

Starvation drives a threshold triggering communication

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Summary

The decision for an ant forager to launch recruitment is governed by an internal response threshold. Here, we demonstrate that this threshold (the desired volume) triggering trail-laying increases under starvation. As a consequence, highly starved foragers lay a recruitment trail and bring back to the nest higher quantities of food from large unlimited resources. In contrast, when the volume of the food source is under their crop capacity, the

percentage of trail-communicating foragers is lower following a prolonged period of starvation. Such starvation-dependent changes in the ‘desired volume’ threshold explain how ants optimize recruitment and select liquid food resources in order to prevent collective exploitation of low profitability.

Key words: threshold, starvation, foraging, ant, *Lasius niger*.

Introduction

The ecological success of animals depends on their ability to adjust their foraging strategies to many parameters characterizing their physiological status and/or their environmental conditions (see Bateson, 2002; Bautista et al., 1998; Cristol, 1992; Soto et al., 2005; Lendvai et al., 2004; McNamara and Houston, 1987; Rothley et al., 1997). In social insects, an interesting question about animals that cooperate during foraging is the relation between the physiological status (e.g. food deprivation level), modulation of inter-individual communication and the resulting collective behaviour. Currently, this relation between starvation level and the probability that an individual will initiate, maintain or stop collective foraging is still poorly studied.

Many studies have shown that social insects select efficient foraging strategies according to food quality, food quantity, distance to food source, risk of predation, or competition. Among all these variables, starvation level is one of most important parameters affecting collective foraging behaviour in ants (Cassill and Tschinkel, 1995; Cosens and Toussaint, 1986; Hölldobler, 1971; Roces and Hölldobler, 1996; Traniello, 1977), honeybees (Seeley, 1995; Schulz et al., 1998; Schulz et al., 2002; Toth and Robinson, 2005; Toth et al., 2005) and bumble bees (Cartar and Dill, 1990). Aphid-tending ant species, such as *Lasius niger*, are good biological models to study the behavioural flexibility of animals faced with fluctuations of nutritional supplies. Honeydew is the main source of protein and carbohydrates for aphid-tending ants (Auclair, 1963; Hölldobler and Wilson, 1990) and its production undergoes important temporal variations in the course of year (El-Ziady and Kennedy, 1956; Sakata, 1994;

Sakata, 1995; Völkl et al., 1999). At the beginning of spring, honeydew resources are limited and aphid colonies are scarce. As the year goes by, some aphid colonies spread out and offer huge amounts of honeydew while others disappear abruptly, or steeply change their honeydew production according to the weather conditions. Due to the high variability of honeydew amount, aphid-tending ants have to undergo long periods of starvation (Cosens and Toussaint, 1986; Skinner, 1980) that force them to intensify their food retrieving activities and transport more food (Cosens and Toussaint, 1986; Howard and Tschinkel, 1980; Howard and Tschinkel, 1981; Josens and Roces, 2000; Seeley, 1995; Wallis, 1962; Wallis, 1964). A wide range of explanations have been given for such strategy choice, among which many are considered merely to be cost-benefit problems that foraging animals must solve while the assessment mechanisms of all information are often considered as a black box (Giraldeau and Caraco, 2000). In other words, research has been mainly focused on the functional significance of foraging choice by starved animals (Stephens and Krebs, 1986) while the underlying behavioural mechanisms of communication have been disregarded.

In previous papers (Mailleux et al., 2000; Mailleux et al., 2005), we demonstrated that an ant forager’s decision to communicate its finding and then to launch recruitment appropriate to food source productivity is governed by an internal response threshold. If foragers are given the opportunity to ingest a desired volume of their own, they lay down a trail and recruit nestmates. If they cannot obtain this volume, after a brief exploration of the foraging area, they return to the nest without initiating recruitment. The desired

volume acts as a response threshold that determines the proportion of trail-laying individuals among returning ants who will spread information about food discovery through the ant colony. Collective regulation of foraging results from the interplay between the distribution of these desired volume thresholds among colony members and the food volume available (Mailleux et al., 2003).

How this critical response threshold depends on individuals and/or colony physiological status is still unknown. In the present study, we investigate experimentally whether the 'rule of thumb' described above remains valid when colonies are food deprived for different durations. More precisely, we quantify whether the starvation level of foragers influences the distribution of their individual response threshold ruling their recruitment decision (Mailleux et al., 2000). Therefore, we compared values of desired volume under different starvation levels and for different food volumes. Our results are discussed in the general context of social foraging and in the case of ant-aphid mutualism.

Materials and methods

We collected three *Lasius niger* (L.) colonies of 1000–1300 workers in Brussels and reared them in the laboratory in plaster nests placed in plastic arenas (50 cm×38 cm), whose borders were coated with fluon to prevent the ants from escaping. Each nest was subdivided into three connected sections (15 cm×5 cm×0.5 cm) covered by a glass plate. Nests were regularly moistened. They were reared at a temperature of 22±3°C with a 12 h:12 h L:D photoperiod and were fed three times a week with a sucrose solution (0.6 mol l⁻¹) and cockroaches *Periplaneta fuliginosa* (Serville).

Foraging patterns of ants are robust to initial variations (e.g. in trail-laying and following behaviour), which can alter the first steps of recruitment (e.g. its time of onset and initial growth rate). Nevertheless, it is known that the first scouts laying a trail back to the nest play a key role in the triggering and built-up of collective foraging patterns in *Lasius niger* as well as in some other mass-recruiting ant species (Mailleux et al., 2005; Beckers et al., 1992; Beckers et al., 1993; de Biseau and Pasteels, 1994). Consequently, we focused our observations on scouts' behaviour.

We studied scouts' behaviour according to different starvation levels and food quantities. Each ant's colony underwent periods of starvation lasting 1, 4 and 8 days. We randomly assigned the sequence of starvation periods to each colony. One to four ants were tested at the end of a starvation period. Afterwards, the colonies were fed *ad libitum* during a resting period of 7 days. We analysed the responses of ants to volumes of 3 µl and 0.3 µl of sucrose solution (0.6 mol l⁻¹). Since 1.8 µl was the maximum ingested volume, each scout that discovered a 3 µl droplet was potentially able to fill its gaster to repletion (Mailleux et al., 2000). The size of 0.3 µl droplets was close to that of honeydew droplets produced by aphids. For instance, the average droplet size produced by

Tuberolachnus salignus (Gmelin) is from 0.06 µl for first instar larvae, and at most 0.8 µl for apterous adults, both aphids being tended by *L. niger* (Auclair, 1963).

During a period of 1 h, nests were connected by a cardboard bridge (length 20 cm, width 0.5 cm) to a small foraging area (6 cm×6 cm) that ants could freely explore. After the exploration phase, a food source was placed in the area centre. The first scout to discover the food droplet and return homewards was gently removed just before entering the nest. By doing this we prevented scouts from communicating with nestmates and limited the scope of this study to scouts' behaviours. Since it is known that the *L. niger* pheromone lifetime on this substrate is about 40 min (Beckers et al., 1993) and that pheromone marks could influence the behaviour of the next ants coming along, only one ant was tested per hour. After the passage of 4 ants, the bridge was renewed. To quantify individual behaviour, we videotaped ants while they were on the bridge and in the foraging area. From a magnified image (×25) we measured two morphological parameters: the length of alitrunk in profile (from the anterior edge of pronotum to the posterior base of propodeum), and the maximal length and maximal height of gaster before and after drinking. By approximating the shape of the gaster to an ellipsoid, the two latter measures allowed us to calculate the volume of sugar solution ingested by each ant (Mailleux et al., 2000). We also measured the following behavioural parameters. (1) Ant's walking velocity, which was measured in the middle of the bridge over a short portion (2.5 cm) on its way from and to nest. (2) Searching time, which started when a scout crossed the middle of the bridge on its way to the foraging area and stopped when it discovered the droplet. (3) Drinking time, which lasted as long as the ant's mandibles were in contact with sugar solution. (4) Giving-up time, which started when the ant stopped drinking until it was seen in the middle of the bridge on its way back to nest. (5) Foraging time was the total time spent searching, drinking and giving-up. Consequently, it started when the scout crossed the middle of the bridge on its way to foraging area and stopped when the scout was seen in the middle of bridge on its way back to nest. (6) Percentage of trail-laying scouts, which was the percentage of ants that laid at least one chemical trail mark over the whole length of bridge. When depositing trail pheromone, a worker curves its gaster vertically to the ground (the normal position being horizontal), interrupts its walk for a fraction of a second and backs up to amplify the movement of its gaster (Beckers et al., 1992). This behaviour was taken as the criterion for trail-laying (Hölldobler, 1971; Detrain and Pasteels, 1991). (7) The individual intensity of trail-laying behaviour, which was assessed by the relative amount of time during which each trail-laying ant was seen dragging its gaster on a section (12 cm) of bridge. Indeed, indirect evidence for the correlation between trail-laying intensity and dragging of gaster has been obtained from behavioural experiences and mathematical models (Beckers et al., 1992; Beckers et al., 1993).

Table 1. Individual behaviours of scouts as a function of food availability and food deprivation

Food volume	Starvation duration (days)	Time (s)				Velocity (cm s ⁻¹)			Ingested volume (μl)	% of trail-laying ants	Trail-laying intensity(%)
		Foraging	Searching	Drinking	Giving-up	Outwards	Inwards				
Above crop one: 3 μl	1 (58)	136±51	45±43	70±26	22±14	2.1±1.1	1.8±0.6	0.72±0.36	88%	0.11±0.09 (51)	
	4 (122)	175±80 ^a	56±64	91±24 ^b	28±33	1.8±0.8	1.6±0.6	0.90±0.39 ^c	93%	0.14±0.11 (113)	
	8 (85)	176±75 ^a	59±65	94±22 ^b	28±26	1.8±0.9	1.7±0.6	0.98±0.37 ^c	87%	0.13±0.11 (74)	
Statistical tests		KW=23.12 P<0.0001	KW=2.76 NS	KW=42.16 P<0.001	NS	KW=5.62 NS	KW=2.04 NS	KW=16.8 P<0.001	χ ² =2.32 NS	KW=5.25 NS	
Below crop one: 0.3 μl	1 (28)	126±58	32±23	38±15	56±54	1.8±1.0	1.7±0.4	0.19±0.08	37%	0.09±0.10 (10)	
	4 (23)	197±95 ^d	64±73	47±17	86±68 ^e	1.8±0.8	1.9±0.7	0.21±0.14	17% ^f	0.16±0.05 (4)	
	8 (25)	178±97 ^d	46±26	41±13	93±93 ^e	1.9±0.9	1.8±0.6	0.23±0.11	12% ^f	0.06±0.06 (3)	
Statistical tests		KW=11.37 P<0.005	KW=5.13 NS	KW=5.68 NS	P<0.05	KW=0.67 NS	KW=1.00 NS	KW=1.14 NS	χ ² =6.13 P<0.05*	KW=3.70 NS	

Values are means ± s.d. (N).

Parameters were compared using Kruskal–Wallis tests except for the percentage of trail-laying ants (χ² test). Values of P and results of statistical tests (α=0.005, NS=non statistical difference) are given in last row for each parameter. Values with identical superscript letters are not statistically different under *post-hoc* Dunn test (a–e) and χ² test (f) at 0.05 level of significance.

Results

Food volume exceeding crop capacity: a 3 μl sugar droplet

The individual foraging behaviour of scouts undergoing 1, 4 or 8 days of starvation (1_{ds}, 4_{ds} or 8_{ds}) differed by the ingested food volume that increased with longer starvation periods (Table 1). Experimental distribution of this parameter could be fitted by a model that assumes that the probability [$=P(V)$] of a scout ingesting a desired volume V and then laying a recruitment trail is not constant but increases close to a critical volume V_c (Mailleux et al., 2000). This probability follows a response threshold function:

$$P(V) = \frac{\eta \Delta V}{1 + e^{-\eta(V-V_c)}}, \quad (1)$$

where the constant η measures the sensitivity of ants to difference between V and the response threshold V_c (desired volume). According to this probability, the fraction of ants (Fr) having ingested at least a volume V before laying a trail (Fig. 1) is:

$$Fr = \frac{1}{1 + e^{\eta(V-V_c)}}, \quad (2)$$

where V_c is defined as the threshold volume at which 50% of trail-laying ants have reached their desired volume.

When starvation was prolonged, η did not vary ($\eta=5$; t -test comparing regression slopes, $t=1.89$, $N=239$, NS) but V_c values statistically increased (t -test comparing regression elevations, $t=33.64$, $N=239$, $P<0.001$). After 1_{ds}, $V_c=0.64$ μl ($R=0.99$, $N=51$, $P<0.001$); after 4_{ds}, $V_c=0.86$ μl ($R=0.99$, $N=113$, $P<0.001$); and after 8_{ds}, $V_c=0.90$ μl ($R=0.99$, $N=74$, $P<0.001$). V_c values after 4_{ds} and 8_{ds} were not statistically different (t -test comparing regression elevations, $t=0.73$, $N=188$, NS). According to our model, as long as the food volume exceeded ant crop capacity, all ants should lay a trail whatever their starvation level and the percentage of trail-laying ants should not vary with the starvation length. This seemed to be the case (Table 1). The majority of ants that found the 3 μl droplet participated in the communication trail: 88, 93, 87% of ants dragged their abdominal tip at least once on their way back to nest after 1_{ds}, 4_{ds} and 8_{ds}, respectively (Table 1). Therefore, when the amount of available food exceeded the crop volume of a scout, neither the percentage nor the intensity of individual trail-laying behaviour changed with the starvation level (Table 1). The percentage and intensity of the individual trail-laying behaviour did not differ with starvation duration. In consequence, under unlimited food availability, trail-laying behaviours of scouts tested after different starvation durations were similar.

After 4_{ds} and 8_{ds}, foraging time increased as a result of longer searching, drinking and giving-up times (Table 1). The mean values of the searching and giving-up time parameters increased, respectively, by 24% and 31% after 4_{ds}, and by 27% for both times after 8_{ds}, even if the differences were not statistically significant. Searching and giving-up time increases did not result from differences in the ants' velocities (Table 1)

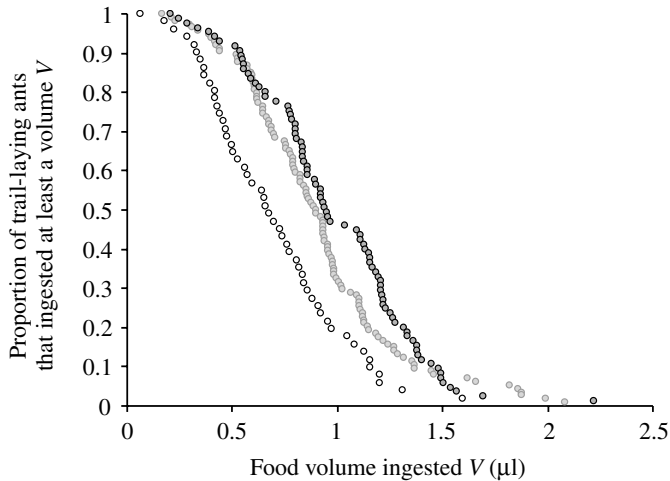


Fig. 1. Proportion of trail-laying ants that ingested at least a volume V as a function of the food volume ingested when the droplet volume exceeded crop capacity ($3 \mu\text{l}$) and when ants were food deprived for 1 day (open circles, $N=58$), 4 days (shaded circles, $N=122$) or 8 days (filled circles, $N=85$).

but from the behaviour of scouts that circled around and around on the foraging area (before and after drinking to find additional food). The mean values of drinking time increased, respectively, by 30% after 4_{ds} and by 34% after 8_{ds}, since starved scouts drank longer to reach their larger desired volume. There were no correlations between any measured time parameters and food volumes ingested by scouts.

Food availability below crop capacity: a $0.3 \mu\text{l}$ sugar droplet

We investigated how scouts behaved when they found smaller food droplets that were below the capacity of the scout's crop. According to our model (Eqn 1), under conditions of limited food availability (food quantity $<1.8 \mu\text{l}$, which is the maximum ingested volume), the percentage of satisfied ants that decided to communicate their finding and lay a trail after having ingested a volume (V) should decrease with starvation duration. This percentage decrease was a consequence of the starvation-dependent increase of the threshold. When food volume was $0.3 \mu\text{l}$, the percentage of trail-laying ants decreased significantly as a function of starvation level: 37, 17, 12% of the observed ants dragged their abdominal tip at least once on their way back to nest after 1_{ds}, 4_{ds} and 8_{ds}, respectively (Table 1). Among those ants that laid a trail, the individual intensity of marking did not vary whatever the offered food volume or the starvation duration (Kruskall–Wallis test: $KW=5.90$, $N=255$, NS). Foraging time increased with starvation level in a similar way to the one observed when food volume exceeded crop capacity (see Table 1). Consequently, the time spent by a scout on the foraging area was not influenced by food availability (Mann–Whitney test: 1_{ds}, $U=637$, $N=86$, NS; Kruskal–Wallis test comparing foraging times after 4_{ds} and 8_{ds}, $KW=1.24$, $N=260$, NS) but was increased by starvation (Table 1). The mean searching and giving-up times increased, respectively, by 97% and 53% after

4_{ds} and by 42% and 65% after 8_{ds}. Actually starved scouts searched for food before and after drinking more intensively when the food volume was below their crop capacity. When they were offered $0.3 \mu\text{l}$, starved scouts tried to drink for longer at the food source but were limited by food availability. Therefore, drinking time was unaffected by starvation. There were no correlations between measured time parameters and the food volumes ingested by scouts.

Discussion

In social species, many studies provide evidence that between-individual differences account for the division of tasks in various collective behaviours such as nest defence, foraging or brood care (Beschers and Fewell, 2001). What determine these individual differences are response thresholds they had for tolerating the task not being done. In ants, honeybees and bumblebees, response thresholds of a given individual are regulated by several internal factors such as genetic predisposition, physiology, physical caste, age or individual experience (e.g. Detrain and Pasteels, 1991; Detrain et al., 1999; Fewell and Page, Jr, 2000; Huang and Otis, 1991; Page et al., 1997; Robinson, 1992; Robinson and Page, 1995; Sempo and Detrain, 2004; Weidenmüller et al., 2002). However, such thresholds can also vary in relation to several external factors such as the ant's demand for food (Suds and Suds, 1985), distance from nest to food patches (Breed et al., 1996), or presence of amino acids in honeydew (Lanza et al., 1992).

Previous studies (Mailleux et al., 2000; Mailleux et al., 2003; Mailleux et al., 2005) provided evidence for the 'rule of thumb' used by foragers to assess the volume of single or multiple food sources in which the ability of scouts to ingest their own desired volume plays a key role. Ants' trail-laying behaviour is under the control of a threshold response (the desired volume) triggered by an internal stimulus (the ingested volume). The present study is the first evidence that the recruitment response threshold increases with starvation. Moreover, we demonstrate that this 'rule of thumb' remains valid for different starvation durations and extends into the regulation of chemical communication.

Consequently to the threshold increase resulting from starvation, when food sources are large (e.g. aphid colonies composed of highly productive individuals), the food volume ingested by foragers and hence the amount of food retrieved to nest increases. Such an increase of retrieved food quantities has been reported for many ant species (Cosens and Toussaint, 1986; Howard and Tschinkel, 1980; Howard and Tschinkel, 1981; Josens and Rocés, 2000; Wallis, 1964). Likewise, honeybee foragers counter depletion of pollen stores by increasing pollen load size per forager (for a review, see Seeley, 1995). However, such increased food retrieval following a prolonged starvation period is not always the rule in social insects: when highly starved, *Atta cephalotes* (L.) foragers cut smaller leaf pieces (Rocés and Hölldobler, 1994). According these authors, a lightening of food load could reduce the time spent by fungus-growing ants cutting leaves at the foraging

area. In trail-recruiting ants as *L. niger*, this time saving is not necessary as the ingestion of the food is rapid and does not strain the time that a scout spends exploiting food.

In social insects, it is known that the number of individuals participating in food recruitment increases with starvation (Cosens and Toussaint, 1986; Hölldobler, 1971; Howard and Tschinkel, 1980; Howard and Tschinkel, 1981; Josens and Rocés, 2000; Rocés and Hölldobler, 1996; Seeley, 1995; Traniello, 1977; Wallis, 1962; Wallis, 1964). Our work shows that this phenomenon does not result from an increase in individual trail marking. We have shown that, quite unexpectedly, when a huge amount of food is available, the duration of starvation does not alter the percentage of *Lasius niger* trail-laying scouts or the individual intensity of their trail-laying behaviour. Our results do not mean that the global recruitment of workers will not increase with starvation but show that this phenomenon is not the result of increased trail marking. This differs from the increased trail-laying reported for *Solenopsis geminata* (Fabricius) after a long starvation period (7 and 14 days) (Hangartner, 1969). Because of the occurrence of brood cannibalism (Lenoir, 1979), we never imposed such a long starvation period on *L. niger*. Our work also shows that the total time spent on the foraging area unexpectedly increased with starvation and therefore slows down collective food collection. Communication between scouts and nestmates inside the nest probably plays the key role in the regulation of foraging as a function of starvation. A study of social interactions between foragers and nestmates would certainly cast light on mechanisms boosting recruitment in highly deprived colonies.

As the threshold increases with starvation, the percentage of trail-laying ants decreases when small food amounts are available. We hypothesize that, in the field, a starvation period elicits a shift in the activity profile of the colony: non-starved ants exploit small and large sources while starved ants concentrated their foraging effort merely on large sources. The smaller sources are not abandoned; they can still be exploited by one or a few individuals. Therefore, this 'rule of thumb' and its modulation in periods of starvation prevents recruitment to small and poorly productive food sources but allows starved colonies to focus their foraging activity on food sources with high expected profitability such as large and/or high-density aphid colonies.

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