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Orientation and navigation during adult transport between nests in the ant *Cataglyphis iberica*

Abstract *Cataglyphis iberica* is a polydomous ant species in which adult transports between nests are frequently observed. When pairs of workers were captured and released at the same location, the transporters (Ts) fled directly towards their destination nest and reached it in most of the cases. The transportees (Te), on the other hand, fled in the opposite direction and only a third of them eventually reached their nest of departure. Additional experiments suggest that this result may be explained by the fact that the Ts ants have a memory of the compass direction of the nest they are heading to and that they adjust their course by using a sequence of memorised landmarks. As regards to the Te, the reversal of their direction of transport seems to be based essentially on celestial cues.

Introduction

Cataglyphis iberica is a monogynous and polydomous ant species (colonies have several nests, one of them with the queen). Adult transports between nests (Fig. 1) are maximum in spring and decrease during summer (Cerdá et al. 1994). Laboratory studies show that transporters (Ts) occupy an intermediate position between intranidal workers and foragers and that transportees (Te) are younger workers (Cerdá and Retana 1992; Dahbi et al. 1997). Dahbi et al. (1997) have sug-

gested that transport may be a means by which colonies are able to maintain a uniform odour: young workers could be distributed through satellite nests in order to acquire the colony odour via trophallaxis and allo-grooming. Since inter-nest traffic does not occur along chemical trails in this species, these authors also hypothesised that transport could have another function, namely to familiarise naive individuals with the spatial surroundings of their colony. We tested this hypothesis in the field by performing various orientation and navigation tests on Ts and Te ants.

General methods

Field experiments were carried out in Bellaterra (Barcelona, NE Spain) at the beginning of May. We worked on a colony located on a flat part of a wasteland without trees and with small bushes and sparse patches of grass. The colony was composed of two groups of three nests about 35 m apart. Transports occurred within as well as between the two groups of nests.

Experiments were run between 1000 and 1700 hours at an average air temperature of 36.5 °C (range: 31.5–41 °C). In each experiment, several Ts/Te pairs

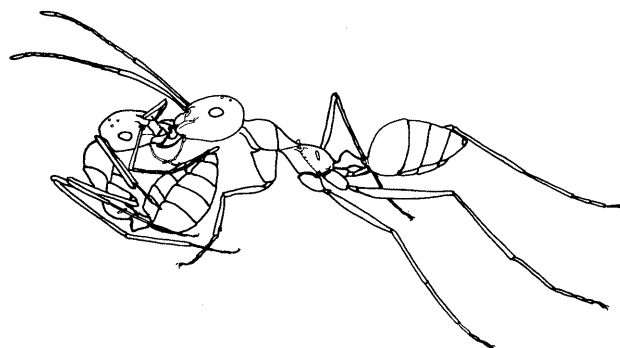


Fig.1 Drawing showing an adult transport of *Cataglyphis iberica*

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were captured. Each pair was gently dissociated and workers were kept in separate tubes and tested individually. Ants were released directly on the ground, at the centre of two concentric circles of 1 m and 2 m radius. The time taken by an ant to reach each circle, as well as the direction in which it crossed the circles for the first time, was noted. We used circular statistics (Batschelet 1981) to compute the direction and length of the mean vector of the distribution of the fleeing directions. The analysis was conducted on each category of individuals and on each circle. The zero direction was set to the direction of the nest of destination. The Wilcoxon test was used to compare the time performance of the Te and the Ts in each pair of ants.

Results

Experiment 1

We first tested whether ants captured between their nest of departure and their nest of destination were able to find their way towards one of the two nests. Fifteen pairs of ants were captured while moving between the two groups of nests in the colony and nine pairs while moving within one of the two groups of nests. Ants were released at the same point as their point of capture and followed for up to 15 min or until reaching a nest, in which case their homing performance (HP) was assessed by dividing the homing time by the distance travelled from the release point.

For each pair of ants the Ts set their bearings significantly quicker than the Te, both at 1 m and 2 m from the release point (Table 1; Wilcoxon: $z = -2.74$ and

$z = -3.00$, $P < 0.01$, respectively). The Ts fled on average in the direction of their destination nest (Fig. 2a) and their fleeing directions were significantly clustered around the direction of this nest, both at 1 m and 2 m from the release point (V -test: $u = 3.88$ and $u = 0.98$, $P < 0.001$, respectively). When they were followed, 92% of them eventually reached the destination nest while only 8% reached the nest of departure (Table 1). In contrast, the fleeing directions of the Te were significantly clustered around the direction of the nest of departure (Fig. 2a), both at 1 m and 2 m from the release point (V -test: $u = 4.18$ and $u = 5.14$, $P < 0.001$, respectively). Only 33% of the Te eventually reached the nest of departure. The remaining ants behaved as if they were lost, even 15 min after being released (Table 1). The distributions of the angular differences between the fleeing directions of the Ts and the Te for each pair of ants were significantly clustered around 180° , both at 1 m and 2 m from the release point (V -test: $u = 3.35$ and $u = 4.67$, $P < 0.001$, respectively). This means that the Te oriented on average at 180° of the Ts direction. The homing performance was better in the Ts (Table 1; Mann-Whitney: $z = -3.43$, $P < 0.001$). The Ts reached the nest of arrival after following an almost direct course whereas the Te made several great loops before reaching it.

Experiment 2

In the preceding experiment, ants could set their initial fleeing direction by using either celestial or terrestrial cues, or a combination of both. To prevent orientation based on terrestrial landmarks, ants were passively dis-

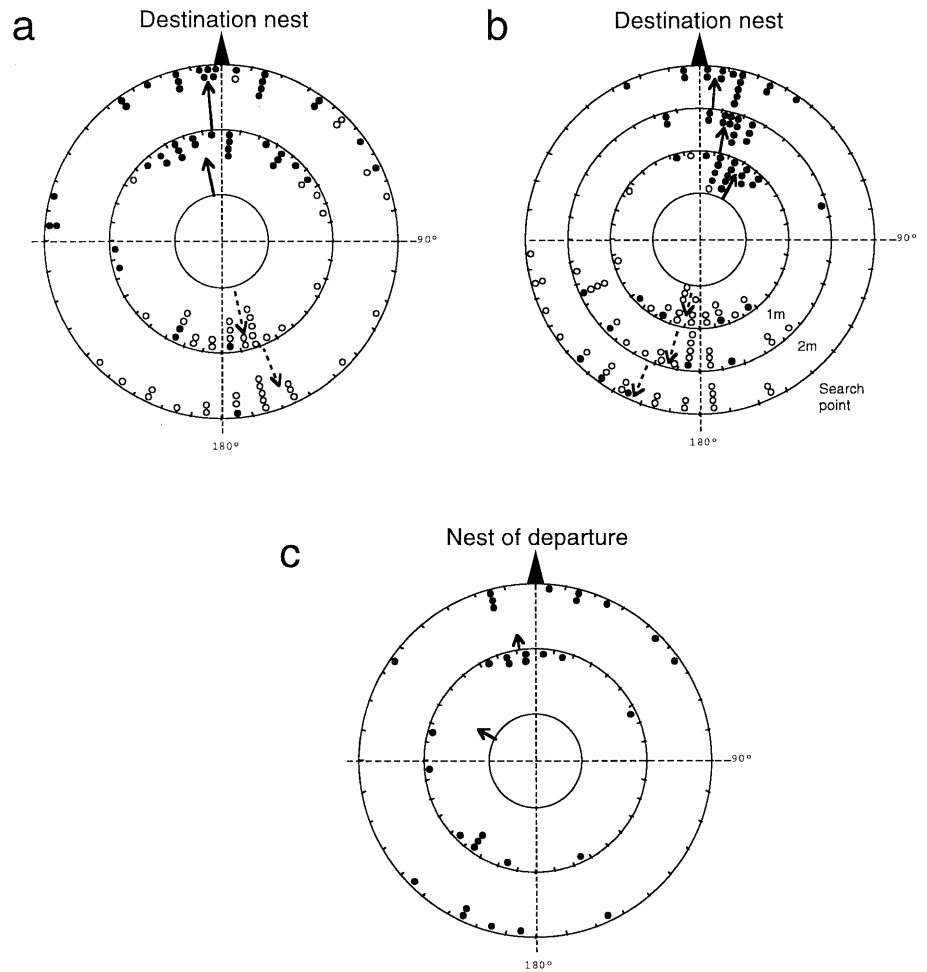
Table 1 Results of the experiments. n : sample size. t_i : mean time \pm SD (s) to reach the circle. α_i , r_i : angle (degrees) and length of the mean vector (with results of the Rayleigh's test) of the distribution of the fleeing directions. Experiments 1 and 3: *Successful run*: number of ants that eventually reached the nest of departure (N_{dep}) or the nest of destination (N_{dest}) within 15 min of their release and average homing performance (HP_{dep} and HP_{dest}) in s

m^{-1} (homing time divided by the distance from the release point to the nest of arrival). *Unsuccessful run*: number of ants that did not reach one of the nests. Experiment 2: *Search point* is the point at which ants began to deviate in their course by an angle greater than 90° . Az_s , r_s , *Dist.*: mean azimuth of the search points, length of the mean vector of the distribution of the azimuths and mean distance of the search point from the release point, respectively

Experiment 1	n	1 m radius circle			2 m radius circle			Successful run				Unsuccessful run
		t_1	α_1	r_1	t_2	α_2	r_2	N_{dep}	HP_{dep}	N_{dest}	HP_{dest}	
Transporters (Ts)	24	34 \pm 35	349	0.57***	46 \pm 38	354	0.72***	2	17	22	22	0
Transportees (Te)	24	53 \pm 34	167	0.71***	97 \pm 88	158	0.62***	8	79	0		16
Experiment 2	n	1 m radius circle			2 m radius circle			Search point			Unsuccessful run	
		t_1	α_1	r_1	t_2	α_2	r_2	Az_s	r_s	Dist.		
Transporters (Ts)	20	20 \pm 11	27	0.62***	33 \pm 11	12	0.59***	4	0.62***	6.1		
Transportees (Te)	20	102 \pm 115	191	0.66***	164 \pm 156	195	0.84***	203	0.85***	2.8		
Experiment 3	n	1 m radius circle			2 m radius circle			Successful run				Unsuccessful run
		t_1	α_1	r_1	t_2	α_2	r_2	N_{dep}	HP_{dep}	N_{dest}	HP_{dest}	
Transporters (Ts)	16	35 \pm 19	298	0.29	89 \pm 85	351	0.21	3	29	8	36	5

*** $P < 0.001$

Fig.2a-c Fleeing directions of *Cataglyphis iberica* workers during different experiments. **a** Experiment 1: ants captured and released at the same point. **b** Experiment 2: ants captured at one point and released 18 m away. **c** Experiment 3: ants captured a few centimetres from their nest of destination and released 2 m behind their nest of departure, on the prolongation of the line linking the two nests between which the transport had occurred. The two concentric circles in **a** and **c** show the directions measured at 1 m and 2 m from the release point. The third circle in **b** shows the directions at which the course of the ants was deviated by more than 90° (search point). Black dots Transporters (Ts); white dots transportees (Te). The zero direction is that of the nest of destination in **a** and **b** and that of the nest of departure in **c**. The mean vector is indicated by an arrow for each distribution (continuous line transporters, Ts; dashed line transportees, Te). The distance between two concentric circles corresponds to a vector length equal to 1



placed in darkness from their capture point to a release point 18 m away (outside the area where transport usually occurred). The same parameters as in experiment 1 were measured. In addition, we noted the direction and distance from the release point of the location at which ants began to deviate in their course by an angle greater than 90°. We will refer to that location, at which the ant seemed to have reached its intended goal as the “search point”. After reaching this point, 11 out of 20 Ts were captured again, released at their initial point of capture and followed for up to 15 min or until reaching a nest.

The Ts were much quicker than the Te to set their bearings at 1 and 2 m from the release point (Table 1; Wilcoxon: $z = -3.74$ and $z = -3.74$, $P < 0.001$, respectively). Moreover, as in experiment 1, their initial fleeing directions were significantly clustered around the compass direction of the nest of destination, both at 1 m and 2 m from the release point (Fig. 2b; V-test: $u = 3.47$ and $u = 3.66$, $P < 0.001$, respectively). A few ants oriented nonetheless towards the nest of departure. In the same way as in experiment 1, the fleeing directions of the Te were significantly clustered around the compass direction of the nest of departure, both at 1 m and 2 m from the release point (Fig. 2b; V-test: $u = 4.00$ and

$u = 5.16$, $P < 0.001$, respectively). The azimuths of the search point were significantly clustered around the compass direction of the nest of destination (V-test: $u = 4.54$, $P < 0.001$; Fig. 2b) and the nest of departure (V-test: $u = 5.29$, $P < 0.001$; Fig. 2b) for the Ts and the Te, respectively. As in experiment 1, the distributions of the angular differences between the bearings of the Ts and the Te were significantly clustered around 180° (V-test: $u = 2.75$, $P < 0.01$; $u = 3.15$, $P < 0.001$ and $u = 2.22$, $P < 0.05$, for the fleeing directions at 1 and 2 m from the release point and for the azimuths of the search points, respectively). The fact that the orientation performance of the ants was comparable in experiments 1 and 2 shows that they did use celestial cues to set their bearings. The distance at which the ants began to search was about twice as far for the Ts than for the Te (Table 1; Wilcoxon: $z = -3.15$, $P < 0.01$). On average however, it was less than half the value of the distance between the initial capture point and the nest of destination. If the Ts had been able to update continuously the distance at which the nest of destination was lying, we would have expected their search points to lie at about 14 m from the release point (the distance between capture point and destination nest). Similarly, if the Te had been able to integrate the distance they had

travelled from the nest of departure while being transported, we would have expected their search points to lie at about 21 m from the release point (the distance between capture point and departure nest). This result suggests that the Ts also use terrestrial cues to reach their destination nest. This is corroborated by the fact that, when 11 of them were released again at their initial point of capture, all travelled immediately and directly towards the nest of destination.

Experiment 3

The last experiment was designed to test whether the terrestrial landmarks should appear in a specific sequence to be used by the ants. Sixteen Ts were captured within a few centimetres of the nest of arrival, and were released 2 m behind the nest of departure, on the prolongation of the line linking the two nests. Ants took more time to take their bearings than in experiments 1 and 2 (Table 1). The distributions of their fleeing directions were not clustered around a definite direction, both at 1 m and 2 m from the release point (Fig. 2c; Rayleigh test: $P > 0.05$ in both cases). However, the samples appear to be bimodal with two modes in opposite directions. In order to check the significance of an axial orientation, we applied the method of doubling the angles as described by Batschelet (1981). If the two modes are in exactly opposite directions, doubling the angles will result in a unimodal sample on which the usual circular statistical tests can be applied. Using this method, we found that the fleeing directions at 1 m and 2 m were significantly clustered along the axis linking the two nests (V -test: $u = 2.30$, $P < 0.05$ and $u = 3.13$, $P < 0.001$, respectively). Five ants did not reach a nest within 15 min whereas three eventually arrived at their nest of departure and eight at their nest of destination. Ants were hesitant before setting their course in a definite direction. Most of them even passed within a few centimetres of the entrance to the nest of departure without stopping.

Discussion

Whether released at their point of capture (experiment 1) or at some distant point (experiment 2), the Ts and the Te oriented in opposite directions. This shows that the Ts use celestial cues to orient during transport and that the Te are able to use these cues to assess the compass direction from which they have been passively displaced. This result concurs with that reported by Duelli (1973) on *Cataglyphis bicolor*. Why the Te head in a direction opposite to the Ts may be explained by the typical posture adopted by formicine ants during transport (see Hölldobler and Wilson 1990): the Te are held by the mandibles, their abdomens curled under the heads and the thorax of the Ts and their appendages folded in a pupal position (Fig. 1). The head posture of

the Ts and the Te is exactly the same except that they are in a reverse position (Duelli 1973). The upper part of the compound eyes of the Te, where the polarisation detectors are located, thus looks at the same portion of the sky but in the opposite directions.

Experiment 1 shows that the Te found it difficult to return to the nest of departure. Most of the workers behaved as if they were lost and those that eventually reached it made several search loops. In experiment 2, both the Ts and the Te began to search well before they had travelled the distance between their capture point and the nest in which compass direction they were moving after being released. This would have been the case for the Ts if they were relying on a memory of the direction and distance at which the nest of destination was lying. Similarly, this would have been the case for the Te, if they had been able to integrate their trajectories while being passively transported. We conclude therefore that the Ts may be either totally unable to assess the distance they have to travel or that their system of distance assessment only works in conjunction with the use of specific landmarks. The Te, on the other hand, may be unable to assess the distance they have travelled while being carried because an active movement may be required to achieve this performance (Ronacher and Wehner 1995). In any case, this result is at variance with that of Duelli (1973) who claimed that carried ants of *C. bicolor* are able to integrate the distance they have travelled during transport.

The Ts indeed seem to need terrestrial landmarks in order to determine their position on the route to the goal. In experiment 2 when they were released again at their capture point, they all headed immediately and directly towards their nest of destination. Furthermore, in experiment 3, their orientation was clearly impaired, as if they had some expectations as to which landmarks might be encountered at specific points along the route. In contrast to the Ts, the Te had poor homing performances in experiment 1. This may be explained in two different ways. First, ants, in the same way as bees (Geiger et al. 1994; Schöne et al. 1995), may be unable to use the visual information passing by in their visual field during passive displacement in order to retrace the path they have travelled. In this case, the Te that reached the nest of departure in experiment 1 may have done so after achieving a systematic search (Wehner and Srinivasan 1981), by making a series of search loops of increasing size biased in its direction. Second, since Te ants are young, inexperienced workers (Dahbi et al. 1997), one can speculate that more than one transport may be required before they can memorise the sequence of landmarks between two nests. For example, in *C. bicolor* Wehner and Menzel (1969) found that the visual knowledge of digger ants whose displacements are limited to the immediate nest surroundings was much poorer than that of foragers. Long-term observations on individually marked workers would be necessary to confirm the second hypothesis.

As a general conclusion, we propose the following mechanisms to explain the orientation performances of the Ts and Te ants in our experiments. When exiting the nest of departure, the Ts use celestial cues to set their bearings in the compass direction of the nest of destination that they have memorised during previous runs. They then pursue their course in the direction they have set and adjust it by using a sequence of landmarks they have memorised during previous runs. As regards to the Te, they seem unable to integrate the distance travelled while being passively transported. There are some doubts however as to whether they can integrate part of the visual information they encountered during their transport. In any case, their ability to reverse the direction of their passive displacement by using celestial cues may allow them to regain their nest of departure after achieving a systematic search biased in its direction.

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References

- Batschelet E (1981) Circular statistics in biology. Academic Press, London
- Cerdá X, Retana J (1992) A behavioural study of transporter workers in *Cataglyphis iberica* ant colonies (Hymenoptera, Formicidae). *Ethol Ecol Evol* 4:359–374
- Cerdá X, Retana J, Haro A de (1994) Social carrying between nests in polycalic colonies of the monogynous ant *Cataglyphis iberica* (Hymenoptera, Formicidae). *Sociobiology* 23:215–231
- Dahbi A, Cerdá X, Hefetz A, Lenoir A (1997) Adult transport in the ant *Cataglyphis iberica*: a means to maintain a uniform colonial odour in a species with multiple nests. *Physiol Entomol* 22:13–19
- Duelli P (1973) Astrotaktisches Heimfindvermögen tragender und getragener Ameisen (*Cataglyphis bicolor* Fabr., Hymenoptera, Formicidae). *Rev Suisse Zool* 80:712–719
- Geiger K, Kratzsch D, Menzel R (1994) Bees do not use landmark cues seen during displacement for displacement compensation. *Naturwissenschaften* 81:415–417
- Hölldobler B, Wilson EO (1990) The ants. Belknap Press, Harvard University, Cambridge
- Ronacher B, Wehner R (1995) Desert ant *Cataglyphis fortis* use self-induced optic flow to measure distances travelled. *J Comp Physiol A* 177:21–27
- Schöne H, Kühme WD, Schöne H (1995) Take-off behavior and vanishing bearings of honeybees after displacement with open view or in a sight-proof box. *Naturwissenschaften* 82:343–345
- Wehner R, Menzel R (1969) Homing in the ant *Cataglyphis bicolor*. *Science* 164:192–194
- Wehner R, Srinivasan MV (1981) Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J Comp Physiol A* 142:315–338