by the G-test of independence (Zar, 1996).

Results

How does distance per se influence foraging behaviour of
Lasius niger *scouts?*
In this part, we analyse results obtained on unmarked set-ups
of different lengths.

Foraging times
When the bridge was free of any home-range marks, the *time
it took to discover the foraging platform* increased signifi-
cantly with bridge length (Table 1a Dunn's test) and was
proportionally longer than expected over the 120 cm bridge
(Table 1a). This longer lasting discovery of remote foraging
areas was probably due to a higher number of U-turns made
by scout workers (Table 2 Dunn's test).

As soon as a scout had reached the foraging platform, it
took her only around half a minute to find the food source due
to the small size of the platform. This *time it took to discover
the food source* did not change significantly with distance.

All the ants which found the food source, started to feed
on the sugar droplet but as a rule, they *spent more time drink-
ing* when they were far from the nest (Table 1c). However, no
difference was found between 60 and 120 cm (Table 1c
Dunn's test) suggesting that beyond a certain distance, ants
behaved similarly at the food source.

After drinking, scouts always took around 2 min to *leave
for the first time the platform* whatever its distance from the
nest and began to head homewards (Table 3). However, in
most cases, homing ants did not return straight to the nest but
made U-turns (Table 2b). As a result, *the last departure from
the foraging platform* occurred significantly later as a func-
tion of feeder distance (Table 1d Dunn's test). This was due
to the concurrent increase of U-turns by seemingly disorien-
tated ants walking more sinuously over long bridges (Table
2b Dunn's test).

As expected, the *return time of homing ants* increased
with distance but ants walked at similar speed whatever the
bridge length.

Finally, the *total duration of a foraging cycle* increased
significantly with food distance (Table 1f Dunn's test). This
resulted mainly from the increasing number of U-turns over
longer bridges that lengthened the time spent by ants to reach
the foraging area or to leave it definitively.

Trail-laying behaviour
Since we learned from an earlier study (Devigne and De-
train, 2002) that scouts exploring a new area and/or a new
bridge never lay a trail during their return trip, trail-laying
values observed over US reliably accounted for recruitment
modulation by homing scouts with regard to food distance
alone (and not according to a newly discovered place).

The number of trail marks laid over the foraging platform
was similar whatever its distance from the nest (Table 4a
Kruskal-Wallis' test). More than 80 % of those trail spots
were laid around the food source as soon as the ants stopped
drinking. This strongly suggests that the trail-laying behav-
iour of ants wandering around food is mainly influenced by
the characteristics of food resources and not by their distance
from the nest.

As scouts headed homewards, left the foraging area and
walked over the US bridge, trail-laying dramatically
dropped to the minimal value of less than one trail mark per
section on average (Fig. 1a). Even the trail amount laid at
the nest-side end of the 30 cm and 60 cm bridges (Table 4b)
was weak and still lower than one spot per 10 cm. This
small number of deposits for all unmarked set-ups ques-
tions the actual informative value of such trail-laying be-
haviour. Such steep trail decrease (Fig. 1a) was mainly due
to the ants (70 %) which stopped laying trails as they depart
from the foraging area for their home journey, instead of
ants which laid marks at a lower rate. Trail intensity de-
creased similarly whatever the feeder distance from the
nest: both the number of trail marks per section (Fig. 1a)
and the proportion of trail laying ants (Fig. 1b) were the
same over 30, 60 and 120 cm bridges (Fig. 1a, Kruskal-Wal-
lis' test, and Fig. 1b, G test of independence; no significant
difference except for the A section, p<0.05). Hence, neither
the probability of an ant ceasing to lay a trail nor the indi-

Table 1. Duration (in seconds) of the foraging cycle of scouts according to the type of home-range marking and the bridge length. The table gives the medians (and the quartiles).

a. Time to discover the area		Marking			Statistics
		US	MS	HS	
Bridge	30 cm	**30.5** (13–85)	**16** (11–25)	**16** (12–22.5)	us ≠ ms** us ≠ hs**
	60 cm	**64** (39–163)	**51** (27–258.5)	**54** (31.5–115)	NS
	120 cm	**180.5** (99.5–308.5)	**168** (84.5–324)	**136** (74–201.75)	NS
	Statistics	30 ≠ 60** 30 ≠ 120*** 60 ≠ 120**	30 ≠ 60*** 30 ≠ 120***	30 ≠ 60*** 30 ≠ 120***	
b. Time to discover the food source		US	MS	HS	Statistics
	30 cm	**22.5** (11–55)	**19** (9–33)	**20** (11–42)	NS
Bridge	60 cm	**27** (12.5–87)	**26** (12–78)	**15** (8.5–62.5)	NS
	120 cm	**23.5** (11–74.75)	**27** (13–81.5)	**29.5** (12.25–189.75)	NS
	Statistics	NS	NS	NS	
c. Drinking time		US	MS	HS	Statistics
	30 cm	**89** (63.5–98.25)	**111** (86–135)	**108** (94–123)	us ≠ ms*** us ≠ hs***
Bridge	60 cm	**111** (95–136)	**136** (104–165.75)	**122** (95–157.5)	us ≠ ms**
	120 cm	**119.5** (99.25–144.75)	**135.5** (113.75–180.75)	**123.5** (97.75–160.75)	NS
	Statistics	30 ≠ 60*** 30 ≠ 120***	30 ≠ 60** 30 ≠ 120**	NS	
d. Time to leave the area		US	MS	HS	Statistics
	30 cm	**105.5** (76.25–192.75)	**88** (49–147)	**111** (76.5–144.5)	NS
Bridge	60 cm	**246** (127.5–455.5)	**142** (82–253.5)	**218** (149–366)	us ≠ ms*
	120 cm	**421** (260–617.5)	**300.5** (172.75–538.5)	**241** (142.25–353.5)	us ≠ hs
	Statistics	30 ≠ 60*** 30 ≠ 120*** 60 ≠ 120*	30 ≠ 60*** 30 ≠ 120*** 60 ≠ 120*	30 ≠ 60*** 30 ≠ 120***	
e. Time to return to the nest		US	MS	HS	Statistics
	30 cm	**17** (12.75–22.25)	**20** (16–27)	**17** (13–22)	us ≠ ms*
Bridge	60 cm	**30** (23–43.5)	**37.5** (30–47.25)	**37** (29.5–46.5)	NS
	120 cm	**81** (57–136.5)	**65.5** (55–115)	**53.5** (44.75–78.75)	us ≠ hs**
	Statistics	30 ≠ 60*** 30 ≠ 120*** 60 ≠ 120***	30 ≠ 60*** 30 ≠ 120*** 60 ≠ 120***	30 ≠ 60*** 30 ≠ 120***	
f. Duration of foraging cycle		US	MS	HS	Statistics
	30 cm	**355** (243–502.75)	**285** (225–392)	**288** (245.5–343.5)	NS
Bridge	60 cm	**664** (484.5–879)	**552.5** (362.5–953.75)	**579** (421–738)	NS
	120 cm	**1041** (745.75–1397.75)	**860.5** (604.75–1205)	**699** (505.25–871.25)	us ≠ hs**
	Statistics	30 ≠ 60*** 30 ≠ 120*** 60 ≠ 120**	30 ≠ 60*** 30 ≠ 120***	30 ≠ 60*** 30 ≠ 120***	

US = Unmarked Set-up; MS = Marked Set-up; HS = Homogeneously marked Set-up.
Dunn's test with level of significance: NS = p > 0.05, * = p < 0.05; ** = p < 0.01; *** = p < 0.001.
Number of scouts observed: $N_{30US} = 56$; $N_{30MS} = 97$; $N_{30HS} = 51$; $N_{60US} = 63$; $N_{60MS} = 68$; $N_{60HS} = 31$; $N_{120US} = 46$; $N_{120MS} = 32$; $N_{120HS} = 26$

Table 2. Number (mean ± SD) of U-turns before scouts reached the foraging area (2a) or after they drunk at food droplet (2b).

a. Number of U-turn before reaching the area		Marking			
		US	MS	HS	Statistics
Bridge	30 cm	**1.12** (± 2.26)	**0.64** (± 1.67)	**0.14** (± 0.4)	us ≠ ms* us ≠ hs***
	60 cm	**2.16** (± 3.26)	**1.39** (± 2.21)	**1.3** (± 1.84)	NS
	120 cm	**3.04** (± 5.38)	**1.69** (± 1.71)	**1.29** (± 1.81)	NS
	Statistics	30 ≠ 120**	30 ≠ 60* 30 ≠ 120***	30 ≠ 60*** 30 ≠ 120**	
b. Number of U-turn after drinking		US	MS	HS	Statistics
Bridge	30 cm	**1.05** (± 1.14)	**0.85** (± 0.86)	**1.21** (± 0.89)	ms ≠ hs*
	60 cm	**2.98** (± 2.25)	**1.45** (± 1.36)	**3.35** (± 2.68)	us ≠ ms*** ms ≠ hs***
	120 cm	**5.61** (± 4.35)	**2.79** (± 2.57)	**3.65** (± 3.25)	us ≠ ms***
	Statistics	30 ≠ 60*** 30 ≠ 120*** 60 ≠ 120**	30 ≠ 60** 30 ≠ 120*** 60 ≠ 120**	30 ≠ 60*** 30 ≠ 120***	

US = Unmarked Set-up; MS = Marked Set-up; HS = Homogeneously marked Set-up.
Dunn's test with level of significance : NS = p>0.05, * = p < 0.05; ** = p < 0.01; *** = p < 0.001.
Number of scouts observed: $N_{30US} = 56$; $N_{30MS} = 97$; $N_{30HS} = 51$; $N_{60US} = 63$; $N_{60MS} = 68$; $N_{60HS} = 31$; $N_{120US} = 46$; $N_{120MS} = 32$; $N_{120HS} = 26$

Table 3. First departure times (in seconds) of scouts having drunk at the food source. The table gives the medians (and the quartiles).

First time to leave the area		Marking			
		US	MS	HS	Statistics
Bridge	30 cm	**62** (28.75–102)	**49** (29–96)	**47** (33.5–80.5)	NS
	60 cm	**61** (33.5–118.5)	**62.5** (38–111)	**48** (29–80.5)	NS
	120 cm	**73.5** (45–149.75)	**111** (36.25–200)	**57** (37.5–80)	NS
	Statistics	NS	30 ≠ 120*	NS	

US = Unmarked Set-up; MS = Marked Set-up; HS = Homogeneously marked Set-up.
Dunn's test with level of significance : NS = p > 0.05, * = p < 0.05. Number of scouts observed: $N_{30US} = 56$; $N_{30MS} = 97$; $N_{30HS} = 51$; $N_{60US} = 63$; $N_{60MS} = 68$; $N_{60HS} = 31$; $N_{120US} = 46$; $N_{120MS} = 32$; $N_{120HS} = 26$

vidual intensity of its trail-laying is influenced by food distance per se nor any possible odometric measure made during its outbound trip. This supports the idea that scouts did not tune the trail signal according to a direct assessment of feeder's distance.

To sum up, distance alone influenced travel time, time spent at the food source and total foraging time but had no effect on the trail-laying behaviour of scouts whose trail deposits steeply declined during their inbound trip whatever the feeder distance from the nest.

How does a distance-related cue – the level of home-range marking – influence the foraging behaviour of Lasius niger *scouts?*

Here we investigated whether distance has to be combined with a distance-related cue to have an effect on the foraging behaviour and overall on the recruiting decisions of scouts. The behaviour of scouts was then observed on set-ups that showed a gradient of home range marks laid in situ by exploring ants (MS) and compared to a control "homogeneously" home-range marked set-up (HS) deprived of any distance-related cue.

Table 4. Number (Mean ± SD) of trail marks laid per recruiting scout on the foraging platform (4a) and over the last section of the bridge, close to the nest (4b).

		US	MS	HS	Statistics
a.	30 cm	**5.4** (± 5.8)	6.2 (± 6.8)	6.7 (± 6.1)	NS
Total number of trail marks on the foraging platform	60 cm	**6.4** (± 6.5)	**4.8** (± 6.4)	4.8 (± 6.4)	NS
	120 cm	**5.4** (± 6.6)	**5.5** (± 7.1)	3.5 (± 4.6)	NS
	Statistics	NS	NS	NS	
b.	30 cm	**0.96** (± 2.14)	4.13 (± 4.41)	2.72 (± 3.3)	US ≠ MS*** US ≠ HS***
Number of trail marks on the last section of the bridge	60 cm	**0.54** (± 1.22)	2.68 (± 3.28)	0.32 (± 1.08)	MS ≠ US*** MS ≠ HS***
	120 cm	**0.11** (± 0.59)	1.17 (± 2.05)	0.12 (± 0.33)	MS ≠ US*** MS ≠ HS*
	Statistics	30 ≠ 120* 60 ≠ 120*	30 ≠ 120*** 60 ≠ 120*	30 ≠ 60*** 30 ≠ 120***	

US = Unmarked Set-up; MS = Marked Set-up; HS = Homogeneously marked Set-up.
Dunn's test with level of significance: NS = p > 0.05, * = p < 0.05; ** = p < 0.01; *** = p < 0.001. Number of observations: N_{30US} = 75; N_{30MS} = 109; N_{30HS} = 56; N_{60US} = 63; N_{60MS} = 69; N_{60HS} = 31; N_{120US} = 56; N_{120MS} = 58; N_{120HS} = 26.

Foraging times

When home-range marking was present over the set-up, we found the same general trends as those observed on the un-marked set-up (US). Globally, *the total duration of a foraging cycle* as well as the number of U-turns increased with the feeder distance (Table 1f Dunn's test). However, home-range marking tended to reduce differences in foraging times between the medium and long set-ups for which the foraging cycles had similar durations (NS between 60 cm and 120 cm over HS or MS set-ups, Table 1f). Home-range marking substantially improved the discovery time of the foraging area at least for short distances from the nest (Table 1a, Dunn's test, significant only for 30 cm). Similarly, the *time spent by ants until their final departure from the area* (Table 1d) decreased, although not always significantly, in both marked set-ups compared to US. The presence of exploratory marking could thus reduce the need for scouts to further explore the foraging area and hence lead to shorter time spent around the food source.

On the other hand, the perception of home-range marks in HS or MS seemed to lengthen the *drinking times* compared to the US, although this effect was significant only for short or medium distances from the nest (Table 1c, Dunn's test significant for 30 and 60 cm).

Finally, home-range marking improved the orientation of returning scouts over medium and long bridges and thereby reduced the travelling times, notably in the presence of a gradient. Indeed, the number of U-turns over MS (Table 2b, Dunn tests) substantially decreased, for 60 and 120 cm bridges compared to US and for 30 and 60 cm bridges compared to HS. This latter observation suggests that the gradient of home-range marks could somewhat facilitate the orientation of scouts by providing directional information.

Trail-laying behaviour

The number of trail marks laid over the foraging platform was similar whatever the food distance from the nest and the type of marking tested (Table 4a, Kruskal-Wallis' test). This strongly suggests that neither the feeder distance nor the presence of home-range marking influenced the trail-laying behaviour of scouts close to the food source. By contrast, the intensity of trail-laying behaviour during the inbound trip over the bridge differed when home-range marking was present. As a result, the number of trail-marks laid over the nest-side end of the bridge and hence the trail amount perceived by workers at the nest entrance was significantly higher on both home-range marked set-ups compared to the unmarked one (Table 4b, Dunn's test). Home-range marking thus played a key role in the tuning of recruitment trail with relation to food distance. Such impact of home-range marking acted at two levels: the continuation and the resumption of the trail-laying behaviour.

First, ants were more prone to maintain their trail-laying behaviour as they perceived home-range marks. As home-range marks were more numerous at short or medium distances from the nest, the proportion of trail-laying ants remained higher for each section of the 30 and 60 cm bridges compared to the longer 120 cm one (Fig. 2a, b and c, comparison between MS curves for each section A, B and C, χ^2 test: the three p values <0.001 and comparison between HS curves for A, B and C sections, χ^2 test: all p values <0.01 except for A section where p = 0.06).

Second, our results suggest that a gradient of home-range marks (in the MS) increasing towards the nest-end bridge section induced ants to resume their trail laying behaviour. Actually, the percentage of trail-laying ants tended to increase as
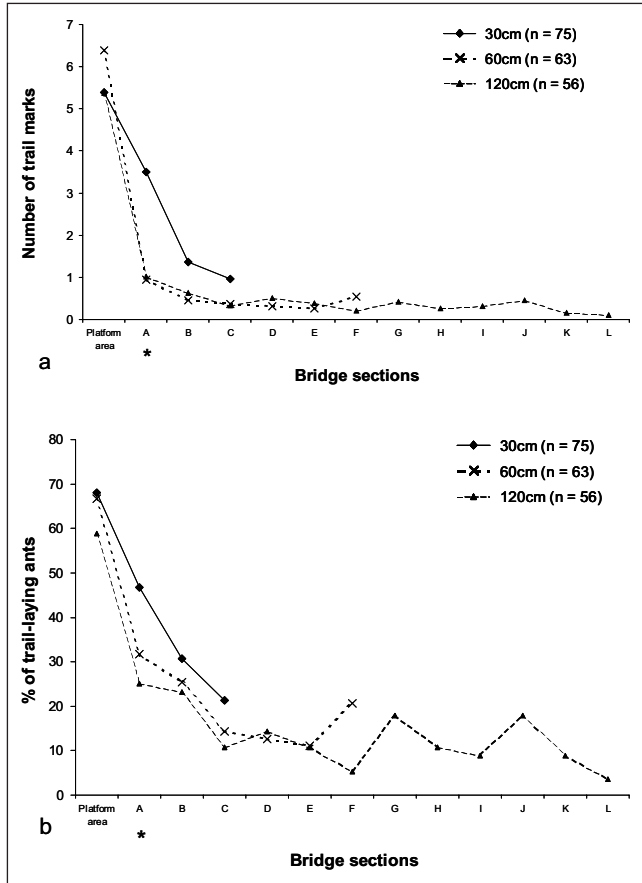
Figure 1. Trail-laying behaviour over the US. Each 10 cm section of the bridge are labelled in alphabetical order following their succession from the foraging platform to the nest.

a: Average number of trail marks laid per forager on its homeward trip on set-ups differing by their length.

Dunn's test with level of significance: * = p < 0.05.

b: Percentage of trail-laying ants as a function of their position (over the foraging platform and each bridge section).

G test of independence. * = p < 0.05.

Figure 2. Percentage of trail-laying ants as a function of their position on the set-up. Each 10 cm section of the bridge are labelled in alphabetical order following their succession from the foraging platform to the nest.

a: 30 cm, b: 60 cm and c: 120 cm.

US = Unmarked Set-up; MS = Marked Set-up; HS = Homogeneously marked Set-up.

G test of independence: NS = p > 0.05, * p < 0.5; **: p < 0.01; ***: p < 0.001.

they approached the nest entrance when a gradient of home-range marking was present (Fig. 2a, b and c; significant difference between the MS and US over the two last sections: G-test of independence, p < 0.001 for 30, 60 and 120 cm).

Owing to these combined effects of home-range marking, the intensity of the trail that reached the nest entrance (and hence the expected rate of nestmates' recruitment) differed according to the feeder distance (Table 4b, Kruskal-Wallis' test, KW = 25.6 and 32.65 for MS and HS respectively, p < 0.001). Notably in the MS, the number of trail marks over the last nest-end section of the 30 cm bridge was around four times higher than for the 120 cm bridge (Table 4b, Dunn's test). Thus, a modulation of recruitment and hence a preferential exploitation of closer food sources can occur provided recruiting scouts perceive a distance-related cue – home-range marking- during their inbound trip.

To sum up, the presence of home-range marking shortens nearly all the stages of a foraging cycle and reduced the dis-
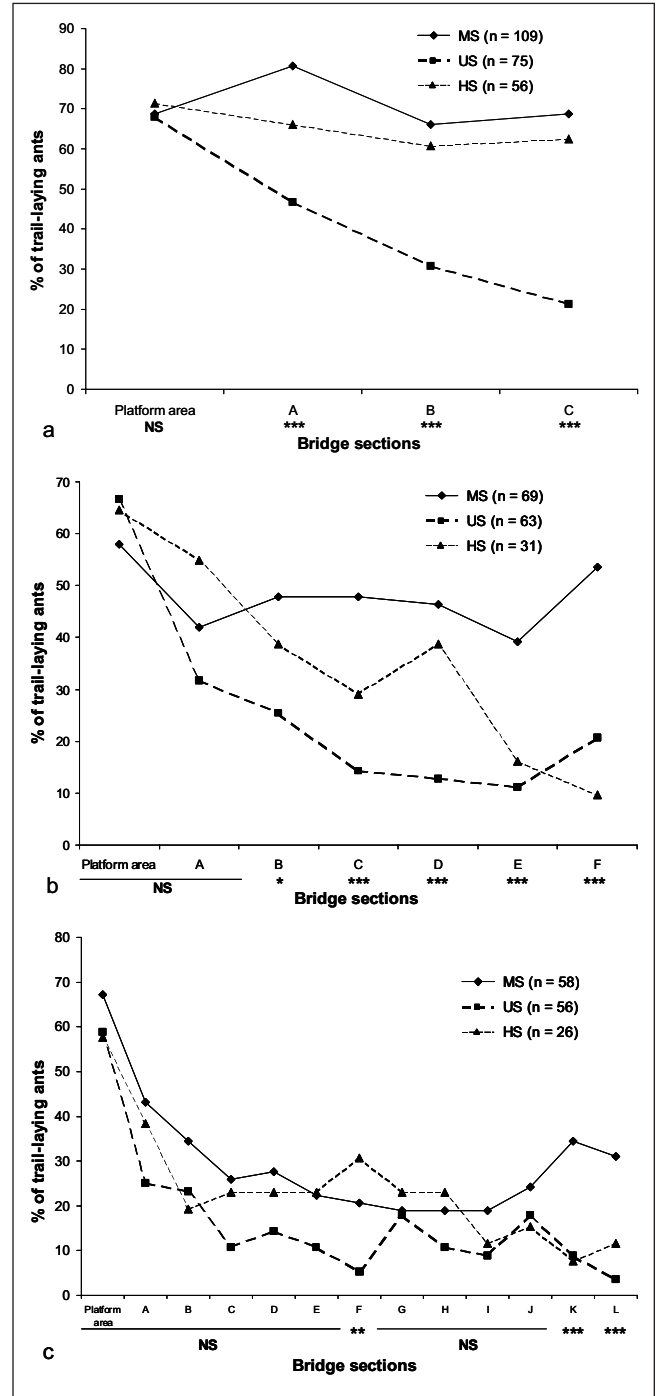
tance impact on foraging times namely between long and medium-sized bridges. Moreover, home-range marking fa-

vours the continuation of trail-laying behaviour during the homeward journey of scouts. Finally, a gradient of home-range marking (in the MS) influences the recruitment behaviour through a resumption of trail-laying behaviour as scouts approached the nest.

Discussion

Food distance is a constraint acting on the foraging decisions of ant colonies. Indeed, with increasing distance, knowledge of the environment decreases while, at the same time, predation risks and/or competition increase. Here we show how food distance can influence the individual foraging behaviour of *Lasius niger* scouts as well as trail recruitment intensity though the use of a distance-related cue – that is the level of home-range marking.

Changing cooperation level with foraging distance

Individual-based foraging is usually favoured with increasing food distance (Caroll and Janzen, 1973; Taylor, 1977; Heinrich, 1978), although the architecture of the foraging habitat may also exert strong influence on the recruitment decision (e.g. in arboreal ant species (Johnson et al. 2003)). Far from the nest, ants are expected to behave in a way that optimises their individual energetic return by increasing their patch residence time (Rissing and Pollock, 1984; Breed et al., 1996), their feeding time (Bonser et al., 1998 but see Hangartner, 1969) and by decreasing investment in nestmates' recruitment (Hangartner, 1969; Hölldobler, 1976; Taylor, 1977; Fewell et al., 1992). By contrast, close to the nest, cooperation and collective food exploitation are often triggered by strong recruitment trail (Hangartner, 1969; Taylor, 1977; Fewell et al., 1992) and facilitated by short patch residence times (Breed et al., 1996), among which variations may occur due to disturbances caused by the ants themselves (Halley and Burd, 2004).

We observe a similar trend in the ant species *Lasius niger*. Indeed, for nearby food sources, the times spent drinking or exploring food surroundings are shorter while the trail amount laid over the nest-end bridge is higher. Therefore, a more intense recruitment will be launched to near feeding sites due to a stronger and quicker information transfer to nestmates. In addition to distance effects, home-range marking influences the level of cooperation during food exploitation and contributes to maintain a high level of trail-laying among homing scouts confirming data from an earlier study (Devigne et al., 2004). Recruitment intensity is thus determined by the feeder distance as well as by other factors related to ant density such as the concentration of home-range marks. This indirect influence of ants' density on the communication dynamics of recruiting scouts strengthens a "democratic" scheme (Jaffe et al., 1985) for information transfer and decision-making in *Lasius niger* in which about 90% of successful scouts are known to lay a recruitment trail to sugary sources (Mailleux et al., 2000).

Choosing the nearest food source: the importance of foraging times

From a theoretical point of view, simulations of binary choices show that the selection of the nearest food source by a colony can simply result from shorter travel times and thereby steeper growth of recruitment dynamics without any modulation of recruitment (Stickland et al., 1992; Detrain et al., 1999b; Devigne et al., 1999). Our results give some support to these predictions since as the walking speed of *L. niger* scouts did not change with food distance (contrary to faster travel speed to far food patches in *Dorymyrmex goetschi* (Torres-Contreras and Vasquez, 2004)), the travel times were strongly correlated with food distance. The higher occurrence of U-turns coupled with longer-lasting drinking and exploring behaviour lengthens even more the duration of a foraging cycle towards remote feeding sites. Hence, distance delays information transfer to nestmates through recruitment trail and impedes the selection of far food sources, the exploitation of which would induce high costs in time and energy.

Tuning recruitment according to distance: what is the cue?

In addition to the role of foraging times the modulation of recruitment trail according to food distance can speed up the selection process of closer resources. We found out how scouts indirectly assess such food distance and accordingly shape their recruiting behaviour.

Whatever the feeder distance or the type of home-range marking, the trail-laying behaviour of ants is similar in the vicinity of the food source. This strongly suggests that ants' recruiting behaviour around the feeding site essentially depends on the food characteristics (Beckers et al., 1993; Mailleux et al., 2000; Portha et al., 2002) rather than on environmental factors such as the distance from the nest or the presence of home-range marking. By contrast, during the homeward trip, the trail-laying behaviour of scouts dramatically changes as a function of the level of home-range marking and the feeder distance.

One may question whether the modulation of recruiting behaviour by scouts relies on some direct measure of distance per se or on a distance-related cue that is the level of home-range marking. Potentially, ants can assess distance through several parameters among which the time and/or energy spent in travelling, step-counting or path integration (the latter being shown in solitarily foraging *Cataglyphis* ants: Müller and Wehner, 1988; Ronacher et al., 2000; Collett et al., 2001; Wohlgemuth et al., 2001; Sommer and Wehner, 2004). To our knowledge, the present study is the first one pointing out that *Lasius niger* scouts do not make a specific assessment and coding of the distance factor per se but rather rely on an indirect cue- the level of home range marking. Indeed, over unexplored set-ups, the probability that a scout lays a trail, as well as the intensity of its trail-laying, decreases along its inbound trip in a similar way whatever the feeder distance. Hence, the travelled distance experi-

enced by a scout during its outbound trip does not determine its further trail-laying behaviour when homing back to the nest. To get a modulation of the recruiting behaviour with respect to distance, bridges have to be previously explored and home-range marked, most probably with footprints cuticular hydrocarbons laid passively by walking ants (Yamaoka and Akino, 1994). In central place foragers such as ants, the density of exploring nestmates and thereby the concentration of home-range marks decrease with distance from the nest. It is thus a relevant cue for ants to assess the location of a feeding site and tune their recruitment accordingly. Here we confirm that home-range marks concentration actually enhances the trail-laying behaviour of returning scouts (see also Devigne et al., 2004) leading to a more intense recruitment trail towards nearby food sources. In addition, the gradient of home-range marks induces some resumption of trail-laying behaviour among ants approaching the nest. This suggests either that ants perceive the gradient of concentration, detecting changes in the amount of home-range marks during their return trip or that ants locally perceive a concentration of home-range marks exceeding a response threshold for trail-laying resumption.

To sum up, instead of "measuring" the absolute distance of food sources, scouts tune their recruiting and foraging behaviour according to a distance-dependent cue – home-range marking- that rates the activity level of the colony. Since in our set-ups visual cues were deliberately suppressed, the interplay between home-range marking and visual landmarks on the recruitment decisions of scouts still needs to be investigated.

Why use home range marking cue instead of distance per se?

This study shows that home-range marking and trail-laying are two chemical communication means with probably different adaptive values that act upon the information transfer in a synergistic way.

The significance of using a home-range cue to shape colony foraging dynamics becomes especially clear when placed in the ecological context of this aphid-tending ant species. It might be useful for scouts to tune their recruiting behaviour not only according to food distance from the nest but also from highly frequented locations such as trunk-trails that, together with the nest, represent the core of daily colony activity (Hölldobler, 1976; Hölldobler and Wilson, 1990). This is actually achieved by *Lasius niger* scouts that modulate trail-laying according to home-range marking concentration. Likewise, regardless of the food distance from the nest, in the arboreal *Gnamptogenys menadensis* ant species, most foragers are recruited from the few return routes and main branches over which the encounter rates with potential recruits are high (Johnson et al., 2003). By using a cue related to local nestmates' density, *Lasius niger* ants integrate information not only about their distance from the nest as well as from main trunk-trails but also about the safety of feeding sites, the local resources productivity or the work-

force available for cooperative food exploitation. Instead of dispersing foragers between multiple food sites, home-range marking helps ant colonies to keep a collective memory of a limited number of rewarding areas and seems to act as a catalyst for recruitment by promoting trail-laying in locations that are close to the nest, safe and/or regularly frequented by nestmates.

References

Anderson C., Theraulaz G. and Deneubourg J.L. 2002. Self-assemblages in insect societies. *Insect. Soc.* **49:** 99–110

Aron S., Beckers R., Deneubourg J.L. and Pasteels J.M. 1993. Memory and chemical communication in the orientation of two mass-recruiting ant species. *Insect. Soc.* **40:** 369–380

Beckers R., Deneubourg J.L. and Goss S. 1993. Modulation of trail-laying in the ant *Lasius niger* (Hymenoptera: Formicidae) and its role in the collective selection of a food source. *J. Insect Behav.* **6:** 751–759

Bonser R., Wright P.J., Bament S. and Chukwu U.O. 1998. Optimal patch use by foraging workers of *Lasius fuliginosus*, *L. niger* and *Myrmica ruginodis*. *Ecol. Entomol.* **23:** 15–21

Breed M.D., Bowden R.M., Garry M.F. and Weicker A.L. 1996. Giving-up time variation in response to differences in nectar volume and concentration in the giant tropical ant, *Paraponera clavata* (Hymenoptera: Formicidae). *J. Insect Behav.* **9:** 659–672

Caroll C.R. and Janzen D.H. 1973. Ecology of foraging by ants. *Annu. Rev. Ecol. Syst.* **4:** 231–257

Collett T.S., Collett M. and Wehner R. 2001. The guidance of desert ants by extended landmarks. *J. Exp. Biol.* **204:** 1635–1639

Depickère S., Fresneau D., Detrain C. and Deneubourg J.L. 2004. Marking as a decision factor in a choice of a new resting site in *Lasius niger*. *Insect. Soc.* **51:** 243–246

Detrain C. and Deneubourg J.L. 1997. Scavenging by *Pheidole pallidula*: a key for understanding decision-making systems in ants. *Anim. Behav.* **53:** 537–547

Detrain C. and Deneubourg J.L. 2002. Complexity of environment and parsimony of decision rules in insect societies. *Biol. Bull.* **202:** 268–274

Detrain C., Deneubourg J.L. and Pasteels J.M. 1999a. *Information Processing in Social Insects*. Birkhäuser Verlag, Basel. 415 pp

Detrain C., Deneubourg J.L. and Pasteels J.M. 1999b. Decision-making in foraging by social insects. In *Information Processing in Social Insects* (C. Detrain, J.L. Deneubourg and J.M. Pasteels, Eds), Birkhäuser Verlag, Basel. pp 331–354

Devigne C. and Detrain C. 2002. Collective exploration and area marking in the ant *Lasius niger*. *Insect. Soc.* **49:** 357–362

Devigne C., Detrain C. and Deneubourg J.L. 1999. Impact of food distance on foraging by the ant *Lasius niger*. In *Social Insects at the Turn of the Millenium* (P. Schwarz and K. Hogendoorn, Eds) Proc. 13th Int. Congr. IUSSI. p 139

Devigne C., Renon A.J. and Detrain C. 2004. Out of sight but not out of mind: modulation of recruitment according to home-range marking in ants. *Anim. Behav.* **67:** 1023–1029

Ferster B. and Traniello J.F.A. 1995. Polymorphism and foraging behavior in *Pogonomyrmex badius* (Hymenoptera, Formicidae) – worker size, foraging distance, and load size associations. *Env. Entomol.* **24**: 673–678

Fewell J.H., Harrison J.F., Stiller T.M. and Breed M.D. 1992. Distance effects on resource profitability and recruitment in the giant tropical ant, *Paraponera clavata*. *Oecologia* **92**: 542–547

Halley J.D. and Burd M. 2004. Nonequilibrium dynamics of social groups: insights from foraging Argentine ants. *Insect. Soc.* **51**: 226–231

Hangartner W. 1969. Structure and variability of the individual odor trail in *Solenopsis geminata* Fabr. (Hymenoptera: Formicidae). *Z. vergl. Physiol.* **62**: 111–120

Heinrich B. 1978. The economics of insect sociality. In *Behavioural Ecology – an Evolutionary Approach* (J.R. Krebs and N.B. Davies, Eds), Blackwell Scientific Publications, Oxford. pp 97–128

Hölldobler B. 1976. Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. *Behav. Ecol. Sociobiol.* **1**: 3–44

Hölldobler B. and Wilson E.O. 1990. *The Ants*. The Belknap Press of Harvard University Press, Cambridge, Mass. 732 pp

Horton P.M., Hays S.B. and Holman J.R. 1975. Food carrying ability and recruitment time of the red imported fire ant. *J. Georgia Entomol. Soc.* **10**: 207–213

Jaffe K., Villegas G., Colmenares O., Puche H., Zabala N., Alvarez M., Navarro J. and Pino E. 1985. Two different decision-making systems in recruitment to food in ant societies. *Behaviour*, **92**: 9–21

Johnson C.A., Lommelen E., Allard D. and Gobin B. 2003. The emergence of collective foraging in the arboreal *Gnamptogenys menadensis* (Hymenoptera: Formicidae). *Naturwissenschaften* **90**: 332–336

Le Breton J. and Fourcassié V. 2004. Information transfer during recruitment in the ant *Lasius niger* L. (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* **55**: 242–250

Mailleux A.C., Deneubourg J.L. and Detrain C. 2000. How do ants assess food volume? *Anim. Behav.* **59**: 1061–1069

McIver J.D. and Loomis C. 1993. A size-distance relation in homoptera-tending thatch ants (*Formica obscuripes*, *Formica planipilis*). *Insect. Soc.* **40**: 207–218

Müller M. and Wehner R. 1988. Path integration in desert ants, *Cataglyphis fortis*. *Proc. Natl. Acad. Sci. USA* **85**: 5287–5290

Nonacs P. 2002. Patterns of energy allocation within foragers of *Formica planipilis* and *Pogonomyrmex salinus*. *West N. Am. Nat.* **62**: 188–196

Portha S., Deneubourg J.L. and Detrain C. 2002. Self-organized asymmetries in ant foraging: a functional response to food type and colony needs. *Behav. Ecol.* **13**: 776–781

Rissing S.W. and Pollock G.B. 1984. Worker size variability and foraging efficiency in *Veromessor pergandei* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* **15**: 121–126

Roces F. 1990. Leaf-cutting ants cut fragment sizes in relation to the distance from the nest. *Anim. Behav.* **40**: 1181–1183

Ronacher B., Gallizzi K., Wohlgemuth S. and Wehner R. 2000. Lateral optic flow does not influence distance estimation in the desert ant *Cataglyphis fortis*. *J. Exp. Biol.* **203**: 1113–1121

Roschard J. and Roces F. 2003a. Fragment-size determination and size-matching in the grass-cutting ant *Atta vollenweideri* depend on the distance from the nest. *J. Trop. Ecol.* **19**: 647–653

Roschard J. and Roces F. 2003b. Cutters, carriers and transport chains: distance-dependent foraging strategies in the grass-cutting ant *Atta vollenweideri*. *Insect. Soc.* **50**: 237–244

Sommer S. and Wehner R. 2004. The ant's estimation of distance travelled: experiments with desert ants, *Cataglyphis fortis*. *J. Comp. Physiol. A* **190**: 1–6

Stickland T.R., Tofts C.M.N. and Franks N.R. 1992. A path choice algorithm for ants. *Naturwissenschaften* **79**: 567–572

Taylor F. 1977. Foraging behavior of ants: experiments with two species of Myrmicine ants. *Behav. Ecol. Sociobiol.* **2**: 147–168

Torres-Contreras H. and Vasquez R.A. 2004. A field experiment on the influence of load transportation and patch distance on the locomotion velocity of *Dorymyrmex goetschi* (Hymenoptera, Formicidae). *Insect. Soc.* **51**: 265–270

Traniello J.F.A. 1983. Social organization and foraging success in *Lasius neoniger* (Hymenoptera: Formicidae) : behavioral and ecological aspects of recruitment communication. *Oecologia* **59**: 94–100

Weeks R.D., Wilson L.T., Vinson S.B. and James W.D. 2004. Flow of carbohydrates, lipids and protein among colonies of polygyne red imported fire ants, *Solenopsis invicta*. *Ann. Entomol. Soc. Amer.* **97**: 105–110

Wetterer J.K. 1991. Source distance has no effect on load size in the leaf-cutting ant *Atta cephalotes*. *Psyche* **98**: 355–359

Wohlgemuth S., Ronacher B. and Wehner R. 2001. Ant odometry in the third dimension. *Nature* **411**: 795–798

Wright P.J., Bonser R. and Chukwu U.O. 2000. The size-distance relationship in the wood ant *Formica rufa*. *Ecol. Entomol.* **25**: 226–233

Yamaoka R. and Akino T. 1994. Ecological importance of cuticular hydrocarbons secreted from the tarsus of ants. In: *Les Insectes Sociaux* (A. Lenoir, G. Arnold and M. Lepage, Eds) Université Paris-Nord. p 222

Zar J.H. 1996. *Biostatistical Analysis*. Prentice-Hall, New Jersey. 662 pp

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