

Cooperative prey-retrieving in the ant *Cataglyphis floricola*: an unusual short-distance recruitment

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Abstract *Cataglyphis* ants are mostly scavengers adapted to forage individually in arid environments. Although they are widely thought to have lost the capacity of recruitment, we provide evidence that *C. floricola* foragers that find a large prey near their nest are able to solicit the help of nestmates to carry it cooperatively. After discovering a non-transportable prey, these ants readily return to their nest and stimulate the exit of several recruits. This rudimentary form of recruitment, which is absent in the sympatric species *C. rosenhaueri*, is only employed when the prey is sufficiently close to the nest entrance (<1 m) and does not allow the food location to be communicated. Instead, *C. floricola* recruits search for the prey in all directions until they discover it and transport it cooperatively to their nest.

Keywords *Cataglyphis floricola* · Foraging strategy · Recruitment · Cooperation

In social insects, recruitment is defined as communication that brings nestmates to some point in space where work is required (Wilson, 1971). It allows workers to exchange information about the presence, quality and/or quantity of a food source that is difficult to exploit by a single individual. In ants, it generally consists of a two-step phenomenon

during which a recruiter first uses pheromones and/or vibrations to solicit her nestmates inside the nest. In a second step, the recruits follow chemical marks laid by the recruiter up to the food source (Passera and Aron, 2005). Recruitment is considered an evolved behavioural trait often absent in “primitive” subfamilies of solitary hunters (Hölldobler and Wilson, 1990). By contrast, it is the norm in “evolved” Myrmicinae, Dolichoderinae, and Formicinae, although with some notable exceptions such as the genera *Gigantiops* (Beugnon et al., 2001) and *Cataglyphis* (Wehner et al., 1983; Lenoir et al., 1990; Baroni Urbani, 1993). In the latter, the loss of recruitment is considered a secondary adaptation driven by the cost of using relatively volatile pheromones in very hot environments to communicate the presence of food (Ruano et al., 2000). Nevertheless, during a field study on the ecology of *C. floricola*, we noticed that the return of a forager to the nest was sometimes immediately followed by the sudden exit of several workers. This observation encouraged us to experimentally test the hypothesis that this species had retained some recruitment capacity.

C. floricola is endemic in the Doñana area (southwestern Spain) and its surroundings. It forms small colonies (176 ± 12 workers, mean \pm SE, $n = 99$ nests, Fernando Amor, unpubl. data) that nest in sandy areas and feed on shrub petals and arthropod corpses (Cerdá et al., 1996). At our study site, near Villamanrique de la Condesa (Seville province, Spain), nest density is relatively high (ca. 0.6 nests m^{-2}) and neighbouring nests are separated by about 1 m (F.A., unpublished data). However, foraging areas widely overlap as these ants often forage 8–10 m away from their nest. Recently, killed *Oedipoda* grasshoppers that were too heavy (weight: 0.2 ± 0.02 g, mean \pm SE) to be individually transported by a single worker were offered to 42 colonies. They were placed at

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20, 40 or more than 100 cm from the nest entrance during the main period of foraging activity (June, from 9:00 to 15:00 solar time). Colony activity (i.e. the number of workers exiting their nest) was recorded for 1 min after the forager that first found the grasshopper returned to the nest. As a control, the same nest's activity was measured during 1 min after the return of an ant that had not discovered a prey at the same distance. At least 30 min separated control and experimental tests.

Foragers that found the non-transportable prey tried to drag them and, after a few unsuccessful attempts, returned rapidly to their nest. Their entrance provoked the immediate exit of up to 16 workers in the following minute (Fig. 1a). By contrast, no more than three workers came out of the nest after the return of a nestmate who had not discovered a prey (two-way ANOVA, Prey effect: $F_{1,39} = 55.4$, $P < 0.0001$). Interestingly, nestmate solicitation largely depended on the distance between the prey and the nest (Fig. 1a; Distance effect: $F_{2,39} = 22.7$, $P < 0.0001$; Distance \times Prey interaction: $F_{2,39} = 15.1$, $P < 0.0001$). Hence, ants that discovered prey at more than 1 m from their nests did not recruit nestmates. The recruits that looked very nervous and agitated leaved the nest in all directions without any information on the direction to the

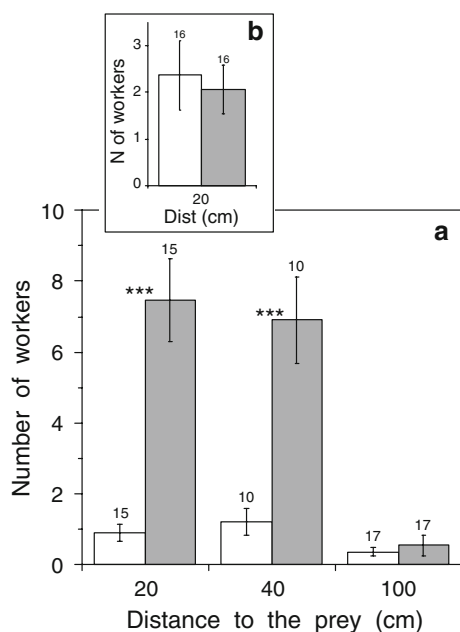


Fig. 1 Mean number of workers coming out of the nest during 1 min after the arrival of a forager that either found a large prey (grey bars) or not (white bars, control). **a** *C. floricola*: prey was placed at 20, 40 and more than 100 cm from the nest. **b** *C. rosenhaueri*: prey was placed at 20 cm. Error bars SE. Values on the top of error bars indicate sample size. Stars denote significant differences between control and experimental groups for each distance separately, *** $P < 0.001$

food. They searched randomly around the nest entrance and eventually discovered the prey.

In order to test the specificity of this result, we placed similar prey at 20 cm from the nest entrance of *C. rosenhaueri*, a species that frequently lives in sympatry with *C. floricola*. Both species are thermophilic scavengers that forage alone at the central daylight time up to 10–11 m from their nest entrance (F.A., unpubl. data; Cerdá and Retana, 2000). Workers of *C. rosenhaueri* are approximately the same size as *C. floricola* and were similarly unable to move the prey. However, instead of alerting nestmates, the foragers that first discovered the prey tried to dismember them. Their return to the nest was followed by the exit of 2.1 ± 0.9 workers which did not differ significantly from control assays in which the return of a forager that had not discovered a prey was followed by the exit of 2.4 ± 0.7 ants (Fig. 1b; Student's t test, $t = 0.26$, $P = 0.8$, $n = 16$ nests).

In a second experiment using *C. floricola*, dead prey was pinned to the ground at 20 cm from 11 nests. The dynamics of ant accumulation on the prey was then monitored every minute from the time it was discovered by an ant until 10 min after this ant had returned to the nest. Discovery was rather variable, ranging from 0.15 to 6.12 min (mean discovery time \pm SE: 4.3 ± 1.0 min, $n = 11$). Before the first ant that discovered the prey returned to the nest (Fig. 2; time < 0), the number of ants on the prey increased very slowly (slope of ant accumulation on the prey: 0.079 ant min^{-1}). However, the number of ants on

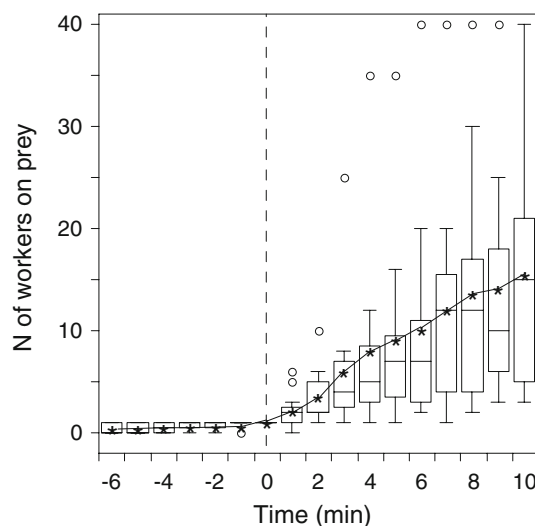


Fig. 2 Number of *C. floricola* workers on a prey fixed on the ground at 20 cm from the nest entry. Time 0 is the moment at which a forager that had discovered the prey first returned to her nest. Each box encloses upper and lower quartiles (50% of the data) with the median displayed as a line and the mean as an asterisk. Open circles are outliers

the prey increased much faster after the first one returned to the nest (slope: $1.473 \text{ ant min}^{-1}$).

Our results clearly demonstrate that *C. floricola* use a rudimentary form of recruitment by which they alert their nestmates to the presence of a heavy prey near the nest. This represents an important difference with other species of the same genus that completely lack the capacity of recruitment, including *C. bicolor* (Wehner et al., 1983), *C. cursor* (Lenoir et al., 1990) and *C. rosenhaueri* (this study). Ants can greatly expand the range of prey sizes they collect by recruiting nestmates (Traniello, 1987, 1989; Cerdá et al., 1998, 2009). Nonetheless, foraging on small, unpredictable prey and the cost of producing high-temperature proof pheromones may have selected for the loss of chemical marking in most species of the genus *Cataglyphis*. Recruitment in *C. floricola* does not seem to contain information about food location, and solicitation of nestmates probably relies exclusively on a “motor display” as, e.g., in *Camponotus socius* (Hölldobler, 1971) and *Rossomyrmex minuchiae* (Ruano and Tinaut, 1999). It also recalls the “social facilitation” described in some Ponerines in which solitary hunters stimulate other workers to leave the nest to help retrieve large prey (Traniello, 1982; Lachaud, 1985; Schatz et al., 1997; Cogni and Oliveira, 2004). In the case of *C. floricola*, solicitation of nestmates may be advantageous for prey located near the nest, so the likelihood of recruits discovering them, even without explicit information on their location, is sufficiently high. However, given the high nest density, mobilizing workers to retrieve a prey located at a greater distance (>100 cm) without being able to indicate its position are probably useless. By the time recruits reached the prey’s location, it would have been robbed by neighbours. From a mechanistic point of view, this result also demonstrates that the recruiter uses her knowledge of the distance from the prey to the nest in order to decide whether to recruit or not, either by means of visual or chemical landmarks or by estimating the distance upon return to the nest (Müller and Wehner, 1988; Collett et al., 1999; Wehner, 2003; Wohlgenuth et al., 2001; Wenseleers et al., 2002; Steck et al., 2009).

A tentative hypothesis for the difference of behaviour between *C. floricola* and *C. rosenhaueri* is that the former belongs to a relatively primitive group among the *Cataglyphis* with some ancestral characteristics (Tinaut, 1993). This hypothesis is supported by phylogenetic evidences that suggest a very old separation between *C. floricola* and other species of the same genus (including *C. rosenhaueri* and *C. bicolor*) in which recruitment is completely absent (Hasegawa et al., 2002). However, more data on a larger set of species and accounting for phylogenetic relationships among species are necessary to determine the evolution of recruitment capacities in *Cataglyphis*.

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