

Links between worker polymorphism and thermal biology in a thermophilic ant species

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The role of the broadly polymorphic worker caste of the thermophilic ant *Cataglyphis velox* is discussed. Two different hypotheses have been tested: 1) worker polymorphism allows colonies to collect different-sized prey more quickly and with greater energetic efficiency; 2) it implies greater variability of responses to temperature, which increases the overall period of external activity, and enhances colony success. The relationship between worker polymorphism and size matching was not confirmed by the data: large *C. velox* workers retrieved neither proportionately nor absolutely heavier loads than did small foragers, they did not collect greater amounts of prey or with greater efficiency than smaller foragers, and they were only more effective than smaller ones in a reduced percentage of their foraging trips. On the other hand, thermal tolerance of *C. velox* workers was size-related: large workers withstood temperatures 6 to 8°C higher than smaller ones. This led to a diurnal rhythm in which the mean size of workers foraging outside the nest at different times of the day increased with temperature. Small workers foraged preferentially when temperatures were lower, while large workers preferentially foraged at high temperatures. At the colony level, this resulted in a longer daily activity period, and an increased benefit in prey collection for *C. velox* colonies. From this point of view, large *C. velox* workers represent a specialized group which preferentially forages at temperatures that smaller workers cannot tolerate.

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Division of labour among workers is widely assumed to be important in the ecological success of ants and other social insects (Oster and Wilson 1978, Wilson 1985, Hölldobler and Wilson 1990). In ants, polymorphism has been found to be closely linked to division of labour: the variation in worker size benefits colony fitness by allowing the colony to perform certain tasks more efficiently than it could if only one size of workers were present (Calabi and Porter 1989, and references therein). Economic benefits of division of labour are more evident in species that possess highly polymorphic workers and show extensive division of labour among different worker castes (Wilson 1980a, b, Franks 1985,

1986, Roces and Hölldobler 1994, Wetterer 1994). A generalization applied to ants is that physical polymorphism has usually been created by the addition of a major caste (Oster and Wilson 1978). The addition of ever more physical castes may be limited by both ergonomic and ecological factors. An ergonomic constraint to polymorphic species is imposed by the energetic cost of producing physically large castes: majors are energetically expensive to manufacture and maintain. Moreover, the advantage of increased efficiency contributed by additional physical specialization may not offset the disadvantage of decreased flexibility in response to environmental variability (Wheeler 1991).

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For these reasons, major workers of various ant species appear to arise only as specialists for very few primary tasks: foraging, defence, food storage, and the milling (chewing) of seeds (reviewed in Hölldobler and Wilson 1990).

Since prey items in the field usually vary substantially in size, Oster and Wilson (1978) suggest that polymorphic ant species may have evolved their size-frequency distributions to approximate the size-frequency distributions of their prey. Foragers of polymorphic ants frequently harvest prey that correspond in mass to ant size (Wilson 1978, Rissing and Pollock 1984, Retana and Cerdá 1994, Wetterer 1994), what is called size matching, or the pairing of forager size and food item size. From this relationship, it is expected that, if the range of worker sizes increases substantially, there will be a corresponding increase in the range of prey masses that can be exploited (Reyes 1987). Size matching is the criterion to be expected if the foragers are acting as a relatively untroubled economic system, attempting to maximize their net energetic yield in optimal environmental conditions and with relatively plentiful food resources (Wilson 1980b). Nevertheless, these conditions do not always hold, and polymorphism could be related to the performance of tasks other than food collection. In fact, differences in longevity (Calabi and Porter 1989), respiratory rates (Lighton et al. 1987, Bartholomew et al. 1988, Nielsen and Baroni-Urbani 1990), running speed (Bartholomew et al. 1988, Heinrich 1993), duration of foraging trips (Lighton and Feener 1989), or diel patterns of activity (Wetterer 1990) of different-sized workers have been well documented. Thus, worker polymorphism could be a way of achieving better exploitation of external environmental conditions. This could be especially important for climate specialists living in extreme thermal environments, such as species of *Melophorus* (Christian and Morton 1992), *Ocymyrmex* (Marsh 1985a, b), or *Cataglyphis* (Harkness and Wehner 1977, Wehner et al. 1983, 1992).

The ant genus *Cataglyphis* is a fairly homogeneous genus which is widespread over the arid regions of the Old World, with a strictly diurnal activity and high thermophily (Wehner et al. 1983, Cerdá et al. 1989, Lenoir et al. 1990). Although many species of the genus have a monophasic worker polymorphism with limited size variation, in accordance with expectations concerning individually foraging ants (Oster and Wilson 1978), certain *Cataglyphis* species, such as the recently re-described *C. velox* (Tinaut 1990a), show a broad worker polymorphism. In the present study, we try to determine the advantages of this broad polymorphism for a species specialized in living in such extreme thermal environments. We shall analyse two different hypotheses:

1. The first hypothesis is based on the size variability of *C. velox* workers being considered as an adaptive polymorphism in which small workers tend to collect

small prey and large workers favour large prey. If true, this property of the worker caste would allow colonies to collect different-sized prey more quickly and with greater energetic efficiency. Larger workers may be better foragers because a) they enlarge the range of prey collected by carrying large prey that cannot be retrieved by small foragers, b) they carry to the nest some sizes of prey with greater net benefit for the colony, or c) they collect greater amounts of prey and/or with greater efficiency (greater proportion of loaded workers).

2. The second hypothesis considers that a greater range of worker sizes implies greater variability of responses to temperature, since large workers have greater thermal tolerance than small workers. If true, this property would increase the range of hours in which colonies engage in outside activity, since large foragers can enlarge the overall activity period of the species to times of the day at which temperatures are too high for small workers. Colonies can thus increment prey collection by having greater periods of activity, and colony success is enhanced.

Methods

This study was conducted in Roblehondo, Sierra de Cazorla (Jaén province, southeastern Spain) in the summer of 1995. The climate of the region is Mediterranean, characterized by cold rainy winters and hot dry summers. At this site, *C. velox* nests were quite abundant. *C. velox* is considered an endemic species of the Iberian Peninsula, limited to La Mancha and the Guadalquivir depression, in an elevation range between 0 and 2400 m (Tinaut 1990a). Like other species of the genus, *C. velox* displays a thermophilic diurnal activity, a diet consisting mainly of arthropod corpses (21% ants, 18% heteropterans, 10% homopterans, and lower percentage of other insect groups, but only 6.6% of plant remains), and an individual foraging strategy. Although the polymorphism of the species appears to be continuous (Fig. 1), for the sake of convenience in this study, in most analyses workers were categorized as either very small, small, medium or large (Table 1).

To assess size-matching relationships, samples of 50 loaded workers from five colonies were collected with their respective loads. In the laboratory, mass and length of each worker and its load were measured to the nearest 0.01 mg and 0.01 mm, respectively. Since differences in regression coefficients among nests were not significant (test of equality of slopes, $p > 0.1$), both foragers and loads from all nests were considered together.

The efficiency of prey transport by each worker size class was estimated using measurements of prey mass and prey transport velocity. Prey were chosen in a wide range of weights, from 3 to 700 mg. For each selected

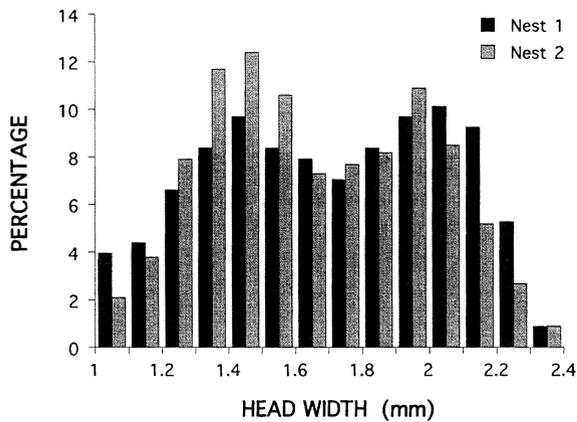


Fig. 1. Head width (mm) distributions of workers in two *Cataglyphis velox* nests.

prey weight, tests were carried out with five workers of each size class. In each test, a prey was directly given to a forager. The time elapsed and the distance covered until it reached the nest were noted. The forager and the prey were collected for later measurement at the laboratory. Two measures of transport efficiency of insect prey were used: prey delivery rate (Orians and Pearson 1979, Traniello and Beshers 1991), and net profit. Prey delivery rate (PDR) was calculated as: $PDR = \text{prey weight} \times \text{transport velocity}$. Net profit (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: $NP = PDR / \text{forager mass}$. This measure counter-balances PDR values of the four categories of workers. It is, to our knowledge, a better index than PDR to evaluate the real benefits obtained by the colony when different-sized workers transport prey to the nest.

Diel patterns of forager size were determined on mid-summer sampling days, when temperatures were hottest. Since soil temperature differences between bare and covered ground areas could be more than 5°C, we evaluated the effect of the herbaceous cover in the activity pattern of different-sized workers. The observations were carried out in four *C. velox* nests: two nests were located in open areas, surrounded by bare soil, while the other two were surrounded by 1–2-cm-high herbaceous cover. The number of workers of each size category leaving or entering each nest was sampled

during twenty minutes per hour throughout the whole daily activity period (from 08.00 to 20.00). Loaded and unloaded workers arriving at the nest were counted separately in order to calculate the efficiency of prey collection. Different temperatures were also measured at each hourly sampling with glass-headed thermocouples connected to a Univolt DT-830 digital multimeter: temperature at the nest entrance of each nest, temperature in the shade, and sun temperatures on bare soil, on soil covered by 1–2-cm-high grasses and at 2–3 cm height.

Live workers were not measured directly in the field. Instead, they were placed in one of the four previously described size categories by reference to a standard array of preserved specimens whose head widths and total body lengths had previously been measured to the nearest 0.01 mm. Periodic checking showed that most ants were placed in the correct size class and that the remainder were misplaced by only one size class. This technique has proved reliable in recording similar size-frequency data (Wilson 1980a, b, 1983). One-, two-, and three-way ANOVAs were used to investigate differences between the worker sizes, degrees of soil cover and sampling days, for the different parameters examined. Values were square root transformed. A Fisher's protected least significant difference was used to separate means in one-way ANOVAs. In order to evaluate whether or not larger workers performed longer foraging trips, fifteen foragers of each size category of three *C. velox* nests were followed when leaving their nest. The maximum distance from the nest that they reached was considered as a measurement of trip length.

Thermal resistance of workers of each size category was measured at the laboratory by means of an electric Plactronic Selecta hot plate of 5–200°C temperature range and 1°C accuracy. Ants were exposed to temperatures from 48°C to 62°C, at intervals of 2°C. At each temperature, ten individuals of each size were placed on the surface of the hot plate in open containers with Fluon-painted inner walls which prevented ants escaping. The time each ant took to exhibit signs of muscle spasms and to die was noted. The critical thermal maximum (CTM) of each size class was defined as the temperature at which at least 50% of workers died or lost muscular coordination after 10 min of exposure. The lethal temperature (LT) of each size class was defined as the temperature at which workers took, on average, less than one minute to die.

Table 1. Categories of *Cataglyphis velox* workers distinguished according to their size.

Worker size	Percentage of nest population	Head width (mm)		Body length (mm)		Body mass (mg)	
		Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
Very small	16.7–21.8	1.16 ± 0.03	1.00–1.35	5.53 ± 0.15	4.5–6	2.56 ± 0.22	1.3–4.0
Small	23.8–34.0	1.51 ± 0.02	1.36–1.70	7.53 ± 0.09	6.1–8	5.84 ± 0.21	4.1–7.0
Medium	32.2–41.0	1.88 ± 0.02	1.71–2.05	9.16 ± 0.06	8.1–10	10.70 ± 0.21	7.1–13.5
Large	12.0–18.5	2.20 ± 0.01	2.06–2.55	10.66 ± 0.05	10–12	16.07 ± 0.22	13.6–27.4

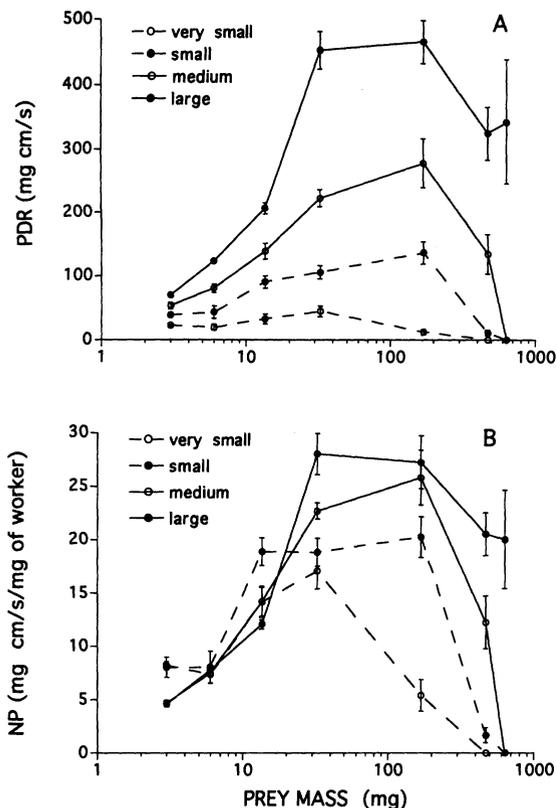


Fig. 2. Prey delivery rate (PDR, measured in $\text{mg cm}^{-1} \text{s}^{-1}$) and net profit (NP, in $\text{mg cm}^{-1} \text{s}^{-1} (\text{mg of worker})^{-1}$) as a function of prey mass (in mg) for workers of the four size classes. Each dot represents the mean value (\pm SE) of five workers.

Results

Size matching and prey collection efficiency of different-sized workers

C. velox foragers weighed between 1.27 and 27.29 mg, a 21.5-fold range, while loads ranged from 0.12 to 112.0 mg, a 933-fold range. More than 80% of foragers analysed carried prey lighter than their own mass. The remainder carried loads up to five times their own mass, and only one forager was found to be carrying a load nine times its own mass. The degree of size matching of forager to load carried was quite small: ant mass (x) and prey mass (y) showed a very low positive relationship ($r^2 = 0.09$, $p = 0.001$, $n = 250$), while the relationship between ant length (x) and prey length (y) was even worse ($r^2 = 0.07$, $p = 0.001$, $n = 250$).

There was a great difference between the weight range of prey loads found in the natural habitat (0.1–112 mg) and the range that could be potentially carried by foragers (large workers were able to transport prey weighing 500–700 mg, Fig. 2). To evaluate which workers would be most likely to transport different-sized prey, the delivery rate (PDR) of each prey type was calculated for each forager class. Although transport

velocity decreased with increasing prey size for all forager classes, the maximum PDR was obtained at prey sizes ranging from 30 to 200 mg (Fig. 2A). According to PDR values, large workers were always the most efficient foragers in transporting prey to the nest, especially for prey over 200 mg. The second measurement of transport efficiency, the net profit (NP), showed a quite different pattern (Fig. 2B). The benefit in prey biomass obtained by the colony per unit of forager biomass was only greater for medium and large carriers when prey mass was above 30 mg. Nevertheless, most prey collected in the field by *C. velox* foragers (80%, $n = 250$) weighed less than 10 mg, and less than 5% were greater than 30 mg. This means that large workers were more efficient than smaller ones in a very small proportion of their foraging trips.

Both the percentage of foragers outside the nest and the percentage of prey collected were significantly different according to worker size (Table 2), but not according to soil cover or sampling day. Nevertheless, there was not an increasing or decreasing trend according to ant size: the most abundant trend classes outside the nest were small and medium foragers, which collected percentages of prey proportional to their abundance. Differences between size distributions of foragers outside the nest and workers of the whole nest were significant ($\chi^2 = 196.1$, $p < 0.0001$), because there were more very small workers and fewer large workers in the whole nest populations (Table 1). Foraging efficiency (measured as the percentage of loaded workers) also varied with worker size: less than 6% of very small workers reached the nest carrying prey, while large workers showed the greatest percentage of loading (not significantly different from values of small and medium workers, Table 2).

Thermal resistance and diel patterns of forager size

Thermal resistance decreased when temperature increased in the four worker size classes (Fig. 3), larger workers showing greater survival time at all temperatures tested (Fisher LSD F -test, $p < 0.05$). The critical thermal maximum (CTM) was also different in each size class: 50, 52, 54 and 56°C for very small, small, medium and large workers, respectively. Lethal temperature (LT) was 4°C higher than CTM for very small and small workers, and this difference increased to 6°C for medium and large workers. Associated with this different temperature tolerance, significant differences (ANOVA, $p < 0.01$) were found in the maximum distance reached from the nest by different-sized workers: large workers performed longer trips (mean \pm SE: 12.41 ± 1.29 m, $n = 15$) than medium, small and very small workers (7.47 ± 0.89 m, 6.25 ± 1.05 m and 4.37 ± 0.65 m, respectively).

Table 2. Analysis of variance of worker size, soil cover and sampling day on percentage of foragers outside the nest, percentage of prey collected and foraging efficiency (number of loaded foragers/total number of foragers). ***, $p < 0.001$; ns, not significant. Mean (\pm SD) values of the four forager sizes are indicated. The values that are significantly different, based on Fisher LSD F -test (at the $p = 0.05$), are indicated by different letters.

Source	% Foragers			% Prey collected			Foraging efficiency		
	df	F	p	df	F	p	df	F	p
Size (A)	3	134.45	***	3	91.19	***	3	61.09	***
Soil cover (B)	1	0.01	ns	1	0.02	ns	1	4.22	ns
A \times B	3	0.96	ns	3	1.22	ns	3	1.98	ns
Day (C)	2	0.10	ns	2	0.01	ns	2	0.06	ns
A \times C	6	0.34	ns	6	0.10	ns	6	0.17	ns
B \times C	2	0.08	ns	2	0.09	ns	2	0.35	ns
A \times B \times C	6	0.54	ns	6	0.14	ns	6	0.31	ns
Error	24			24			24		

Mean \pm SD for each worker size	% Foragers	% Prey collected	Foraging efficiency
Very Small	10.4 \pm 3.2 ^d	7.0 \pm 5.5 ^c	5.8 \pm 4.8 ^b
Small	29.1 \pm 6.8 ^b	29.3 \pm 7.3 ^b	9.6 \pm 2.0 ^a
Medium	36.5 \pm 6.5 ^a	35.8 \pm 5.5 ^a	9.4 \pm 2.4 ^a
Large	24.0 \pm 6.0 ^c	27.9 \pm 7.9 ^b	12.0 \pm 5.4 ^a

Diel changes in forager weight followed quite well daily temperature rhythms (Fig. 4A): maximum values were found at midday, when large foragers were the most abundant size class outside the nest. A significant linear relationship between temperature (x) and mean forager weight (y) was found (Fig. 4B; $y = 0.14x + 2.94$, $r^2 = 0.94$, $p = 0.001$). This activity at high temperatures was associated with an enhanced foraging success: total hourly amount of prey collected significantly increased with soil temperature ($y = 0.33x - 7.46$, $r^2 = 0.22$, $p = 0.0001$).

Discussion

Large castes are energetically expensive to manufacture and maintain, because construction and maintenance

costs are reasonably assumed to be a more or less linear function of the dry weight of the adult (Oster and Wilson 1978, Wilson 1980b). This would imply that one large worker should provide services equivalent to several small workers to justify the colony's energy investment, or to perform some special service of exceptional importance to make their creation profitable to the colony. Most studies about these topics have been carried out with leaf-cutting ants, which represent one of the best examples of polymorphic ant species (workers within a single colony may range 250-fold in mass, Wetterer 1990). In these ants, size-related foraging and division of labour among foragers have been widely reported (Wilson 1980a, b, Waller 1989, Wetterer 1990, 1994, Roces and Nuñez 1993), which has led to the generalization that ant polymorphism seems to be a coarse adaptation to increase diet breadth and the efficiency of food retrieval (Traniello and Beshers 1991). Nevertheless, the hypothesis of the close relationship between size matching and polymorphism does not always hold (Rissing and Pollock 1984, Rissing 1987, Christian and Morton 1992). This is the case of the species of the present study, *C. velox*, which is one of the most polymorphic *Cataglyphis* species in the Iberian Peninsula (Tinaut 1990a, b), with a continuous 22-fold range in body mass. The degree of size matching of forager to load carried in *C. velox* was smaller than that found for other species of ants (Traniello 1989, Retana and Cerdá 1994, Wetterer 1994), i.e. large *C. velox* workers did not retrieve either proportionately or absolutely heavier loads than did small foragers. Kaspari (1996) suggests that the relationship between prey size and worker size may be weak when prey are scarce, but stronger when prey are abundant. In this study, prey were abundant (samples were collected in early sum-

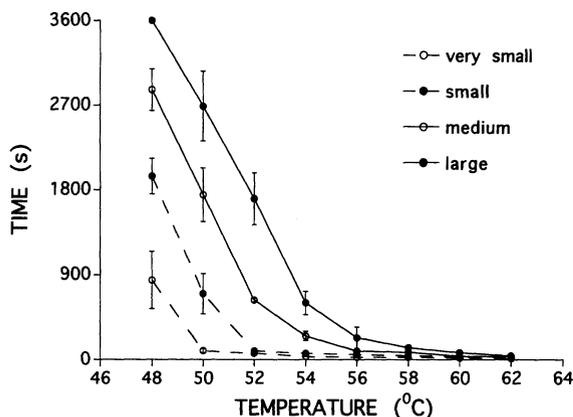


Fig. 3. Mean survival time (\pm SE) of *Cataglyphis velox* workers of the four size categories considered in relation to temperature ($^{\circ}$ C).

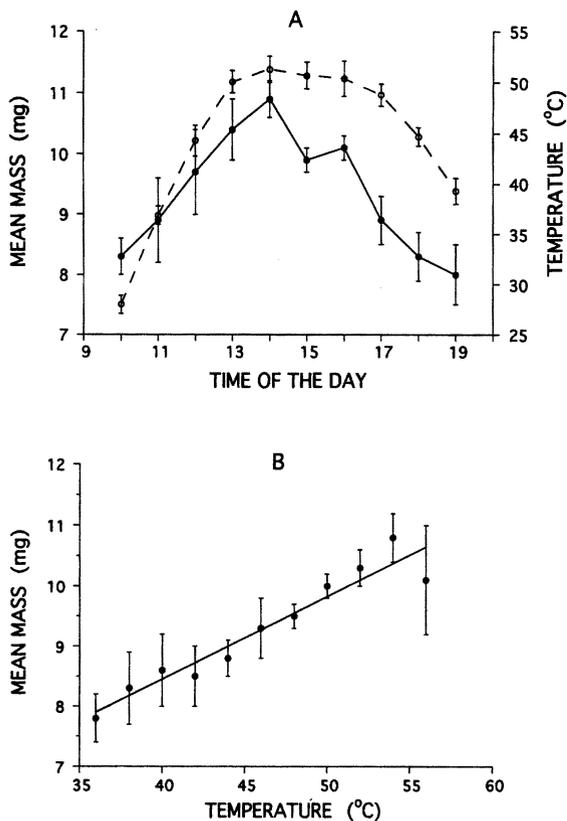


Fig. 4. A) Diel patterns of mean weight of *Cataglyphis velox* foragers (black dots and unbroken line) and temperature (white dots and broken line). B) Relationship between temperature (°C) and the mean weight (mg) of *Cataglyphis velox* foragers. Each point represents the mean value (\pm SE) of all measurements at each period of the day or with the same temperature (in 2°C-classes) from all nests and all sampling days.

mer, when populations of many insect taxa were at their maximum), but such a linear relationship was not found. If the correlation between ant mass and load mass is low, one would expect larger ants to be able to carry to the nest prey of certain sizes with greater net benefit to the colony. As predicted by foraging models (Reyes 1987), the greatest possible yield in prey biomass obtained by the colony per unit of forager biomass for small prey was provided by very small and small *C. velox* foragers, and it was only higher for medium and large workers when prey mass was over 30 mg. Since prey of this weight or greater represent less than 5% of loads collected by *C. velox* foragers and are also very seldom found in the arthropod distributions in the field (Oster and Wilson 1978, Stork and Blackburn 1993), the conclusion is that large foragers are substantially larger than necessary to carry prey commonly found in their habitat, being only more effective than smaller ones in a very small percentage of their foraging trips. The last hypothesis proposed to explain the role of large workers in prey collection, i.e. that they should

collect greater amounts of prey and/or with greater efficiency, is also not confirmed by the results of this study. Large workers were not the size group that collected most prey (medium and small workers carried more prey than large ones) and, although they showed the highest percentage of loading, differences with small and medium workers were not significant.

If they are not specialized in finding and delivering greater amounts of prey or proportionately larger prey, what is the role outside the nest of large *C. velox* workers? In other species, the largest workers do not commonly participate in foraging; they appear to specialize as soldiers defending the colony (Hölldobler and Wilson 1990, Wetterer 1994). But *C. velox* majors are good foragers that leave the nest and perform long foraging trips (more than 20 m far from the nest). Moreover, they are not the most abundant size group outside the nest, but their proportion there is considerably higher than their proportion in the entire nests (24.0% versus 12.0–18.5%, respectively). This fact could be related to large workers' greater ability to tolerate external environmental conditions. Thermal tolerance of *C. velox* workers is related to size: both critical thermal maximum and lethal temperature increase with body size. Several studies (see review in Kaspari 1993) also suggest this relationship between heat tolerance and body size in ants: variables such as desiccation (Hood and Tschinkel 1990, Kaspari 1993), maximum foraging time (Lighton and Feener 1989) or foraging temperature (Rissing and Pollock 1984, Porter and Tschinkel 1987) increase with body size. Although there is not always a close relationship between thermal tolerance and activity periods (Wetterer 1990, Cros 1995), a clear relationship between heat tolerance and foraging times has been found in *C. velox*. Larger foragers are less temperature-limited than smaller ones, and, as far as foraging is concerned, this leads to a diurnal rhythm in which the mean size or weight of workers foraging outside the nest at different times of the day increases with temperature, a phenomenon that has also been observed in other species (e.g. *Formica neorufibarbis*, Bernstein 1976, or *Solenopsis invicta*, Porter and Tschinkel 1987). This is an especially interesting feature for a thermophilic ant species such as *C. velox*, where the thermal polymorphism could have an adaptive value to withstand the critical environmental conditions to which foragers are exposed. Large workers can be active at higher temperatures and perform longer trips than small workers because of their longer legs, which allow them to stilt above the hot substrate, or their greater running speed (Heinrich 1993). Notwithstanding, the close relationship between polymorphism and thermal biology of species is not universal among thermophilic ants. Other species that are also active at very high temperatures and faced with the economic problem of thermal tolerance do not show a temperature-related polymorphism (Shalmon 1982, Christian and Morton 1992), or even a broadly

polymorphic worker caste (Marsh 1985a, b, Retana and Cerdá 1990).

The results of this study indicate that *C. velox* colonies enjoy important advantages because of their broadly polymorphic caste. Very small and small foragers forage preferentially when temperatures are lower, while medium and large workers, which withstand temperatures 6 to 8°C higher than smaller ones, preferentially forage at high temperatures. At the colony level, this means longer and more continuous daily activity periods. As also seen in other *Cataglyphis* species (Wehner 1987, Cros 1995), *C. velox* colonies benefit from foraging in these harsh thermal conditions by collecting larger amounts of prey, both because there are more prey available, and/or because there are fewer potential competitors. Foragers usually suffer high mortality and have short half-lives (Porter and Jorgensen 1981, Johnson and Wilson 1985), but this is especially important in species living in hot dry habitats (Schmid-Hempel and Schmid-Hempel 1984). Less polymorphic *Cataglyphis* species, such as *C. cursor* (Cerdá et al. 1989) or *C. floricola* (pers. obs.), are forced to reduce their midday activity because of very high temperatures on some summer days, or to accept a high forager mortality risk (Schmid-Hempel and Schmid-Hempel 1984). For *C. velox*, polymorphism could represent a mechanism to reduce this high risk of mortality while foraging at very high temperatures. In this context, large *C. velox* workers could be considered a specialized group foraging at temperatures which other size groups cannot withstand outside the nest. Nevertheless, factors maintaining size polymorphism may be variable and additive, and it is not necessary to find only one functional explanation of polymorphism for a given ant species. As proposed for other polymorphic species (Calabi and Porter 1989), the proportion of large workers in *C. velox* colonies might represent an average selective trade-off between the proportionately greater expense of their production and maintenance, and their behavioural contribution in different ways to colony fitness.

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