Regulation of ants' foraging to resource productivity

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We investigate the behavioural rule used by ant societies to adjust their foraging response to the honeydew productivity of aphids. When a scout finds a single food source, the decision to lay a recruitment trail is an all-or-none response based on the opportunity for this scout to ingest a desired volume acting as a threshold. Here, we demonstrate, through experimental and theoretical approaches, the generic value of this recruitment rule that remains valid when ants have to forage on multiple small sugar feeders to reach their desired volume. Moreover, our experiments show that when ants decide to recruit nest-mates they lay trail marks of equal intensity, whatever the number of food sources visited. A model based on the 'desired volume' rule of recruitment as well as on experimentally validated parameter values was built to investigate how ant societies adjust their foraging response to the honeydew productivity profile of aphids. Simulations predict that, with such recruiting rules, the percentage of recruiting ants is directly related to the total production of honeydew. Moreover, an optimal number of foragers exists that maximizes the strength of recruitment, this number being linearly related to the total production of honeydew by the aphid colony. The 'desired volume' recruitment rule that should be generic for all ant species is enough to explain how ants optimize trail recruitment and select aphid colonies or other liquid food resources according to their productivity profile.

Keywords: aphid; ant; foraging; food partitioning; food productivity; trail recruitment

1. INTRODUCTION

Many ant species find their energy supply in honeydew produced by aphids (Breton & Addicott 1992), membracids (Del-Claro & Oliveira 2000) or scale insects (Itioka & Tamiji 1996), as well as in plant nectar (Lawton & Heads 1984) or in nutritious secretions of lycaenid caterpillars (Wagner & Kurina 1997). These social insects adjust their individual and collective response to these liquid food sources which differ in their chemical composition (Sudd & Sudd 1985; Breed *et al.* 1987, 1996*a,b*; de Biseau *et al.* 1992; Beckers *et al.* 1993; de Biseau & Pasteels 1994; Bonser *et al.* 1998; Völkl *et al.* 1999) or their spatial distribution (Addicott 1979; Breed *et al.* 1987; Itioka & Tamiji 1996).

The available quantity of honeydew has been shown to influence the collective foraging response of ants, as well as their choice of an aphid colony (Breed *et al.* 1987, 1996*a,b*; de Biseau & Pasteels 1994; Mercier & Lenoir 1999; Völkl *et al.* 1999). In a previous paper, Mailleux *et al.* (2000) demonstrated that the decision for a scout to return to the nest and lay a trail is governed by an internal response threshold. If ants are given the opportunity to ingest a desired volume of their own, they lay down a trail and recruit nest-mates. If they cannot obtain this volume after a brief exploration of the foraging area, they go back to the nest without initiating recruitment. The response is all-or-none and the intensity of chemical marking is independent of the ingested volume. It is therefore the proportion of trail-laying individuals among returning ants that spreads information about total food volume through the society.

The total amount of honeydew produced by an aphid colony depends on the number and/or population density of aphids as well as on the size and rate of renewal of honeydew droplets emitted per individual. As the size of honeydew droplets scales on average from 0.06 to 0.8 µl in homopterans (e.g. Mittler 1958; Völkl *et al.* 1999), foragers usually have to visit several aphids before filling their crop up to their desired volume (mean desired volume of *Lasius niger*, 0.9 µl; Mailleux *et al.* 2000). In the present paper, we investigate through an experimental approach and with the help of a model, whether the rule of thumb evidenced for a single food source remains valid when a scout has to collect several droplets to reach its desired volume. To this end, we extend the one-source experiment initially developed by Mailleux *et al.* (2000) to a multisources set-up mimicking a group of aphids.

Using Monte Carlo simulations, based on our experimental values, we then make theoretical predictions on how the 'desired volume' rule of thumb can regulate trail recruitment and adjust the collective foraging response of ants to the productivity of the aphid colony.

2. MATERIAL AND METHODS

(a) *The experiment*

Experiments were carried out on the black garden ant, *L. niger*, a common palaearctic species, which feeds on the honeydew of several aphid species which differ in their honeydew productivity (El-Ziady & Kennedy 1956; Mittler 1958; Klingauf 1987; Sakata 1994, 1995; Völkl *et al.* 1999; Offenberg 2001). We followed the experimental procedure developed by Mailleux *et al.* (2000) to test the behaviour of *L. niger* foragers when faced with six droplets of sucrose solution. The concentration of the tested sucrose solution was 0.6 M, within the density limits

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found in honeydew droplets actually emitted by aphids tended by *L. niger* (Völkl *et al.* 1999). We chose to deliver a 0.3 µl droplet at each food source, a volume that compelled most foragers to search for additional sources in order to reach their desired volume. This value is also comparable to the amount of honeydew actually produced per aphid individual (Mittler 1958; Auclair 1963; Völkl *et al.* 1999). Six micropipettes delivering sucrose droplets hung at the centre of the foraging area (6 cm × 6 cm) and were arranged into two rows of three micropipettes (the distance between adjacent micropipettes was 1 cm). Potentially, each tested ant had the opportunity to reach its desired volume as the total amount of food available in the foraging area (1.8 µl) was close to the maximal crop capacity of *L. niger*. Each forager had to climb on a metal stick before reaching the food source. Once it had ingested the first droplet, the forager could either return to the nest or keep on searching for additional food droplets. Ingested droplets were not renewed and micropipettes were removed after the departure of the ant. To prevent evaporation, we started delivering a droplet only when the ant was seen climbing on the metal stick associated with the corresponding micropipette. We videotaped the behaviour of 88 foragers while in the foraging area and while they walked along the bridge connecting the nest to the food source. On the 10-times magnified image, we measured the maximal length and maximal height of the ant abdomen before and after drinking. By approximating the gaster to an ellipsoid, those measures allowed us to calculate the volume of sugar solution ingested by each ant (see Mailleux *et al.* 2000). We also measured the following additional variables: (i) the number of food sources visited by each forager during its whole stay in the foraging area; (ii) the exploitation time, defined as the time elapsed between the ant starting to drink at the first droplet and leaving the last visited micropipette; (iii) the percentage of trail-laying foragers, defined as the percentage of ants laying at least one trail mark over the bridge; and (iv) the individual intensity of trail-laying behaviour, that is the percentage of video frames on which a trail-laying ant is seen dragging its gaster on a 2.5 cm section of the bridge.

Two key parameters for the model (see below) are also the giving-up time and the discovery time. Both were estimated using data from our previous experiments (Mailleux *et al.* 2000), with one droplet (volume of the droplet was 0.3 µl).

The giving-up time is the time spent by non trail-laying ants exploring the foraging area after having drunk at the micropipette until they leave the foraging area. It is exponentially distributed, which means that the probability of leaving the foraging area per time unit is constant, $1/85\ \mathrm{s}^{-1}$ ($n = 35$, $r^2 = 0.98$, $p < 0.001$).

The discovery time is the time spent by an ant to discover another micropipette. It is estimated by the time elapsed between successive visits to the micropipette in the single source set-up (from unpublished data of Mailleux *et al.* (2000); $n = 30$, $\bar{x} \pm$ s.d. $= 20.4 \pm 17.2$). This estimated discovery time is similar to the time ($n = 55$, $\bar{x} \pm$ s.d. $= 19.4 \pm 18.9$) spent by a scout to discover a new micropipette in a multisources set-up (Kolmogorov–Smirnov test: $D = 0.12$, n.s.). Like the giving-up time, the discovery time is exponentially distributed and the probability to discover a new micropipette is constant, $1/20\ \mathrm{s}^{-1}$ ($n = 30$, $r^2 = 0.94$, $p < 0.001$).

(b) The model

We built a model based on the recruitment rule evidenced in the case of a single source and we applied it to a multisources situation (figure 1). The only difference was that 'unsatisfied' ants that had not yet ingested their desired volume still had the

opportunity to discover additional food by exploring the foraging area. With this model, we simulated the following behavioural sequence of a scout using parameter values drawn out from the single source experiment of Mailleux *et al.* (2000).

A scout begins by exploring the foraging area (see figure 1). At this point, it can either discover a food droplet (P_d) or it can leave the area and return to the nest without laying a trail (P_l). The scout has also the option of continuing to explore the foraging area. The probability that an ant will leave the foraging area (P_l) is constant and equals $1/85\ \mathrm{s}^{-1}$. This probability is calculated from the average giving-up time that 'unsatisfied' scouts spent searching for additional food before leaving the area in a single source experiment (Mailleux *et al.* 2000). The probability that ants will discover a food source (P_d) equals $1/20\ \mathrm{s}^{-1}$; this constant value is calculated from the time elapsed between successive visits to the micropipette in the single source set-up (Mailleux *et al.* 2000).

The second branch point applies to ants that succeed in finding a food source and is crucial in the process of regulation of trail recruitment to food productivity. Two variables affect the proportion of scouts returning to the nest: (i) the amount of food available and (ii) the probability that an ant reaches its 'desired volume'. If food is available, an ant is assumed, for each second spent at the food source, to ingest a volume ΔV ($= 10^{-2}$ µl for *L. niger* based on Mailleux *et al.* (2000)). The probability of stopping ingesting food and leaving the source $S(V)$ grows with the volume already ingested (V) and follows a response threshold function:

$$S(V) = \frac{\eta \Delta V}{1 + e^{-\eta(V - V_c)}}, \tag{2.1}$$

where the constant η ($= 4.3$) measures the sensitivity of ants to the difference between V and the threshold V_c ($= 0.9$ µl) and is drawn from the experimental threshold curve (Mailleux *et al.* 2000). V_c is defined as the threshold volume for which 50% of the ants' population have reached their desired volume and left the food droplet. The scout repeats the cycle that ends either when food is exhausted or when the ant moves to the next compartment and returns to the nest. Among those returning ants, a majority (90%), but not all individuals, engage in trail-laying behaviour. The remaining 10% do not lay a trail during their homeward trip, while they behave similarly to trail-laying foragers and ingest similar amounts of food. Therefore, the probabilities that a scout becomes a trail-laying ant (P_t) or not ($1 - P_t$) are equal to 0.9 and 0.1, respectively.

When the source is depleted as a result of food ingestion by the scout and/or other nest-mates, a fraction of ants has to leave despite not having reached their desired volume. For an initial volume of the droplet (V) this fraction of unsatisfied ants (U) is

$$U(V) = \frac{1}{1 + e^{\eta(V - V_c)}}. \tag{2.2}$$

Those 'unsatisfied' ants start exploring the area again, searching for additional food without laying a trail.

We made the further assumptions that (i) whatever the number of visited sources, ants that are still unsatisfied retain the same probability of leaving the foraging area ($1/85\ \mathrm{s}^{-1}$), in which case they do not lay a trail; and (ii) satisfied ants that succeed in ingesting their desired volume lay the same amount of trail pheromone during their homeward trip, whatever the number of visited sources and/or the ingested volume. The latter assumption is supported by experiments with a single source
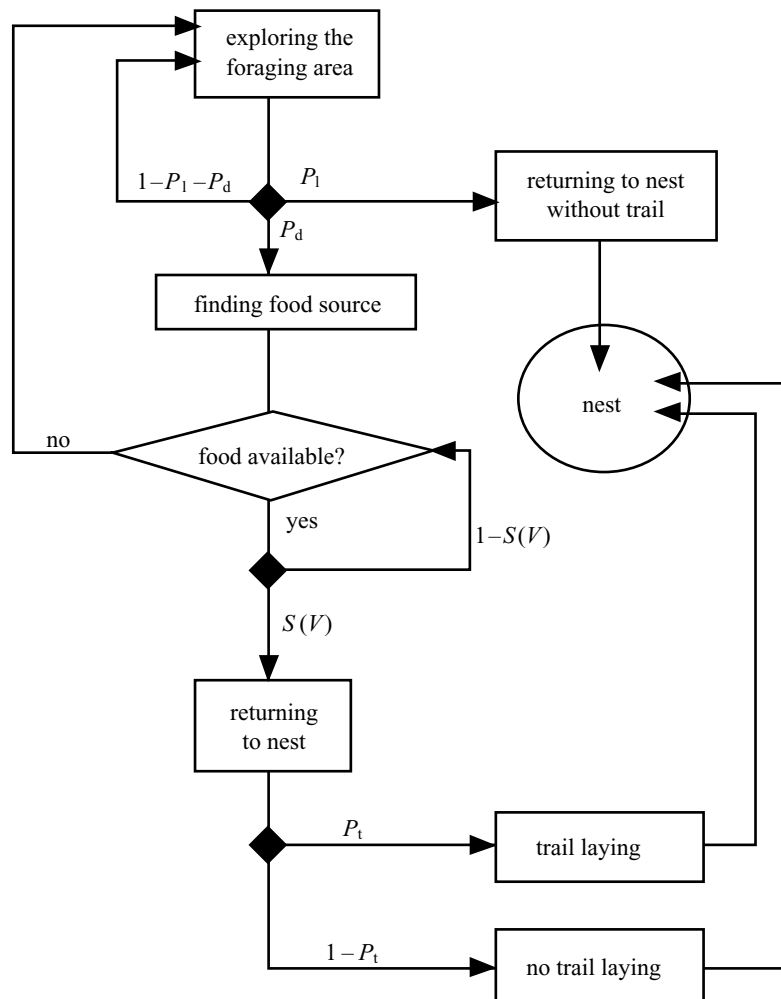
Figure 1. Graphical representation of the model on how ant colonies adjust their foraging to resource productivity. The model is based on the following empirically determined cycle of foraging behaviour. An ant begins exploring the foraging area and then either discovers a food droplet or abandons its search for food. As a food source is discovered, the ant starts drinking. At this point, if the ant succeeds in ingesting its 'desired volume' (see § 2b), it returns to the nest with a high probability of laying a trail. If no more food is available and if the ant is not yet satisfied with the amount of food ingested, it has the option of continuing to explore the area and forage for additional food. The model predicts an adjustment of the number of trail-laying ants as a function of the amount of food available at a given time and the probabilities associated with each of the three decision points. The black diamonds along the arrows denote such decision points. P_d, probability of food discovery is $1/20 \text{ s}^{-1}$; P_l, probability of leaving the area is $1/85 \text{ s}^{-1}$; $S(V)$, probability of stopping ingesting food (see equation (2.1)); P_t, probability of laying a trail among returning ants is 0.9.

(Mailleux *et al.* 2000) and confirmed in a multisources set-up (see below).

Monte Carlo simulations based on the behavioural rules described above were at first conducted in a set-up comprising six small food droplets (0.3 µl), each of them being below the desired volume of most ants. We then compared resulting theoretical values to experimental data from the six micropipette set-up to test the validity of the behavioural rules implemented in our model.

Having experimentally validated the model and its behavioural algorithms, theoretical predictions were made on how the partitioning of food, the productivity of aphids and the number of foragers (depending on ant's colony size and nutritional needs) influence the trail recruitment behaviour of aphid-tending ants. The simulations involved varying values of the model parameters while keeping constant the density of aphids. As aphids are highly aggregated in natural conditions, the time needed for an ant to move from one aphid to another was assumed to be equal to 1 s.

3. RESULTS

(a) *Foraging and trail-laying behaviour of scouts in a multisource set-up*
(i) *The experiment*

The trail-laying intensity (table 1; $\bar{x} \pm \text{s.d.} = 9 \pm 8\%$, $n = 45$) measured for each recruiter varied from one individual to the other but was independent from either the number of sources it had visited ($r_s = 0.10$, $n = 45$, $p > 0.05$), the amount of food ingested ($r_s = 0.12$, $n = 45$, $p > 0.05$) or the exploitation time ($r_s = -0.04$, $n = 45$, $p > 0.05$). The individual trail-laying intensity observed in this set-up of six micropipettes (0.3 µl) was similar to that found when a large single source (3 or 6 µl) was offered ($\bar{x} \pm \text{s.d.} = 13 \pm 11\%$, $n = 137$ from Mailleux *et al.* (2000) data) (Mann–Whitney test: n.s.; $Z = 1.35$, $n_1 = 45$, $n_2 = 137$). But, the percentage of trail-laying ants (57%) was lower when foragers had to feed on six small food sources to attain their desired volume than if a single large

Table 1. Comparison of experimental and theoretical behaviours of ants.

(Means are given ± s.d.; *n*, number of scouts observed experimentally. Theoretical values were obtained for 500 000 Monte Carlo simulations and compared with experimental data by means of one-sample Kolmogorov–Smirnov tests (except for that marked with an asterisk which was a χ^2-test).)

	experimental results (*n*)	theoretical results	statistical tests
percentage of trail-layers	57% (88)	58%	$\chi_1^2 = 0.04^*$, n.s.
individual trail-laying intensity	9 ± 8% (45)	—	—
ingested food volume (µl): by all ants	0.8 ± 0.5 (65)	0.7 ± 0.4	$D = 0.16$, n.s.
ingested food volume (µl): by trail-laying ants	0.9 ± 0.5 (37)	0.8 ± 0.4	$D = 0.10$, n.s.
ingested food volume (µl): by non-trail-laying ants	0.8 ± 0.5 (28)	0.6 ± 0.3	$D = 0.27$, n.s.
number of micropipettes visited: by all ants	2.8 ± 1.3 (88)	2.5 ± 1.2	$D = 0.11$, n.s.
number of micropipettes visited: by trail-laying ants	2.9 ± 1.3 (50)	3.0 ± 1.1	$D = 0.23$, n.s.
number of micropipettes visited: by non-trail-laying ants	2.5 ± 1.3 (38)	1.9 ± 1.0	$D = 0.23$, n.s.
exploitation time (s): for all ants	115 ± 67 (86)	105 ± 57	$D = 0.02$, n.s.
exploitation time (s): for trail-laying ants	127 ± 71 (48)	115 ± 56	$D = 0.10$, n.s.
exploitation time (s): for non-trail-laying ants	101 ± 58 (38)	91 ± 54	$D = 0.12$, n.s.

droplet (3 or 6 µl) was available (in the latter case, we found more than 90% of trail-laying ants; Mailleux *et al.* 2000). On average, all ants drank 0.7 µl of sugar solution, visited 2.5 micropipettes and spent 105 s exploiting food sources.

(ii) *Testing the validity of the model*

We compared experimental results to expected values from the model in which the 'desired volume' recruitment rule was implemented in a set-up of six micropipettes. First, the observed decrease in the proportion of trail-laying ants in our multisources set-up (where the discovery time is rather long) was confirmed by theoretical results in which only 58% of foragers laid a trail on their homeward trip (table 1). In addition, the model shows that this lower proportion of trail laying ants in the multisources compared with the single source set-up depends on the ratio between the giving-up time (T_2) and the discovery time (T_1). According to the model, the difference in the fraction of trail-laying ants between single and multisource set-ups decreases as this ratio increases. In other words, the impact of food partitioning on trail laying is expected to weaken as the giving-up time increases and/or as the discovery time of an additional source decreases (e.g. to highly aggregated aphid colonies, see § 3b).

Second, a good agreement between experiments and theoretical simulations was observed for averaged values of ingested volume, number of micropipettes and exploitation time (table 1). Actually, the theoretical distributions of these parameters were not statistically different from their experimental counterparts (one-sample Kolmogorov–Smirnov test): no significance for ingested food volume (figure 2*a*), number of micropipettes visited (figure 2*b*) and exploitation time (figure 2*c*).

The good agreement between theory and experiment was confirmed when considering separately either trail-laying or non trail-laying behavioural groups. The averaged values of ingested volumes or exploitation times generated from simulation data did not differ from their experimental counterparts, either within the trail-laying or the non trail-laying behavioural group (table 1). In both experiments and simulations, some trail-laying ants left the foraging area as soon as they found one micropipette while others with a higher desired volume threshold did so after visiting several micropipettes. As a result, the cumulative proportion of individuals that left the area and laid a trail increased with the number of micropipettes visited (and the related amount of food available) (figure 3*a*,*b*). Such dynamics of departure from the area of trail-laying ants was similar in the experimental and theoretical approach (Kolmogorov–Smirnov test: $D = 0.10$, $n = 50$, n.s.). Likewise, the experimental and theoretical dynamics of departure from the foraging were similar for non-trail-laying ants (Kolmogorov–Smirnov test: $D = 0.20$, $n = 38$, n.s.; figure 3*a*,*b*).

In conclusion, the general quantitative agreement between theoretical and empirical data validates the behavioural algorithms used in the model. There is no need to evoke other behavioural rules (e.g. based on some analogical counting of the number of food sources visited) to account for the foraging response of ants faced with several micropipettes. This combined theoretical and experimental approach demonstrates that the same recruitment rule based on the 'desired volume' criterion applies when ants forage on a single micropipette or when they have to collect food from multiple food sources.

(b) *Theoretical predictions of the model*

Having validated the behavioural algorithms, theoretical predictions using Monte Carlo simulations were then made on how the partitioning of honeydew, the global productivity of the aphid colony, as well as the number of foragers tending aphids, influence the trail recruitment behaviour of ants.

The first set of predictions dealt with the behaviour of ants tending aphid colonies delivering the same total volume of honeydew (VT) but differing in the number of producing aphids (N_a). The amount of honeydew produced per homopteran thus decreased as an inverse function of the increasing size of the aphid colony. For a given number of foragers (N_f), simulations showed that the percentages of trail-laying ants remained unchanged whatever the partitioning of the honeydew source (figure 4). This result is obtained when the time to discover a new aphid is short (1 s). However, as this new aphid may have been
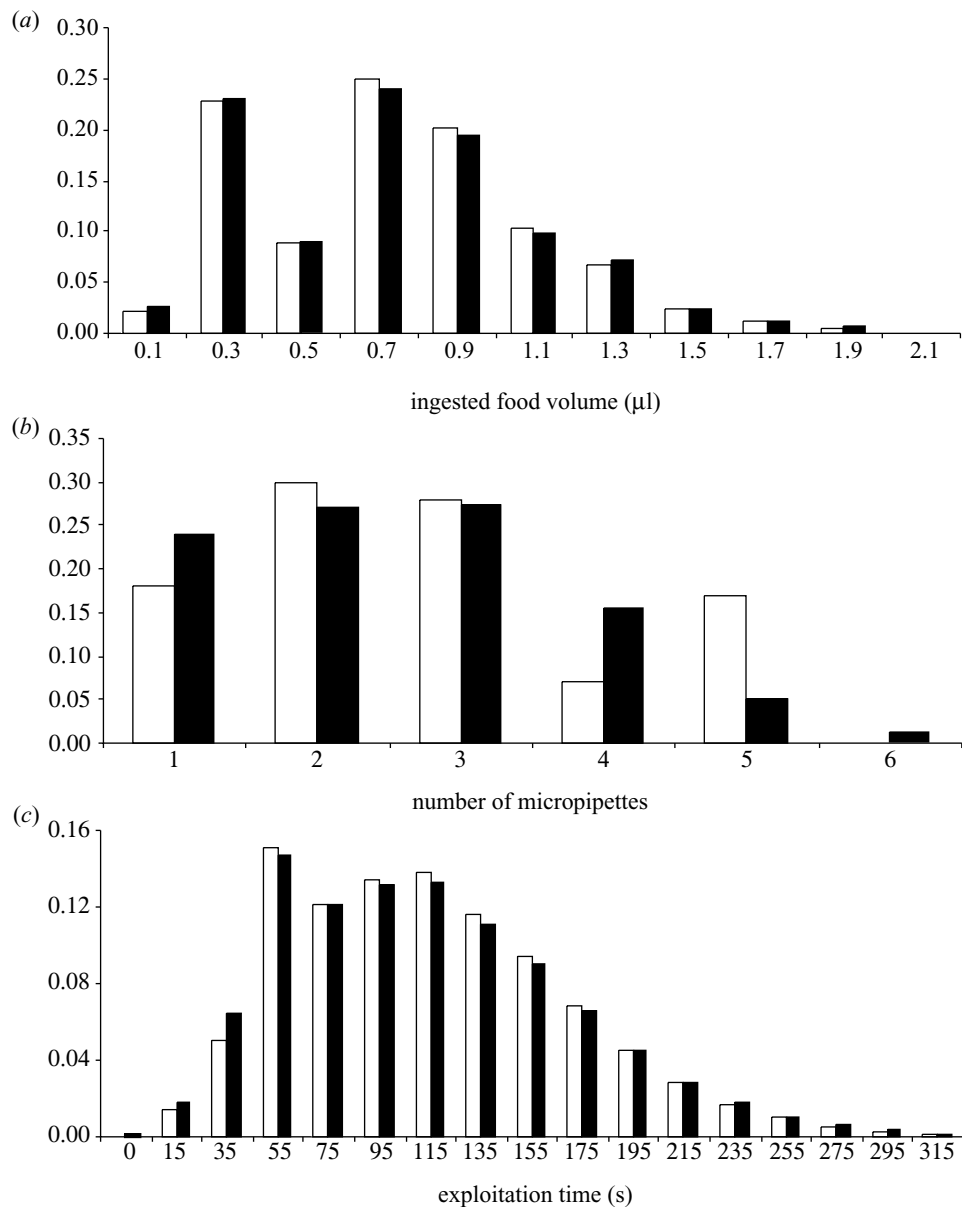
Figure 2. Distribution of theoretical (number of simulations, $n = 5000$, filled bars) and experimental values (number of ants observed, $n = 88$, open bars), for (a) ingested food volume, (b) number of visited micropipettes and (c) exploitation time.

tended by another forager, the time spent by a scout before finding additional food may be longer than 1 s.

For a given productivity (VT), large colonies of poorly excreting aphids elicited the same proportion of recruiters among foragers as small colonies of highly productive individuals. As a general rule, the proportion of recruiters was related to the total productivity of the aphid colony but did not depend on the pattern of honeydew delivery.

A second set of numerical experiments aimed to investigate how the absolute number of trail layers changes with the foraging force of the ant colony (N_f), for a given total productivity of the aphid colony (VT) (figure 5). The number of trail-laying ants started increasing with the foraging force to reach a maximum (number of foragers attending aphids, X_o) before declining when an even larger number of ants was present. Whatever the size of the aphid colony, curves showed that the maximum was always positioned at *x*-axis values close to the VT/V_c ratios ($X_o = $VT/$V_c$). Simulations predicted that X_o was linearly

related to the total productivity of the aphid colony (figure 6; $r^2 = 0.99$, $n = 25$, $p < 0.001$). Hence, ants are expected to regulate their numbers at the food resource in proportion to its productivity. Functionally, it means that the global trail intensity increased with the foraging force as long as the total quantity of honeydew oversupplied the total demand of foragers. Conversely, when the demand of the foraging force overcame the offer of honeydew, fewer workers were able to ingest their desired volume and lay a trail. As a result, the foraging force is automatically driven back to values where the recruitment (the number of trail-laying ants) is maximized.

4. DISCUSSION

Our previous study (Mailleux *et al.* 2000) provided a direct support to the rule of thumb used by foragers to assess the volume of a single food source. The key criterion that triggers the trail-laying behaviour of foragers is
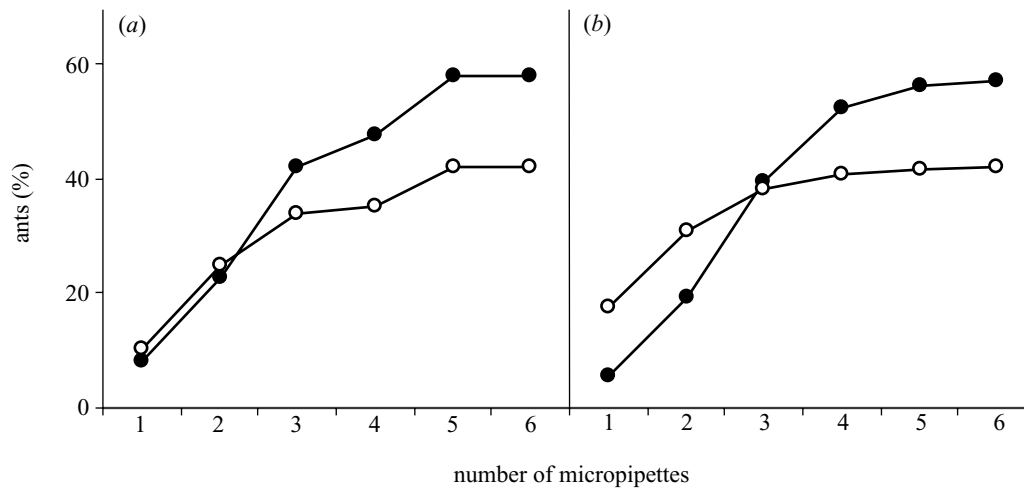
Figure 3. Cumulative percentage of trail-laying ants (filled circles) or non trail-laying ants (open circles) leaving the foraging area after having visited between one and six micropipettes. For a value on the *x*-axis of for example three micropipettes, this figure gives the summated proportions of trail-laying ants that left the area after visiting one, two or three micropipettes. The curves were obtained from (*a*) experiments (*n* = 88) or (*b*) from theoretical simulations (*n* = 5000).
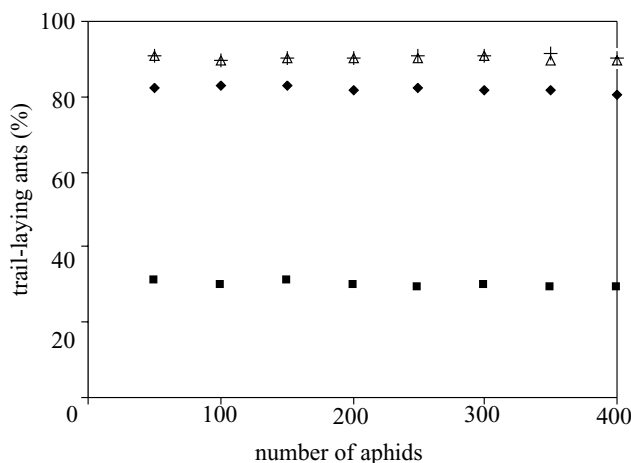

Figure 4. Percentage of trail-laying ants as a function of the number of aphids for a given honeydew productivity (VT = 10 µl). The number of aphids (N_a) within the colony ranges from 50 to 400 individuals, each emitting from 1/40 to 1/5 µl of honeydew. Curves were drawn for different numbers of foragers attending the aphid colony (N_f = 1 (plus symbols), 5 (triangles), 10 (diamonds) or 15 (squares) foragers). Each theoretical dataset results from 2000 simulations.
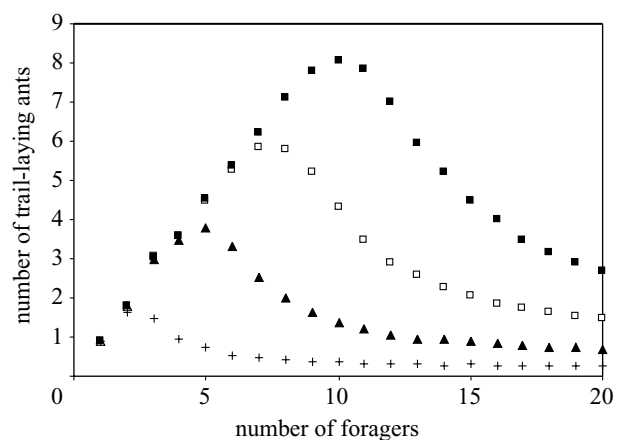

Figure 5. Average number of trail-laying ants as a function of the number of foragers attending aphids. Curves were drawn for several aphids' colonies differing in their total productivity (VT): these colonies are composed of either 100 (plus symbols, VT = 2.5 µl), 200 (triangles, VT = 5 µl), 300 (open squares, VT = 7.5 µl) or 400 (filled squares, VT = 10 µl) individuals (N_a); each emitted 0.025 µl of honeydew. Each theoretical dataset results from 2000 simulations.

their ability to ingest their own desired volume. Information about the total volume of a food source is thus conveyed to the society by the percentage of trail-layers among returning ants. The good agreement between theory and experiments in a set-up of six small feeders validates the behavioural algorithm used to model *L. niger* recruitment behaviour: the 'desired volume' criterion is not restricted to a single source situation but can be generalized to the context of multiple food droplets. Moreover, the model shows that the lower fraction of trail-laying ants when workers have to feed on several food sources results from the ratio between the time needed to discover a new food source and the giving-up time spent before leaving the foraging area.

For a high density of droplets (corresponding to a short time of discovery) as actually occurs in the aphid colony

(Addicot 1979), the model predicts that the partitioning of the honeydew food source does not affect the proportion of ants laying a trail and hence the number of attending ants. For a same global productivity, large colonies of weakly excreting aphids are expected to attract the same number of foragers as small colonies of highly productive individuals. However, this theoretical prediction currently lacks validation in natural conditions. Indeed, it is difficult to experimentally isolate the impact of food partitioning on aphids' attendance by ants, as aphid species that differ in the size of emitted droplets are likely to differ also in the quality of honeydew (e.g. Mittler 1958; Sakata 1994).

The model also investigates how a rule of thumb based on a desired volume criterion allows ants to adjust their foraging force to the productivity of aphid colonies. A hypothetical regulatory mechanism—not supported by our
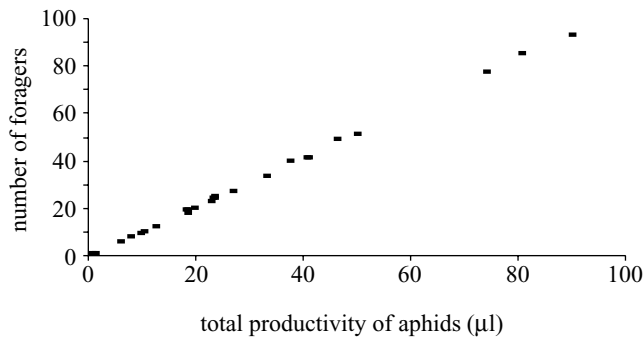
Figure 6. Number of foragers for which global trail-laying is maximized, as a function of the productivity of the aphid colony (a significant linear relationship was found between these two parameters, $y = 1.04x - 0.15$, $r^2 = 0.99$, $n = 25$, $p < 0.001$). Each theoretical dataset results from 100 simulations. The number of aphids (N_a) within the colony ranges from 0 to 400 individuals, each emitting from 0.05 to 0.25 μl of honeydew.

data—might be that the amount of pheromone laid down by each ant is directly related to the quantity of food it has ingested. Instead, an all-or-nothing response is at work that regulates the fraction of workers laying a trail: the ingested volume acts as a threshold that rules the decision to lay a trail but does not influence the amount of pheromone emitted per trail-laying ant. One of the main consequences of this threshold response is that there is a number of foragers for any given productivity that will maximize recruitment. This all-or-nothing response is a powerful and economical means for the society to adjust the number of potential food carriers to the global quantity of available honeydew. In effect, trail recruitment of nest-mates simply stops when ants present at the food source no longer succeed in ingesting their desired volume. Such feedback is both functional and energy saving as it slows down recruitment to temporarily exhausted or overcrowded food sources, a likely situation in the case of small-sized colonies of aphids producing a limited amount of honeydew.

Finally, our simulations show that the optimal number of foragers that maximizes recruitment is linearly related to the number of homopterans and to their global honeydew productivity. A similar linear dependence between the number of foragers and the aphid productivity has been reported for several ant–aphid associations (Dreisig 1988; Breton & Addicott 1992), which suggests the widespread presence of our rule-of-thumb. If this is indeed the case, then interspecific variation in the foraging regulation could result from a simple quantitative difference in the values of behavioural and physiological parameters (e.g. desired volume, ingestion time) between species, but not in the decision-making process governing trail recruitment.

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