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ORIGINAL PAPER

Individual and collective foraging decisions: a field study of worker recruitment in the gypsy ant *Aphaenogaster senilis*

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Abstract In social insects, the decision to exploit a food source is made both at the individual (e.g., a worker collecting a food item) and colony level (e.g., several workers communicating the existence of a food patch). In group recruitment, the recruiter lays a temporary chemical trail while returning from the food source to the nest and returns to the food guiding a small group of nestmates. We studied how food characteristics influence the decision-making process of workers changing from individual retrieving to group recruitment in the gypsy ant *Aphaenogaster senilis*. We offered field colonies three types of prey: crickets (cooperatively transportable), shrimps (non-transportable), and different quantities of sesame seeds (individually transportable). Colonies used group recruitment to collect crickets and shrimps, as well as seeds when they were available in large piles, while small seed piles rarely led to recruitment. Foragers were able to "measure" food characteristics (quality, quantity, transportability), deciding whether or not to recruit, accordingly. Social integration of individual information about food emerged as a colony decision to initiate or to continue recruitment when the food patch was rich. In addition, group recruitment allowed a fast colony response over a wide thermal range (up to 45°C ground temperature). Therefore, by combining both advantages of social foraging (group recruitment) and thermal tolerance, *A. senilis* accurately exploited different types of food sources which procured an advantage against mass-recruiting and behaviorally dominant species such as *Tapinoma nigerrimum* and *Lasius niger*.

Keywords Foraging · Ants · Group recruitment · Food size · Thermophily

Introduction

Foraging is a central component of animal behavior. Considering that animals may forage "optimally" in order to maximize their fitness (Pyke 1984) led to the development of the optimal foraging theory. According with Begon et al. (2006, p. 282), "the aim of optimal foraging theory is to predict the foraging strategy to be expected under specified conditions, and it considers that the foraging behaviour that is exhibited by present-day animals is the one that has been favored by natural selection in the past but also most enhances an animal's fitness at present." Although the consequences of individual foraging decisions on fitness are relatively straightforward in most solitary animals, they may be more complicated to disentangle in social animals. Hence, while the errors made by solitary animals impact on them alone (in terms of fitness reduction), those of social animals have negative consequences both at the individual and colony levels. To

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prevent such errors, insect societies have developed efficient collective mechanisms for conveying information about food sources (Portha et al. 2002; Mailleux et al. 2003) or new nest sites (Sendova-Franks and Franks 1995; Pratt et al. 2002; Pratt 2008).

Foraging in ants is a complex process by which individual and social aspects interact to determine food intake for the colony as a whole (Roces and Hölldobler 1994). Ant colonies show a wide range of strategies based on individual or cooperative food gathering. Worker recruitment is the behavioral sequence that allows a worker, the recruiter, to bring a given number of nestmates, the recruits, to a food source. Recruitment strategies can be classified into three main categories (Wilson 1971) of which tandem recruitment or tandem running is considered least efficient because it allows the recruitment of only one worker; during tandem running, the recruit follows the recruiter in close antennal contact. Mass recruitment is the most efficient strategy by which recruiters returning from a food source to the nest lay a chemical trail that guides their nestmates to the source. Group recruitment stands between these extremes: the recruiter first lays a chemical trail upon return to the nest and subsequently leads a small group of recruits along this trail to the source. Therefore, a main difference between mass and group recruitment is that the former type is "anonymous" while the latter type involves a leader (Bonabeau 1997). Moreover, in mass-recruiting species, chemical signaling results in the formation of longer-lasting trails and the recruitment of hundreds of workers that monopolize the source. By contrast, group recruitment is mainly used to collect solid food items by recruiting a few workers through temporary chemical trails.

From an adaptive perspective, the more flexible the foraging behavior, the more readily colonies may adjust to environmental changes (Schatz et al. 1997). Gordon (1991) defines behavioral flexibility as the process by which an animal changes its behavioral patterns when the environment changes. In ants, for example, an individual worker may change from individual retrieving to group recruitment. This decision may be influenced by many factors such as colony size (Beckers et al. 1989; Thomas and Framenau 2005), presence of brood (Portha et al. 2004), mortality risk due to competitors (Nonacs and Dill 1990; Dejean et al. 2005), amount, type, and distribution of food (Breed et al. 1987; Detrain and Deneubourg 1997; Portha et al. 2002; Mailleux et al. 2003; Johnson et al. 2003; Cogni and Oliveira 2004), and temperature (Cerdá et al. 1998a; Ruano et al. 2000). The integration of these factors by individual workers (recruiters or recruits) determines the outcome of the recruitment process (Lopes et al. 2004).

At a community level, species coexistence and diversity depend on various mechanisms that provide many kinds of refuges and ensure the persistence of inferior competitors (Toda et al. 1999). For small-bodied ectotherms, one such kind of refuges may be high temperatures tolerated by thermophilic species. In Mediterranean habitats, as in other thermally stressing environments, temperature plays a determinant role in structuring insect communities. As an example, thermal constraints may generate within- and between-habitat variations in the composition and size structure of insect pollinator assemblages (Herrera 1997). Patterns of resource use in Mediterranean ant communities, which have also been studied in depth, are affected by species-specific traits such as foraging strategies and thermal preferences (Cros et al. 1997; Cerdá et al. 1997, 1998a). Selection of particular thermal environments on a daily and seasonal basis provides certain advantages for ants (Cerdá et al. 1998a). Hence, subordinate species (those within the community with lesser capacity to win confrontations with competitors) are often more thermophilic, being able to tolerate warmer temperatures than dominant species, which increases their exploitative ability and foraging efficiency (Cerdá et al. 1997, 1998a).

Surprisingly, as Mailleux et al. (2000) pointed out, although many studies have focused on the functional and evolutionary significance of the observed patterns of resource use, the behavioral mechanisms and decision-making processes that underlie such foraging strategies have often been disregarded. For that reason, the major goal of our research was to study these behavioral and ecological processes in one of the most common species of open Western Mediterranean habitats, the gypsy ant *Aphaenogaster senilis*, a subordinate group-recruiting species. We conducted a series of field experiments to determine the role of behavioral flexibility of foragers and the collective decision-making process in this species. More precisely, we analyzed the dynamics of recruitment by examining the relationships between the social response of the colony (number of recruits), the individual response of workers (decision to recruit or not), the "transportability" of the resource (non-transportable and cooperatively or individually transportable prey), and the efficiency in resource exploitation by the species when compared with others of the community. We hypothesized that (1) group recruitment is modulated and adjusted to different quantity and quality of prey and (2) the combination of both social foraging strategies and thermophily gives a competitive advantage in resource exploitation.

Material and methods

Model system and field sites

A. senilis Mayr is a common ant distributed around the western Mediterranean basin (Cagniant et al. 1991).

Colonies are monogynous (one single queen), monodomous (one single nest), and comprise between 200 and 3,000 monomorphic workers (Boulay et al. 2007). Individual body length and weight range from 6 to 10 mm and from 5 to 8 mg, respectively (unpublished data). It is a diurnal and thermophilic species, with an optimal foraging temperature of 42°C and a critical thermal limit (CTM) of 46°C (Cerdá et al. 1998a). It feeds on a large variety of food items, including animal (mainly insect corpses) and plant (flower petals, twigs, or seeds) remains (Cerdá et al. 1988). Maximum individual load that a single worker of *A. senilis* is able to carry is 150 mg (Cerdá et al. 1998b).

Field experiments were performed in two different localities of the Iberian Peninsula where nests of *A. senilis* were conspicuous and abundant. The Canet area was an open grassland near Canet de Mar (41° 25′ N, 2° 37′ E; Barcelona, NE Spain) at 50 m above sea level, 750 m away from the coastline (see Cerdá et al. 1997 for a detailed description of the vegetation). The Doñana area was located in Las Beles, in the Doñana Biological Reserve of the Doñana National Park (37° 1′ N, 6° 33′ W; Huelva, SW Spain) at sea level, 4 km away from the coastline. It consists of an open shrubland composed mainly by *Halimium halimifolium*, *Halimium commutatum*, *Stauracanthus genistoides*, and *Lavandula stoechas*. The climate in both study sites is Mediterranean. Ant species composition was similar between both localities, with small geographic differences due to species distribution that did not affect the competition outcome. In Canet de Mar, dominant species were *Tapinoma nigerrimum*, *Tetramorium semilaeve*, and *Pheidole pallidula*, while in Las Beles dominant species were *T. nigerrimum*, *Tetramorium impurum*, and *Lasius niger*; in Canet de Mar, the highly thermophilic ant species was *Cataglyphis cursor*, while in Las Beles it was *Cataglyphis floricola*.

All experiments were done (1) during the peak of seasonal activity of the species (May–June; X. Cerdá et al. personal observation), that is, when presence of brood is largest; (2) during the normal daily activity period of the species (from 09:00–14:00 h and 17:00–20:00 h LST); and (3) with the most active colonies in the area. Colonies with similar levels of foraging activity were chosen the day before the experiments in order to homogenize the sampling units. Each colony was tested only once. During all experiments, soil surface temperature was monitored every 3 min with an electronic digital probe thermometer (Brannan, UK, mod. 38/660/0).

Group-recruitment experiments: the effect of food transportability

We analyzed differences in the recruitment process of *A. senilis* colonies to two different types of food source according to transportability: (1) a shrimp of mean weight 3,705±171 mg (mean±SE, $n=20$) which is not transportable, either individually or cooperatively (~500 times heavier than one worker and ~24 times heavier than the maximum individual load that one worker can carry), and must be cut in small individually transportable pieces; and (2) a pile of *ad libitum* decorticated sesame seeds, one seed is 3.45±0.13 mg (mean±SE, $n=20$), weight and individually transportable by workers (0.5 times lighter than one worker). Food items were deposited at 2 m from the nest entry. Preliminary experiments showed that both food items were very attractive to the ants.

Group-recruitment events occurred as follows: a worker (the recruiter) discovered the food item, came back to the nest, and left the nest followed by a small group of relatively excited workers (the recruits). In order to optimize the observation effort, when more than 30 min elapsed without a colony finding the food item, it was not considered for the experiments and another colony was used instead. From the moment of food discovery to the end of the experiment (30 min later), we recorded the following variables: (1) time of the first recruitment (time elapsed between the food discovery and the arrival of the first group of recruits), (2) frequency of recruitment events, and (3) the number of recruits in each observed recruitment event.

To test differences in group-recruitment dynamics between non-transportable (shrimp) and individually transportable (seeds) food items, we compared the following five variables: (1) time of first recruitment, (2) number of recruitment events per nest, (3) average number of recruits per recruitment event, and (4) total number of recruits per experiment (sum of all recruits from all observed recruitment). Independent statistical models were fitted to each of these four dependent variables with the type of food (shrimp or *ad libitum* seeds) as fixed effect.

Normality of dependent variables was always tested before fitting statistical models and we selected the distribution of errors that minimized the deviance of the model (Herrera 2000). We used either general linear models with normal distributions and identity link functions (hereafter $\mathrm{GLM_N}$) or generalized linear models with Poisson or gamma distributions and log link functions (hereafter $\mathrm{GLM_P}$ and $\mathrm{GLM_G}$, respectively).

Group-recruitment experiments: the effect of food availability

We tested the effect of food availability on recruitment by offering ants 5, 20, or an *ad libitum* pile of sesame seeds. In the 5- and 20-seed experiments, when a worker collected one seed, another seed was immediately added to the pile to maintain constant food availability so that seed collection (or recruitment behavior) did not stop due to the absence of seed. We compared (1) time of first recruitment, (2) number of recruitment events per nest, (3) average number of recruits per recruitment event, (4) total number of recruits per experiment, and (5) the total number of seeds retrieved when we offered seed piles of different quantity. We analyzed differences of these three variables as a function of the quantity of food (fixed effect) by fitting GLMs to the data. When models were significant, we performed post hoc comparisons to test between-level difference significance.

Occupation dynamics to different food sources

The occupation of the food source through time is a process that depends on worker traffic between the food item and the nest. We measured this occupation by counting every 2 or 3 min the number of workers on prey (cricket and shrimp, respectively) and the number of workers coming back to the nest carrying a seed (crossing a mark point in 3-min intervals). Similar to shrimp and seeds, young crickets averaging 321±12 mg (mean±SE, $n=20$; ~45 times heavier than one worker) were deposited at 2 m from the nest entry. We compared the occupation of the different food types during the first 30 min, as the maximum number of workers was always attained before this time. We standardized the data of each colony by defining its maximum accumulated number of counted workers as the 100% value. Maximum absolute values were: 33 workers for crickets, 67 workers for shrimps, and 261 workers for seeds. We used the cumulative number of workers on prey (shrimp and cricket) or carrying a seed in 3-min intervals as dependent variables in general regression models. Each of these variables was fitted against time after discovery, by simple or polynomial regression. The best fit was chosen on the basis of the regression coefficient (R^2) and the F and p statistics associated to the whole model. Because we aimed at comparing the occupation processes in optimal conditions, we did not consider experimental colonies with low recruitment values (e.g., less than a total of ten workers for cricket, 30 worker for shrimp, or 50 seeds carried to the nest before 30 min) to fit recruitment dynamics curves of different food items through time.

We analyzed the effect of temperature on the occupation dynamics. The number of workers in the shrimp or carrying a seed in 3-min intervals was fitted by simple or polynomial regressions to ground temperature in the same time intervals (the best fit was chosen on the basis of the regression coefficient, R^2).

Cooperative prey transport dynamics and foraging efficiency

To analyze the cooperative transport efficiency of prey by *A. senilis*, two types of non-individually transportable items were offered: (1) a young cricket averaging 321±12 mg (mean±SE; ~45 times heavier than one worker) and (2) an adult cricket averaging 870±285 mg (~125 times heavier than one worker). Both items are cooperatively transportable by a group of workers. Young crickets were deposited at 2 m from the nest entry and surveyed during 30 min, while the adult crickets were deposited at 0.5 m from the nest entry and surveyed during 15 min; in both cases, we noted every 2 min the number of workers on the prey and the distance between the prey and the nest. As our previous observations indicated that the mean foraging distance of *A. senilis* workers was 4.1±0.01 m (mean±SE, $n=545$), young crickets were deposited at 2 m from the nest entrance, while adult crickets were placed at a shorter distance to diminish the time of prey transport and, consequently, the risk of prey robbing by mass-recruiting ant species (Cerdá et al. 1998b). Our interest was to quantify the efficiency (velocity of transport and number of workers involved) of *A. senilis* during the cooperative transport of prey.

In order to compare the foraging efficiency for the different prey types (both adult and young cricket corpses cooperatively transportable and individually transportable sesame seeds), two other measures of transport efficiency were used: prey delivery rate (PDR; Orians and Pearson 1979; Traniello and Beshers 1991) and net profit (NP; Cerdá and Retana 1997). PDR was calculated as: PDR= prey weight×transport velocity. NP was defined as the benefit in prey biomass obtained by the colony per unit of biomass invested in the forager (assumed to be a linear function of the forager's mass) and was calculated as: NP= PDR/forager mass (Cerdá and Retana 1997). This measure counterbalances PDR values according to the number of workers involved in the prey delivery. It evaluates the real benefits obtained by the colony when different-sized teams of workers transport different-sized prey to the nest. For these calculations, we grouped number of workers by pair categories (e.g., category 2: included cases with one and two workers; category 4: cases with three and four workers, etc); we used the value of 7.25 mg as the weight of one forager (obtained as the average weight of 20 foragers caught during experiments).

Recruitment to baits: competition within the community

The potential competitive advantage of group recruitment for food exploitation was determined by placing 12 series of four baits regularly in a 50×50-m plot in Las Beles site (see Cerdá et al. 1997 and references therein for methodological justification). Baits were plastic discs with four non-individually transportable food rewards (honey, bacon, cheese, and biscuit). Baits were installed at 07:00 and the number of ants of each species feeding at them was recorded every hour from 08:00 to 23:00. Ground surface temperature

Table 1 Effect of food transportability on the recruitment process of *A. senilis*‘

Variable	Non-transportable (shrimp; *n*=32)	Transportable (ad libitum seeds; *n*=15)	GLM error distribution	*df*	$\chi 2$	*p*
First recruitment time (min)	13.2±1.4	13.7±2.8	Gamma	1	0.17	0.681
Number of recruitments per nest	3.2±0.4	2.1±0.6	Poisson	1	2.77	0.096
Number of recruits per recruitment	10.4±1.2	4.9±1.7	Poisson	1	**7.67**	**0.006**
Total number of recruits per nest	33.9±4.9	10.1±2.7	Poisson	1	**13.52**	**<0.001**

Values are mean±SD. GLM error distribution refers to the distribution of the dependent variable; *n* represents sample size (each colony was tested only once); χ^2, *df*, and *p* are the GLM statistics, in bold when significant

was also measured every hour with an electronic digital probe thermometer (Brannan, UK, mod. 38/660/0).

Bait occupation of *A. senilis* (the target species, subordinate, group-recruiting) was compared to that of *C. floricola* (hot specialist, thermophilic species, subordinate, solitary forager) and the dominant species *T. nigerrimum* and *L. niger* (baits occupied by both species were considered together).

General statistics

Computations of GLM and GLMM were performed with the SAS package v. 8.2, procedure GENMOD and MIXED (SAS Institute Inc. 1999). As temperature has a great effect on the dynamics of ant foraging (Cerdá et al. 1998a), we added temperature as a covariable in all models (even if not explicitly stated). The results are presented as mean±SE.

Results

The effect of food transportability on the dynamics of group recruitment

On average, the first recruitment occurred 13 min after the food source was discovered, irrespective of its transportability (Table 1; sesame seed pile vs shrimp). The average number of recruitments carried out by each colony did not differ significantly between both types of food (Table 1) and only a small proportion of colonies (6.25% and 26.67% for sesame seed pile and shrimp, respectively) did not recruit at all during the course of the experiment.

The number of recruits per recruitment varied greatly, ranging from 1 to 27, although a large majority of recruitments (>70%) involved one to ten workers only (Fig. 1). The number of recruits per recruitment was significantly higher when the source was a large non-transportable shrimp than when it was composed of numerous individually transportable seeds (Table 1). This also resulted in a significantly higher total number of workers recruited to shrimps than to large piles of sesame seeds (Table 1).

Although ground temperature varied greatly from 21°C to 53°C throughout the experiment, it had only a limited effect on the organization of group recruitment. The first recruitment after food discovery occurred significantly sooner when ground temperature was higher (GLM_G, χ^2= 4.34, p=0.037) but the other variables (number of recruitment events per experiment, number of recruits per recruitment, and total number of recruits per experiment) were not significantly affected by ground temperature (GLM_P, χ^2=0.03, p=0.866; GLM_P, χ^2=0.80, p=0.372; and GLM_P, χ^2=0.03, p=0.866, respectively).

Effect of food availability on group recruitment

When considering the effect of food availability by offering different seed quantities, piles with only few (five or 20) or many (*ad libitum*) items, the time elapsed between seed discovery and the first recruitment did not change significantly according to the size of the seed pile (Table 2). By contrast, both the number of recruitments per nest (Table 2)

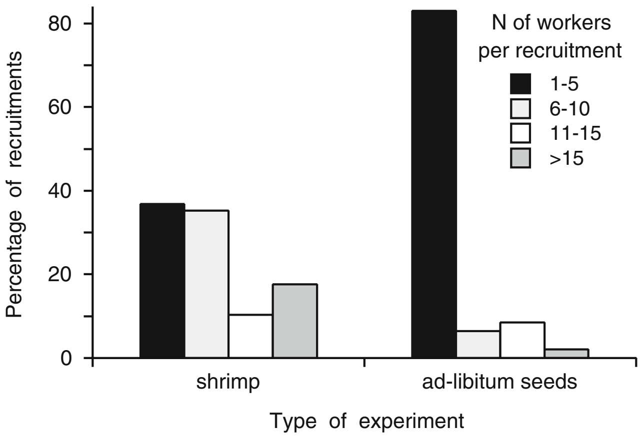

Fig. 1 Percentage of observed recruitments with different number of workers recruited for two types of food item: non-individually transportable (shrimp) and individually transportable (*ad libitum* seeds). Number of cases: shrimp, *n*=68; *ad libitum* seeds, *n*=47

Table 2 Effect of food availability on the recruitment process of *A. senilis*

Variable	Ad libitum seeds (n=15)	20 seeds (n=10)	Five seeds (n=10)	Error distribution	*df*	χ2	*p*
First recruitment time (min)	13.7±2.8	26.13±2.6	22.2±3.7	Gamma	2	5.14	0.076
Number of recruitments per nest	2.1±0.6	0.4±0.3	0.5±0.2	Poisson	2	**10.15**	**0.006**
Total number of recruits per nest	10.1±2.7	3.6±3.1	1.8±2.7	Poisson	2	**7.70**	**0.021**
Number of recruits per recruitment	4.9±1.7	1.5±1.1	1.5±0.7	Poisson	2	5.86	0.053
Number of seeds retrieved per nest	129±37	30±16	19±2	Gamma	2	**14.70**	**0.0006**

Values are mean±SD. GLM error distribution refers to the distribution of the dependent variable; *n* represents sample size (each colony was tested only once); χ^2, *df*, and p are the GLM statistics, in bold when significant

and the total number of recruits per nest (Table 2) differed significantly depending on the number of available seeds. The number of recruitments per nest was significantly higher when sesame seeds were available *ad libitum* than when they were presented by 20 or five, but the difference between 20-seed and 5-seed piles was not significant (*post hoc* pairwise comparison tests). Differences in the average number of recruits per recruitment were not significant (Table 2). Thus, a large seed pile triggered more recruitment events and with more workers recruited than when only 20 or five seeds were available at a time.

Major differences in the recruitment effort with respect to seed amount resulted in large significant differences in the number of seeds that were eventually retrieved by ants (Table 2). Colonies offered *ad libitum* seed piles collected on average four to six times more seeds than those offered 20- and 5-seed piles, in spite of the fact that seed amount was maintained constant throughout the experiment.

Throughout this experiment, ground temperature ranged from 20°C to 54°C and had no effect on the organization of group recruitment to the different seed piles. None of the measured variables (first recruitment, number of recruitment events per experiment, number of recruits per recruitment, total number of recruits per experiment, number of seed retrieved per experiment) were significantly affected by ground temperature ($\mathrm{GLM_G}$, $\chi^2=0.30$, $p=0.584$; $\mathrm{GLM_P}$, $\chi^2=0.38$, $p=0.538$; $\mathrm{GLM_P}$, $\chi^2=0.04$, $p=0.837$; $\mathrm{GLM_P}$, $\chi^2=2.50$, $p=0.113$; and $\mathrm{GLM_G}$, $\chi^2=0.00$, $p=0.961$, respectively).

Occupation dynamics to different food sources

The various recruitment events that followed food discovery progressively led to an accumulation of workers on the source. However, the shape of the slope of occupation through time was very different according to food type (Fig. 2). The colonies of *A. senilis* had a different response according to the type of prey: the fastest response was to cooperatively transport young crickets and the slowest to transport individually the sesame seeds. The relative number of workers on the young cricket as a function of time fitted well a quadratic curve with a very quick increase of the number of workers in contact with the prey ($y=-1.753+0.114x-0.000033x^2$; $R^2=0.994$, $p<0.001$, $n=15$). The number of workers on the shrimp (non-transportable prey) increased linearly to a maximum of approximately 50% of workers ($y=-5.22+0.0612x$, $R^2=0.984$, $p<0.0001$, $n=24$). For the *ad libitum* seed pile, there was an initial small increment in the number of workers in contact with the food and a subsequent large increment until the maximum was reached ($y=0.69+0.005x+0.000029x^2$, $R^2=0.996$, $p<0.0001$, $n=24$). Mean maximum values were: 21±2 workers on the cricket (overall maximum 33, $n=10$); 46±2 workers on the shrimp (overall maximum 67, $n=24$); and 117±18 workers carrying seeds individually to the nest during 30 min (overall maximum 261, $n=16$). Ten minutes after prey discovery, there were 55% of workers (percentages with respect to the maximum number of workers) carrying the crickets (i.e., 18 workers) but only 30% on the shrimp (20 workers) and 10% carrying seeds (26 workers).

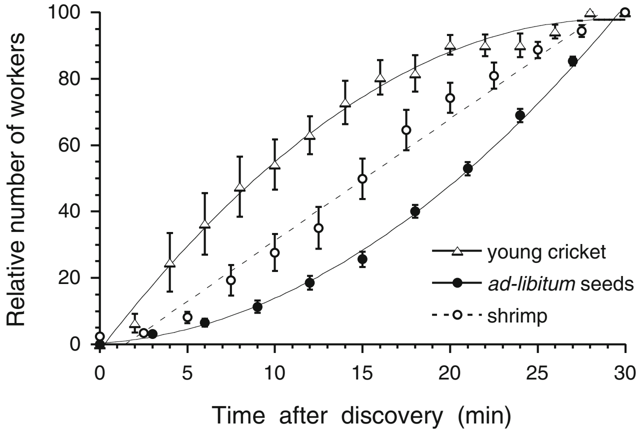

Fig. 2 Recruitment dynamics to different food items over time. Occupation of each food item at 2 m from the nest is represented by standardizing relative number of workers to the maximum accumulated number of workers attained in each experiment. Values represented are means+SE and *lines* show the fit for each food item

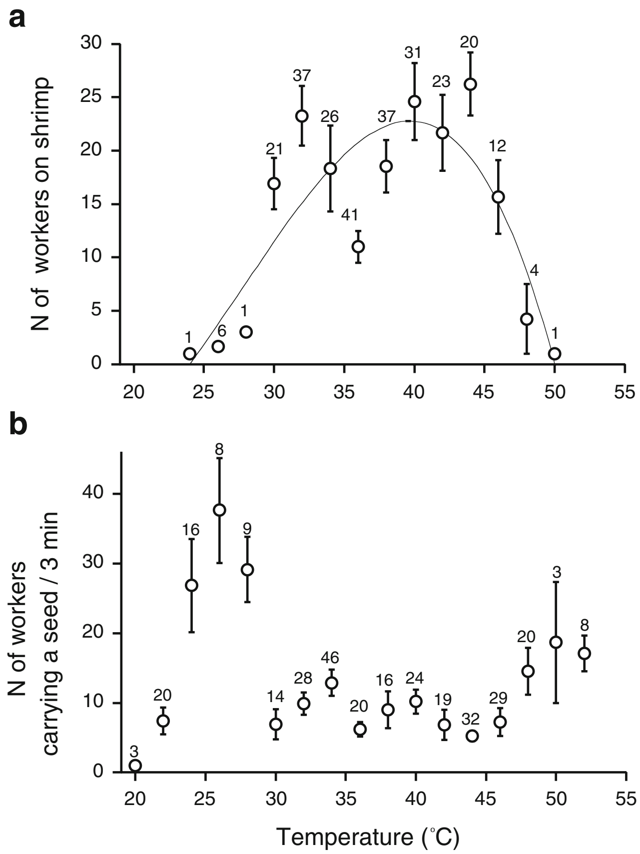

Fig. 3 Effect of temperature on occupation dynamics: **a** recruitment to a shrimp (*y-axis*: number of workers on the shrimp); **b** traffic of workers carrying a seed in *ad libitum* experiments (*y-axis*: number of workers coming back to nest during 3 min). Values represented are means+SE and the *line* shows the curve fit for the shrimp experiment. *Numbers* on the *top* of each value are the sample size

The effect of temperature on food source occupation dynamics differed according to type of food. Figure 3a shows the relation between temperature and number of workers on the shrimp. The observed data fitted well with a third-degree polynomial ($y=53.69-8.90x+0.389x^2-0.00466x^3$, $R^2=0.740$, $p=0.003$, $n=14$), with the maximum values within the temperature range between 32°C and 45°C and an abrupt fall of worker presence beyond this temperature. By contrast, temperature and traffic of seed carriers were not significantly related either for *ad libitum* seed piles ($R^2=0.02$, $p=0.57$, $n=17$) or for 20- and 5-seed piles ($R^2=0.13$, $p=0.43$, $n=15$; $R^2=0.10$, $p=0.58$, $n=13$, respectively), and traffic of workers continued until extreme ground temperatures, near 52°C (Fig. 3b).

Cooperative prey transport and foraging efficiency

To transport the prey cooperatively, the number of workers involved varied according to prey size: for the young (and lighter) cricket, the percentage of observations involving more than ten workers pulling or pushing was 56%, while, for the adult (and heavier) cricket, a large majority of prey transport observations (>80%) involved more than 15 workers (Fig. 4).

The dynamics of prey transport are shown in Fig. 5a. For the case of the larger prey (an adult cricket placed at 0.5 m from the nest), only 4 min after the first ant discovered the prey, we observed that an average of 25 workers were dragging the adult cricket, a number which was already enough to move the prey (Fig. 5a). The number of workers transporting the prey increased slowly up to 35–40 workers. The relationship between the number of workers on the prey and the distance covered to the nest fitted an exponential function (Fig. 5a; $y=0.0407e^{(0.1823x)}$, $R^2=0.978$, $p<0.05$, $n=10$). Cooperative prey transport was very efficient: the adult cricket was transported to the nest in less than 15 min.

For smaller prey (a young cricket placed at 2 m from the nest), we observed that 4 min after the first ant discovered the prey an average of nine workers dragged it, a number that was enough to begin to move the prey (Fig. 5a). The number of workers transporting the prey increased slowly up to 20 workers. The relationship between the number of workers on the prey and the distance covered to the nest fitted an exponential function (Fig. 5a; $y=1.3311e^{(0.2751x)}$, $R^2=0.776$, $p<0.001$, $n=15$). Cooperative prey transport was very efficient: the young cricket was transported to the 2-m nest in less than 30 min; if the cricket were situated at 0.5 m from the nest entry, it would be transported in less than 9 min. The number of cooperative workers carrying the prey was related to the prey size: more workers were recruited for heavier prey (up to 40) than for lighter prey (up to 20).

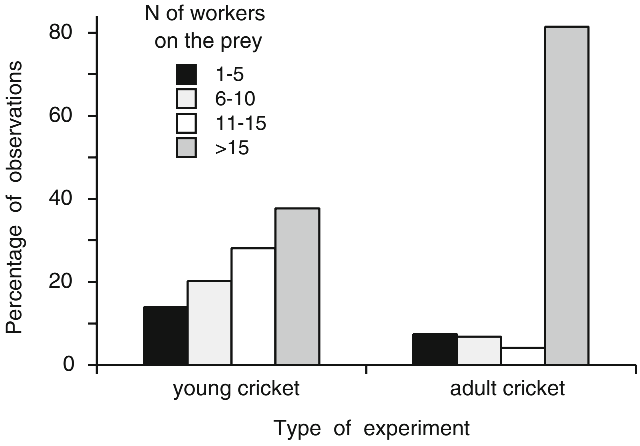

Fig. 4 Percentage of observations on cooperative prey transport with different number of workers on the prey when it was transported to the nest. Number of observations: young cricket, $n=114$; adult cricket, $n=189$

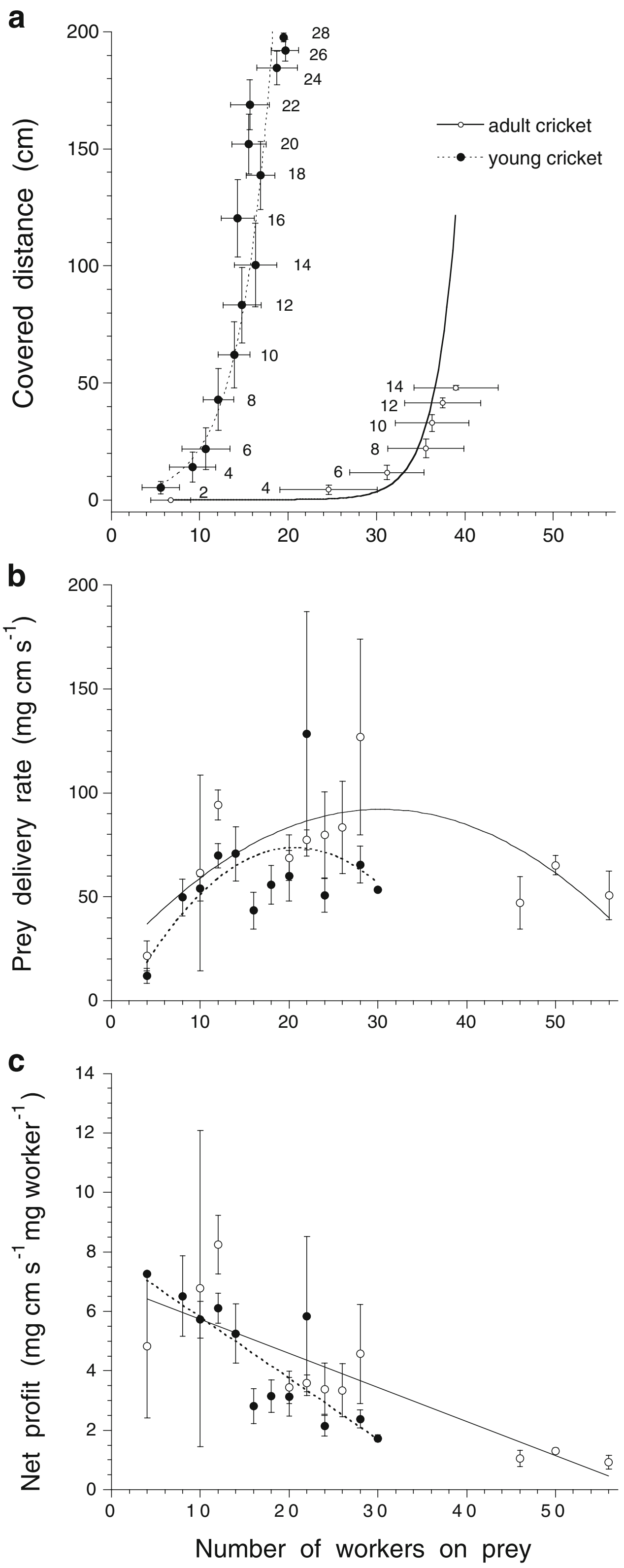

Fig. 5 Efficiency of cooperative transport of young and adult cricket ▶ corpses to the *A. senilis* nest. Young cricket 320-mg weight at 2 m from the nest (total time 30 min). Adult cricket 870-mg weight at 0.5 m from the nest (total time 15 min). Relationships between the number of workers transporting the prey and **a** the distance covered between prey and nest (cm; values of distance and workers are mean± SE measured each 2 min, time interval indicated beside *error bars*); **b** the prey delivery rate (measured in milligram centimeter per second, mean±SE); and **c** net profit (in milligram centimeter per second per milligram of worker, mean±SE)

When analyzing the effect of prey size on transport efficiency by offering one individually transportable sesame seed or cooperatively transportable different-sized crickets, both the PDR and the NP differed significantly, depending on prey item (Table 3). Although transport velocity decreased with increasing prey size, PDR values increased with the prey size; thus, a big adult cricket had a PDR higher than a sesame seed. Differences between sesame seed and both types of crickets were significant (*post hoc* pairwise comparison tests). The second measurement of transport efficiency, NP, was significantly different between the adult cricket and both the sesame seed and the young cricket (*post hoc* pairwise comparison tests). In contrast to PDR, the lowest NP value is that of the biggest, the adult cricket (Table 3).

To evaluate the number of workers that would be most efficient for transporting different-sized prey, the delivery rate (PDR) of each prey type was calculated for each category (see “Materials and methods”). Figure 5b shows the relation between the number of workers and the PDR. For the adult cricket, the observed data fitted well with a second-degree polynomial ($y=18.8+4.8289x-0.079475x^2$, $R^2=0.526$, $p=0.050$, $n=11$); maximum PDR was obtained when transported by 30 workers. For the young cricket, the maximum PDR was obtained when transported by 20 workers, but fit was not significant ($y=-11.123+8.18x-0.19734x^2$; $R^2=0.375$, $p=0.121$, $n=12$). According to PDR values, medium-sized groups of workers were always the most efficient in transporting prey to the nest and, for an equivalent number of workers, PDR is higher for a larger prey. The second measurement of transport efficiency, the NP, showed a quite different pattern (Fig. 5c). The benefit in prey biomass obtained by the colony per unit of forager biomass decreased when the number of foragers increased. The observed data fitted well with a linear regression (adult cricket: $y=6.8726-0.11463x$, $R^2=0.714$, $p=0.007$, $n=11$; young cricket: $y=7.8593-0.2052x$, $R^2=0.720$, $p=0.003$, $n=12$). Maximum NP values were those corresponding to a low or medium number of workers; for both the young and adult cricket, the maximum values corresponded to four to 14 workers carrying the prey. Nevertheless, as we have shown in the previous sections, most prey found in the field by *A. senilis* foragers were collected by teams of less than 15 workers (Figs. 1 and 4), with the exception of the adult cricket, which is in the range limit of cooperatively transportable prey (its weight was 821±285 mg, Cerdá et al. (1998b) considered the uppermost value of 1,000 mg).

Table 3 Effect of prey size on the transport efficiency by *A. senilis* workers

Variable	Sesame seed (*n*=11)	Young cricket (*n*=9)	Adult cricket (*n*=10)	GLM error distribution	*df*	χ2	*p*
PDR	4.0±1.3	60.3±29.3	74.7±26.7	Normal	2	56.83	**>0.0001**
NP	0.55±0.2	0.62±0.3	0.34±0.2	Normal	2	14.87	**0.0006**
Prey weight	3.45±0.6	321±52	870±285	–			

Sesame seeds were individually transportable and crickets were cooperatively transportable prey. Measures of efficiency are prey delivery rate (PDR, in milligram-of-prey centimeter per second) and net profit (NP, in milligram-of-prey centimeter per second per milligram of worker), see "Materials and methods" for calculation details. Values are mean±SD. GLM error distribution refers to the distribution of the dependent variable; *n* represents sample size (each colony was tested only once); χ^2, *df*, and *p* are the GLM statistics, in bold when significant. Prey weight (in milligram) is given only for information, mean weight of a worker is 7.25 mg

Recruitment to baits: daily competition within the community

During early morning and evening, while ground temperature was still cool, baits were mostly occupied by dominant ant species, either *T. nigerrimum* or *L. niger*. Further on, as temperature increased, dominant ants became less abundant on the baits while *A. senilis* started to occupy the baits upon 10:00 (Fig. 6). The daily foraging activity of this species was bimodal with two peaks around 12:00 and 16:00 separated by a period of lower activity. This activity pattern reflected the thermophily *A. senilis*, which occupied the largest number of baits when temperature attained 43°C and 48°C at 12:00 and 17:00, respectively. During the central hours of the day (13:00–15:00 h, when temperature reached 51°C), *A. senilis* disappeared from the baits and was partially replaced by the highly thermophilic ant *C. floricola* (Fig. 6).

Discussion

The ecological success of an ant species depends on its ability to adjust its foraging strategy to ever-changing environmental constraints, including resource characteristics and temperature (Mailleux et al. 2000). Within a colony, the allocation of foraging tasks operates without any central or hierarchical control, which does not imply the absence of social coordination (Gordon 1996, 2007). The aim of our study was to determine whether the process of group recruitment in *A. senilis* is modulated by individual flexibility according to food characteristics and to what extent this contributes to the foraging efficiency of this species.

First, our results indicate that workers respond to variations in food transportability by modulating the process of group recruitment. Hence, facing a large non-transportable food item (a shrimp), they tended to recruit a large number of nestmates, which resulted in the rapid domination of the food item. By contrast, when the food source was large but individually transportable (a pile of sesame seeds), the number of recruits per recruitment was lower.

Second, the fact that individual workers recruited less to 20- or 5-seed piles than to large piles demonstrates that they were able to estimate the size of a food source independently of its transportability. Recruiting nestmates to a poor food patch such as a 5-seed pile is not economic because it

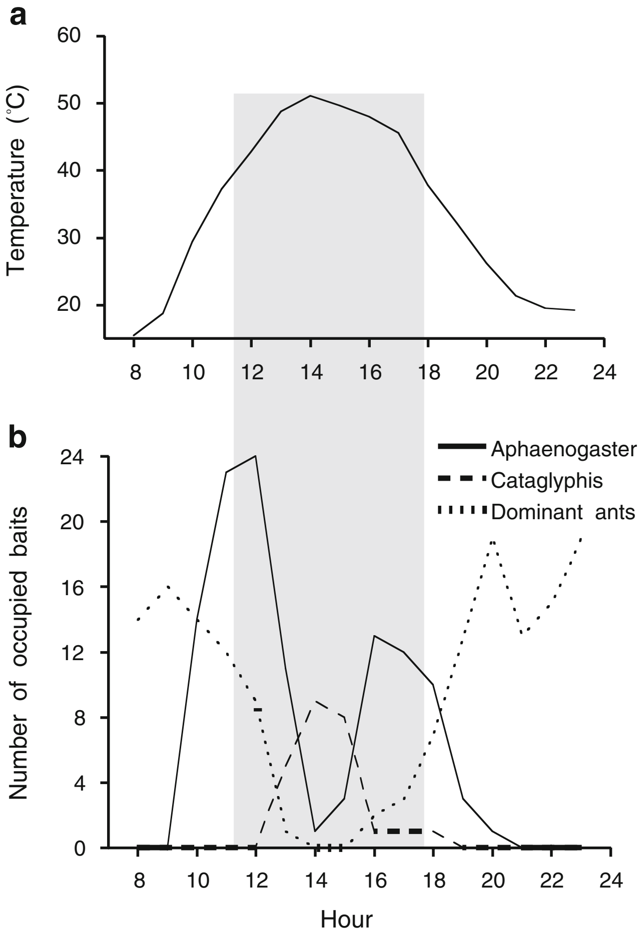

Fig. 6 Daily variation of soil surface temperature (**a**) and bait occupation (**b**) by *A. senilis*, the highly thermophilic *C. floricola*, and the dominant ant species (*T. nigerrimum* and *L. niger*) on May in Las Beles site (Doñana National Park). The area in *gray* represents the hottest period of the day, when temperature exceeds 40°C. Hour is the local standard time (solar time+2 h)

reduces the possibility of rapidly exploiting another richer patch. Interestingly, although some scouts occasionally recruited a few nestmates to 20- or 5-seed piles, these “mistakes” were apparently corrected at the colony level by an absence of feedback in the recruitment process. Such mistakes are rare events and the probability that a recruit repeat the same mistake made by the recruiter by recruiting herself to a poor patch becomes negligible. As Herbers and Choinière (1996) pointed out, ant colonies are characterized by redundancy of operations (Oster and Wilson 1978), which can allow an individual to make mistakes with relative inconsequence to the entire colony's operation (Herbers 1981).

The decision to recruit may respond to different thresholds at the individual and colony level. In *L. niger*, the key criterion that regulates mass-recruiting behavior is the ability of foragers to ingest their own desired volume of liquid food. This volume acts as a threshold from which workers returning from the source lay a trail that provokes recruitment (Mailleux et al. 2000). Similarly, in some harvester ants, the return of successful foragers is sufficient to adjust their foraging intensity to current food availability (Schafer et al. 2006; Gordon et al. 2008). In *P. pallidula*, ants shape their recruiting behavior simply according to the prey tractive resistance, i.e., the passive resistance of a prey to ant retrieval by pulling (Detrain and Deneubourg 1997). Some ant species are able to “measure” food size or patch richness and recruit accordingly: *Formica rufa* scouts that find baits with six fly larvae offered as food source recruit more workers and faster than to baits with only two fly larvae (Lenoir 2002). Other ant species do not initiate recruitment when prey items are small and individually transportable (Cogni and Oliveira 2004; Detrain and Deneubourg 1997). *Aphaenogaster cockerelli* does not recruit to clumps of seeds (Sanders and Gordon 2002), but *A. senilis* recruits when clumps are sufficiently rich (this study, *ad libitum* seeds). We have seen here that a single *A. senilis* worker was able to provoke a group-recruitment event, but to continue increasing the worker force on the food source a social decision is necessary.

The third result of our study concerns the adjustment of the number of workers to transport a large prey to the nest. If we consider the relative number of workers collecting a prey (Fig. 2), *A. senilis* colonies adjusted their foraging effort according to the type of prey: the fastest response was to transport cooperatively young crickets and the slowest to transport individually sesame seeds. Cooperative transport (to young crickets) was faster than recruitment to bigger prey (e.g., shrimp) but only in relative values (standardizing the values by considering the maximum number of workers implied in each behavior) because the absolute values were similar (18 vs. 20 workers) while the dynamics of transport was different. Therefore, colonies tended to adjust the timing of recruitment according to the differential characteristics of the food source. This is in contrast to mass recruitment in which many foragers remain in the nest to be recruited once a new food source is discovered (Roulston and Silverman 2002). As mass recruitment reduces the number of workers that initially search for food, it may reduce food detection rate, but it may increase the post-discovery food retrieval rate. On the contrary, group recruitment requires a lower proportion of workers remaining within the nest, which allowed *A. senilis* colonies to have more scouts to patrol (necessary to search for unpredictable and scattered resources) and fewer inactive individuals in the nest; this system seems adequate to *A. senilis* due to the small size of its colonies. Feener (2000) considers that ant colonies face a tradeoff in the allocation of scouts that search for food versus recruits that remain in the nest awaiting notification of the food discovery. This tradeoff may determine the kind of food that is most profitable for a colony to collect. Mass-recruitment species invest heavily in recruits and exploit large food patches, whereas group-recruitment species such as *A. senilis* preferentially invest in scouts and efficiently exploit smaller resource patches.

Ant colonies are neither alone nor isolated. In Mediterranean open habitats, where no top-dominant ant species (“extirpators” in the sense of Wilson (1971)) are found, most species forage on common areas with other species belonging to the same community (Cerdá et al. 1997). In this community framework, each species develops different foraging strategies aimed at increasing its foraging efficiency. An important question is how group recruitment contributes to the foraging efficiency of *A. senilis*. In a study on prey robbing between ant species in a Mediterranean community, Cerdá et al. (1998b) showed that large prey, such as arthropod corpses whose removal requires the cooperation of several individuals, can represent up to 71.5% of the total biomass collected by *A. senilis* nests. Group-recruitment system allowed *A. senilis* to exploit a much wider range of food items and to retain most large prey during the morning period, when mass-recruiting species were not active (Cerdá et al. 1998b). This is in agreement with the results of our experiments: *A. senilis* could not transport and dissected the large prey (i.e., shrimp) inefficiently, but they rapidly transported medium-sized preys (i.e., cricket) to their nest in a highly cooperative action of several workers (Figs. 4 and 5a). We showed that the speed of cooperative transport of an adult cricket (~870 mg) was 2 m/h; since the home range of the species was ~4 m, any prey of this size would be transported to the nest in less than 2 h, which might be enough to prevent encounters with dominant species. Better performances were obtained with smaller prey such as the young cricket (~320 mg): any prey of this size would be transported to the nest in less than 1 h. For both adult and young cricket transport, PDR and NP values were not excessively high when compared to other subordinate species such as *Cataglyphis velox* as, in the latter species, workers may be very large and run very fast, attaining PDR values up to 450 and NP values up to 30 (Cerdá and Retana 1997). Nevertheless, dominant ant species in Mediterranean open communities are smaller and slower than *A. senilis* (Cerdá et al. 1997). In these habitats, as most arthropod corpses disappear in less than 5 min due to ant collection (Retana et al. 1991), collecting food items as quickly as possible provides an advantage. *A. senilis* workers are not able to defend food resources for a long time but group recruitment allowed them to retrieve medium prey to the nest, before dominants that are often also mass recruiters find them (Cerdá et al. 1998b).

How does the combination of temperature resistance and group recruitment provide an ecological advantage? Temperature may be an important constraint to ectothermic organisms like ants, but *A. senilis* is a relatively thermophilic species that uses group recruitment up to 45°C to exploit a valuable food resource (Fig. 3a), a temperature very close to its critical thermal maximum of 46°C (Cerdá et al. 1998a). It continues foraging even at extreme temperatures (up to 52°C), mainly as a solitary forager and for short durations (less than 10 min), principally to exploit small individually transportable food items like seeds (Fig. 3b). It is a risk-prone species that frequently forages at thermal stress risk conditions: its foraging efficiency increases with ground temperature (see Fig. 5a in Cerdá et al. 1998a) and on some days maximum values of risk activity (foraging performed at temperatures higher than CTM 2°C) accounted for up to 70% of the total daily activity (Cerdá et al. 1998a). In the Doñana ant community, thermophily allows *A. senilis* to occupy numerous food resources (baits) at temperatures exceeding 40°C that other small dominant mass-recruiting species cannot tolerate (Fig. 6). In addition to thermophily, the capacity to recruit nestmate even at high temperature procures *A. senilis* with an ecological advantage over strictly solitary foraging species like *C. floricola* (personal observations). These two advantages (group recruitment and temperature resistance) are important when *A. senilis* competes within the group of subordinate species of Mediterranean communities. High temperatures limit ant foraging activity in open Mediterranean habitats (Cerdá et al. 1997, 1998a). On the one hand, at high ground temperature, chemical signals may disappear quickly, disabling the recruitment process (Ruano et al. 2000). For example, trail pheromones in mass-recruiting species are organic compounds that may evaporate or degrade at high temperatures (Morgan 1984; Ruano et al. 2000). Group recruitment may continue in these harsh conditions because the orientation is not exclusively linked to the pheromone signal and because the mark laid by the leader only needs to remain for a very short time to guide the recruits (contrary to mass recruitment in which there is no leader and chemical mark needs to remain longer). On the other hand, stable pheromone trails can be established only if there is a sufficient number of foragers (trail-laying workers) to maintain them (Bonabeau et al. 1998); but workers of mass-recruiting species are risk averse (Cerdá et al. 1998a) and do not forage at hot temperatures as shown by the low bait occupation values when temperature exceeds 40°C (Fig. 6).

Within a colony framework, we have seen that the behavioral flexibility of individual *A. senilis* foragers optimizes prey retrieving, the individual decisions on whether or not to recruit depending both on the size and quantity of food. Group recruitment may be socially modulated by increasing the number of recruitments to food source or by increasing the number of recruits per recruitment. Workers recruit mainly when the amount of food is large, but individual mistakes (i.e., workers recruiting to small or poor food sources) are socially regulated and prevent the exploitation of poor patches. Within a community framework, group recruitment can be carried out at a wide thermal range (until high temperatures) giving an ecological advantage over dominant, risk-averse, and heat-intolerant ant species. Group recruitment increases the species' foraging efficiency by expanding the range of transportable prey size, allowing a fast colony response to transport large food items and preventing food robbing by other competitors (Cerdá et al. 1998b).

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