Behavioural and physiological traits to thermal stress tolerance in two Spanish desert ants

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Abstract. In Mediterranean open habitats, dominant ant species are heat-intolerant and risk-averser, foraging very far from their critical thermal limits (CTM). Subordinate are heat-tolerant (thermophilic) and risk-proner, foraging very near their CTM, running a high heat mortality risk, but having better performance at high temperatures. Thermal tolerance allows a far greater dominance in the ecosystem by subordinates than might be expected from their relative abundance and fighting abilities. Foraging of subordinates is more influenced by temperature than by competition of dominants. The mutual exclusion between dominant and subordinate species seems the result of physiological specialization to different temperature ranges. Focussing on two *Cataglyphis* species (subordinate and thermophilic), two alternative mechanisms facing extreme heat are described: *C. velox* polymorphism (large workers are more resistant than small ones), and physiological and behavioural adaptations of *C. rosenhaueri* workers (all of them of small size).

Key words: *Cataglyphis*, ants, thermophilia, thermal stress, polymorphism, Mediterranean communities

Resumen. *Caracteres conductuales y fisiológicos de tolerancia al estrés térmico en dos especies de hormigas españolas de zonas desérticas.* En ambientes mediterráneos abiertos, las especies de hormigas dominantes son intolerantes a las elevadas temperaturas, y evitan el riesgo de morir recolectando a temperaturas muy alejadas de sus límites térmicos críticos (CTM). Las especies subordinadas son tolerantes al calor (termofílicas) y asumen el riesgo de recolectar muy cerca de su CTM, lo que aumenta su riesgo de morir pero les permite optimizar la recolección de alimento. Su mayor tolerancia térmica permite a las especies subordinadas una mayor dominancia en el ecosistema del que sería esperable por su abundancia relativa y su capacidad competitiva. La recolección de las subordinadas está más influida por la temperatura que por la competencia con las dominantes. La exclusión mutua entre dominantes y subordinadas parece el resultado de la especialización fisiológica a diferentes rangos de temperatura. Concretando el estudio en dos especies del género *Cataglyphis* (ambas subordinadas y termofílicas), se describen dos mecanismos alternativos para hacer frente a las elevadas temperaturas: el polimorfismo de *C. velox* (las obreras grandes son más resistentes que las pequeñas), y las adaptaciones fisiológicas y comportamentales de las obreras de *C. rosenhaueri* (todas ellas de tamaño pequeño).

Introduction

Traditionally, interspecific competition has been considered as the major factor affecting structure in ant communities (Fellers, 1987; Savolainen & Vepsäläinen, 1988, 1989; Andersen, 1992). Competitive dominance has two components: behavioural and ecological (Cerdá et al., 1997). An ant species is ecologically dominant if it occurs at a large proportion of food resources, monopolizes most of the food resources at which it occurs, and has far greater representation at them than would be expected from its presence in the area (Andersen, 1992). The term 'behavioural dominance' refers to the priority of access to resources that results from successful attacks, fights, chases or supplanting actions: an ant species is behaviourally dominant if it initiates attack and by its presence elicits avoidance behaviour in an encounter with another species. In many cases, there is a direct relationship between behavioural dominance and

ecological dominance, not because levels of aggression determine dominance success, but because aggression is a manifestation of dominance. In these cases, ant species have been grouped into transitive hierarchies of interacting species with superior competitors behaviourally excluding subordinate species (Vepsäläinen & Pisarski, 1982; Mabelis, 1984; Savolainen & Vepsäläinen, 1988). Nevertheless, in Mediterranean communities, where environmental factors (mainly temperature) show important daily and seasonal fluctuations, the limited thermal tolerance of behaviourally dominant species compared with that of subordinates disrupts the expected transitive hierarchies. The lower thermal limitation of subordinate activity not only increased their exploitative ability, but also altered the outcome of interspecific interactions at food resources modifying the interference hierarchy (Cerdá et al., 1997).

Recently, the prevalent view of community structuring by dominant species has moved to one giving more prominence to non-equilibrium and stochastic factors, such as physical disturbance and inconstancy in conditions (Begon et al., 1996). With linear hierarchies, high diversity may be maintained by predation or physical disturbances affecting the top dominant species strongest (Savolainen & Vepsäläinen, 1989). If environmental conditions are changing such that each species is favored alternately, then these competing species could coexist indefinitely (Murray, 1986). We might expect equilibrium communities to be primarily ordered by biotic interactions and developed in situations of moderate to low environmental variation, while non-equilibrium communities are expected to be found in highly variable environments, and to be influenced by independent interactions of species populations with abiotic factors (DeAngelis & Waterhouse 1987, Putman 1994), but even in systems at equilibrium, environmental constraints influence the outcome of assembly rules (Belyea & Lancaster 1999)

For small bodied ectotherms such as insects, temperature may play a very important role in community structure. Temperature determined the outcome of competition in pairwise interspecific interactions between *Drosophila* (Davis et al. 1998) and species-specific thermal tolerances may contribute to large- and small-scale patterns of community structure in mycophagous flies (Worthen & Haney, 1999). Species coexistence and diversity in a community should be understood on a larger spatio-temporal scale, where various mechanisms would act together to ensure the persistence of inferior competitors by providing many kinds of refuges (Toda et al. 1999). One of these kinds of refuges may be the high temperatures at midday. As another example in the hot Mediterranean summer, thermal constraints may generate within- and between-habitat variation in the composition and size structure of insect pollinator assemblages (Herrera, 1997).

A stress can be defined (Parker et al. 1999) as any detrimental effect on some biological entity (individual, population, food web, community, etc) which occurs following some disturbance (or stressor). Many evolutionary and ecological considerations of stress emphasize the unpredictability of environmental heterogeneity, usually abiotic, in terms of ability or inability of organisms to genetically track such changes, leading to the evolution of particular kinds of life histories associated with unpredictable and/or harsh environments (Parker et al., 1999). Grime (1989) has defined stress as the "external constraints limiting the rates of resource acquisition, growth or reproduction of organisms", and Koehn & Bayne (1989) as "any environmental change that acts to reduce the fitness of an organism". According to Bijlsma & Loeschcke (1997), environmental stress may play and may have played a significant role in the evolution of biological systems, from the level of gene to that of ecosystem. For small-bodied ectotherms such as ants, temperatures outside the range between 10 and 45°C may be considered stressful. However, at midday of summer days, when ground surface in Mediterranean open habitats might heat up to 64°C, it is easy to see the *Cataglyphis* worker running outside the nest. How are they able to do it? And what are the advantages of this behaviour? In this work we review previous papers about the role of temperature on Mediterranean ant community structure (Cerdá et al. 1997; 1998a, b) and the different mechanisms of subordinate *Cataglyphis* species to tolerate thermal stress (Cerdá & Retana, 1997, 2000).

Temperature, foraging activity and foraging efficiency in Mediterranean ant communities

As already said above, interspecific competition has long occupied a preeminent position among factors affecting structure and dominance in ant communities (Savolainen & Vepsäläinen, 1988, 1989; Andersen, 1992). Nevertheless, in many Mediterranean ecosystems affected by considerable daily and seasonal environmental fluctuations, physical factors, mainly temperature, can limit niche breadths of behaviourally dominant species in a stronger way than those of behaviourally subordinate species (Cerdá et al., 1997). Temporal differences in foraging rhythms are common among sympatric ant species (Cros et al. 1997). Although the temporal partition of interspecific foraging shifts is considered one of the consequences of interspecific competition, temporal separations in foraging can also result from non-competitive causes such as physiological tolerance to physical conditions (Briese & Macauley, 1980; Fellers, 1989; De Bie & Hewitt, 1990). Selection of particular thermal environments (and consequent body temperatures) on a daily and seasonal basis is a behavioural mechanism leading to certain advantages for animals (Cerdá et al., 1998a).

Table 1. Critical Thermal Maximum (CTM, in ºC) and Maximal Activity Temperature of Foraging (MAT, in ºC) of some dominant and subordinate ant species of different Spanish Mediterranean communities. CTM is the temperature at which at least 50% of workers died or lost muscular co-ordination after 10 min of exposure. MAT is the temperature at which the species has the maximum foraging activity in the field. (Data from Cerdá et al., 1998b and unpublished)

Category	Species	CTM	MAT
Dominant	*Linepithema humile*	40	20
	Tapinoma nigerrimum	42	24
	Camponotus sylvaticus	46	28
	Tetramorium caespitum	42	26
	Tetramorium hispanicum	42	24
	Tetramorium semilaeve	40	24
	Pheidole pallidula	40	24
Subordinate	*Cataglyphis cursor*	50	48
	Cataglyphis floricola	50	44
	Cataglyphis iberica	52	50
	Cataglyphis rosenhaueri	50	44
	Cataglyphis velox	54	46

Figure 1. Representative models of curve shape for the relationship between ground surface temperature (ºC) and foraging activity in a dominant species (*Pheidole pallidula*) and in a thermophilic subordinate ant species (*Cataglyphis cursor*) in a grassland community of Canet de Mar (Barcelona, NE Spain). Data have been standardized by defining the maximum mean activity value observed, which corresponds to the maximal activity temperature (MAT, see Table 1), as 100% of activity. Risk temperatures are those ≥CTM-2ºC, where CTM is the Critical Thermal Maximum (see Table 1). (Modified from Cerdá, 1999)

A number of studies (Marsh, 1985; Cokendolpher & Phillips, 1990; Wehner et al., 1992) have demonstrated that environmental temperatures experienced by worker ants often result in body temperatures that exceed some Critical Thermal Maximum (CTM), defined as the temperature at which the locomotion ability of ants is so reduced that they can no longer escape lethal temperatures (Cokendolpher & Phillips, 1990). Such thermal stress limits worker activity to certain times of day and specific microhabitats, thus restricting worker movement and foraging activity (O'Neill & Kemp, 1990). As Cerdá et al. (1998a) have shown, in Spanish Mediterranean communities, dominant ant species are heat-intolerant. They adopt a "minithermy" strategy by foraging when temperatures are much lower than their CTM. They are crepuscular and/or nocturnal from late spring to late summer, and they have low Maximal foraging Activity Temperature (MAT), with values between 20-28°C (Table 1). On the other hand, subordinates of these communities (the majority belonging to the *Cataghyphis* genus) are heat-tolerant ant species, and they adopt a strategy of "maxithermy" by foraging when temperatures are closer to their CTM. They are strictly diurnal during all seasons, and they have high MAT values, ranging between 44-50°C (Table 1). These thermophilic *Cataglyphis* species are able to run short and fast foraging trips even when ground surface temperatures are greater than their CTM.

However, the risk of mortality caused by environmental conditions during foraging can represent an important cost for colonies of ants. The foraging activity of animals is subject to certain physiological limits, and these critical limits can be near or far from their usual foraging conditions, involving, respectively, a risk-prone (near the critical limits) or a risk-averse (far from the critical limits) strategy (sensu Stephens & Krebs, 1986). Since exploiting only food sources
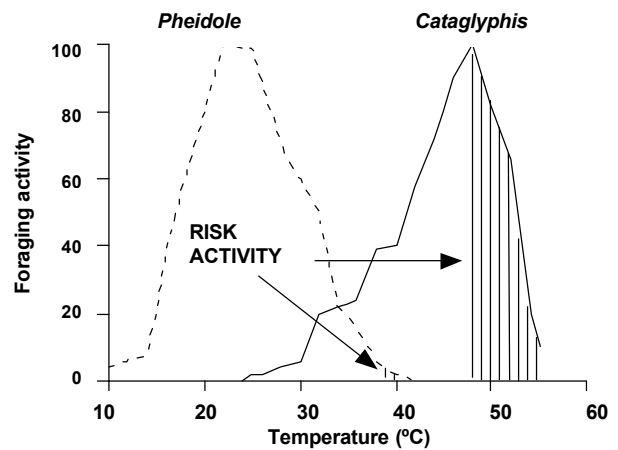
without any associated risk may restrict colonies to an impossibly small set of food items (Nonacs & Dill, 1988), foragers of different species must choose a trade-off between maximizing energy brought back to the colony and minimizing mortality risk (Nonacs and Dill, 1990). In Mediterranean communities, dominant (heat-intolerant) ant species behave as risk-averse species (foraging at temperatures very far from their CTM), while subordinate (heat-tolerant) ant species behave as risk-prone species (foraging very near their CTM and having a high heat mortality risk). Figure 1 shows the foraging activity curves of a dominant and a subordinate ant species from Canet de Mar (Barcelona, NE Spain). Only a small area of the activity curve of the dominant species, *Pheidole pallidula*, is over the risk threshold (near CTM). On the contrary, the majority of the curve of the subordinate species, *Cataglyphis cursor*, is over the risk threshold.

There may be situations in nature in which it is advantageous to suffer near-lethal temperatures to maximize foraging success: heat-tolerant species benefit from this strategy by having better foraging performance at high temperatures. The foraging efficiency of subordinates increases when temperature increases (Marsh, 1985; Cerdá et al., 1998a), while that of dominants decreases with temperature. Results obtained by Cerdá et al., (1998b) confirm that the species foraging at higher temperatures were more efficient than heat-intolerant ones. Since heat-tolerant species are individual-foraging species, while heat-intolerant ones are recruiting species, the different efficiency of both groups of species at high temperature is probably because temperature influences (and even alters at high temperatures) the stability of chemical signals that de-
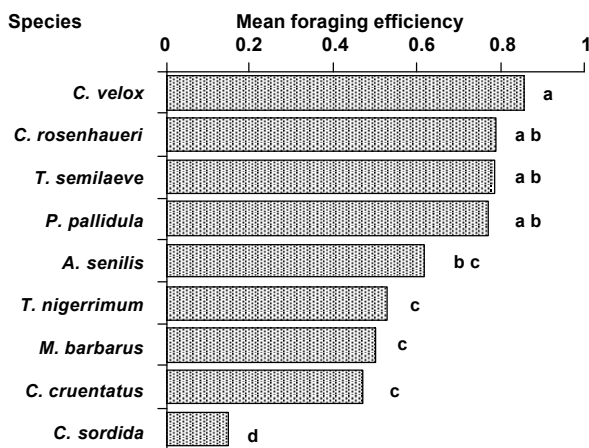
Species   **Mean foraging efficiency**

Figure 2. Foraging efficiency of each ant species in Palomares (Sierra Sur de Jaén, SE Spain). Values were calculated from the abundance of each species at baits and in pitfall traps, following Baroni-Urbani & Aktaç (1981) (see Cerdá et al. 1998b for more details). Those species that were not significantly different (*p*>0.05), based on Fisher's protected LSD *post-hoc* tests for the mean values of different summer sampling days, share a common letter. (J. Retana, X. Cerdá & A. Manzaneda, unpublished data).

termine nestmate recruitment (Ruano et al., 2000). Figure 2 shows the foraging efficiency values of ant species from the Palomares community (Sierra Sur de Jaén, SE Spain). Therein, the most efficient species, *Cataglyphis velox* and *C.rosenhaueri* are both subordinate and thermophilic species. Probably the wide range of thermal niches may be one of the reasons to explain that Mediterranean ant faunas are so diverse in spite of limited vegetation diversity and habitat structure: the daily range of temperature may be sufficiently great to meet the requirements both of heat-adapted and cold-adapted species as well as a spectrum of intermediate forms, each having a sufficient allocation of time so that they can avoid interference competition with one other (Heatwole & Muir, 1989). That is, more species can be packed into a long thermal axis than into a shorter one (Cerdá et al., 1998b).

Effects of ecologically-dominant species and temperature on thermophilic subordinate ants

In the previous section, we have described the role of temperature on the foraging success of dominant and subordinate species. Now we also focus (but from a community structure point of view) on the role of temperature and of a second factor, ecological dominance, on subordinate ant species of the *Cataglyphis* genus. Temperature stress (outside the range of temperatures between 10 and 45°C) has been highlighted as the principal abiotic stress regulating ant community structure in Australia (Andersen 1995), because low temperatures limit the abundance of dominant ants, and therefore largely determines competitive dynamics within the community. In

Mediterranean areas (and also steppes, deserts, and semi-arid subtropics, see Baroni Urbani & Aktaç [1981], Heatwole & Muir [1989] or Bestelmeyer [2000]), temperature (in this case, high temperatures) also controls the structure of communities (Cerdá et al., 1997, 1998a, b). In these areas, the foraging requirements of dominant species are not typical of other ants: as we have seen, dominants are heat-intolerant species that are restricted largely by physical conditions, while subordinates are heat-tolerant species that are active over a wider range of temperatures. The limited thermal tolerance of dominant species compared with that of subordinates may disrupt the expected transitive hierarchies, and allow subordinates to be abundant in certain seasons (summer) and habitats (open and arid habitats) (Cerdá et al., 1997; Cros et al.,1997). By the contrary, in other ant communities, these variations do not affect differentially the activity of dominant species compared to other species, because the foraging activity in relation to temperature of dominant ant species is similar to that of other ants (Vepsäläinen & Savolainen, 1990; Andersen, 1992; Human & Gordon, 1996). In Mediterranean ant communities, a close relationship between activity rhythm in the period of maximum activity and position in the dominance hierarchy has been found: subordinate species are active during the day, when conditions are more severe, while dominants are active during the afternoon and the night; dominants forage at low temperatures (maximum activity at 20-28 °C, see Table 1) quite distant from their CTM, while subordinates forage at high temperatures (maximum activity at 40-50 °C) very close to their physiological thermal limits (Cerdá & Retana, 1997, 2000; Cerdá et al., 1998b).

In a community study conducted in an open grassland habitat in Palomares (Sierra Sur de Jaén, SE Spain), in (Cerdá et al., 1998b), different close areas with the same ant composition and vegetation structure, but differing in the relative abundance of dominant ants were chosen. In this natural scenario, the effect of dominants on foraging of subordinates was evaluated by measuring different variables of foraging populations of subordinate species which can be regulated by competition: forager abundance (by mean of pitfall traps), foraging efficiency (from abundance at baits and in pitfall traps) and foraging times. Moreover, the role of environmental factors (mainly temperature, which may be used as the summary environmental variable to define climatic favourability for ant activity, Hölldobler & Wilson, 1990; Cros et al., 1997) on these variables was also tested by analyzing natural shifts in resource use as conditions change temporally. In summary, the purpose of the analyses below was to evaluate the causes of changes in resource use by subordinate species between zones (with different abundance of dominant ants), and between different periods of the day (with different environmental conditions, mainly temperature).

Aggressive interactions at baits were more

Table 2. Dominance hierarchy of ant species at baits in Palomares (Sierra Sur de Jaén, SE Spain). Species are ranked according to their Dominance Index (% dom), calculated as the relative frequency of expulsion vs. escape interactions (N is the number of observed interactions). In the matrix of dominance a two-dimensional array of the outcome of bait interactions between pairs of species is shown. For abbreviations of column species, note that they are in the same order as row species. A 1 in row *i* and column *j* indicates that the *i*th species excluded the *j*th species; a 0 indicates de opposite; a dash (-) indicates that there were not enough encounters to determine the outcome of the interaction. (Table modified from Cerdá et al., 1998b)

				Matrix of dominance hierarchy at baits					Dominance Index	
Species	*Tsem*	*Ppal*	*Tnig*	*Mbar*	*Asen*	*Csor*	*Ccru*	*Cvel*	*Cros*	N	% dom
Tetramorium semilaeve		1	1	1	1	1	-	-	-	26	96.1
Pheidole pallidula	0		1	1	1	1	1	1	1	65	84.6
Tapinoma nigerrimum	0	0		1	1	1	1	1	-	73	52.9
Messor barbarus	0	0	0		1	-	-	-	-	64	37.5
Aphaenogaster senilis	0	0	0	0		0	1	1	1	76	36.8
Crematogaster sordidula	0	0	0	-	1		-	-	-	14	35.7
Camponotus cruentatus	-	0	0	-	0	-		1	1	8	25.0
Cataglyphis velox	-	0	0	-	0	-	0		1	50	22.0
Cataglyphis rosenhaueri	-	0	-	-	0	-	0	0		20	20.0

Table 3. Relative abundance of ants in pitfall traps (%P: percentage of ants caught in traps per day) and at baits (%B: percentage of baits occupied per day) in plots with low, medium and high density of dominants in Palomares site (Sierra Sur de Jaén, SE Spain) in summer. (Data from Cerdá et al., 1998b)

Density of dominants	Low		Medium		High	
Species	%B	%P	%B	%P	%B	%P
Tetramorium semilaeve	-	-	-	0.6	11.4	19.6
Pheidole pallidula	1.6	6.7	2.9	3.3	27.3	24.9
Tapinoma nigerrimum	12.3	2.8	24.6	36.8	26.1	25.9
Crematogaster sordidula	-	-	-	-	4.9	1.0
Messor barbarus	66.6	51.1	49.1	29.8	18.9	12.1
Camponotus cruentatus	1.2	3.1	0.6	0.1	-	-
Aphaenogaster senilis	5.8	8.5	9.1	6.1	5.4	4.2
Cataglyphis velox	10.7	23.5	10.3	18.9	3.5	8.9
Cataglyphis rosenhaueri	1.8	4.3	2.3	4.4	1.9	3.4
Total values of abundance per day ($\sum$N)	571.2	656.2	659.7	833.5	526.7	668.2

frequent in high dominants' density plots (68% of aggressive interactions in all interspecific encounters at baits) than in medium and lower dominants' density plots (22 and 28%, respectively). Table 2 shows the dominance hierarchy of the ant community obtained from bait observations. There is a very clear transitive dominance hierarchy (4% of intransitivity): most of species of higher rank outcompeted species of lower rank. Two *Cataglyphis* species, *C. velox* and *C. rosenhaueri*, are the least behaviourally dominant species, they quickly leave or are driven away from baits upon encountering a higher-ranked species. But total presence at pitfall and baits of subordinates does not diminish significantly with the increase of dominants' density (Table 3). If foraging times of subordinates are limited by the interference of dominants, they should forage at broader times, although always within their physiological limits, when dominants are absent. Nevertheless, the daily activity rhythms of subordinate species are similar in the three zones with different abundance of dominants, indicating no effect of dominants on foraging times of subordinates (Figure 3). Table 4 summarizes the effects of the density of dominants and of the temperature on the four varia-

bles used to describe the foraging of subordinate species. The relationships between mean daily temperature are significant for the two bait-related variables. Once the effect of temperature has been removed, in most cases (except for *C.velox* number of occupied baits and of foragers in pitfall traps), there is no effect of the density of dominants on the foraging of subordinates. Foraging of subordinate species in these ant communities is much more affected by physical factors than by competition of dominants, in opposition what happens in other areas.

From these results we can conclude that temporal activity patterns found in ant communities of open Mediterranean habitats are basically conditioned by environmental factors rather than by competition (Cerdá et al. 1997, 1998b; Cros et al., 1997). Temporal separation of activity rhythms has been considered advantageous when competition involves intense interference interactions, because subordinate species might be expected to reduce the probability of exclusion by dominants by foraging at different times, mainly at night and/or in low temperatures (Savolainen & Vepsäläinen, 1989; Paulson & Akre, 1991). Nevertheless, in the communities studied, this mutual
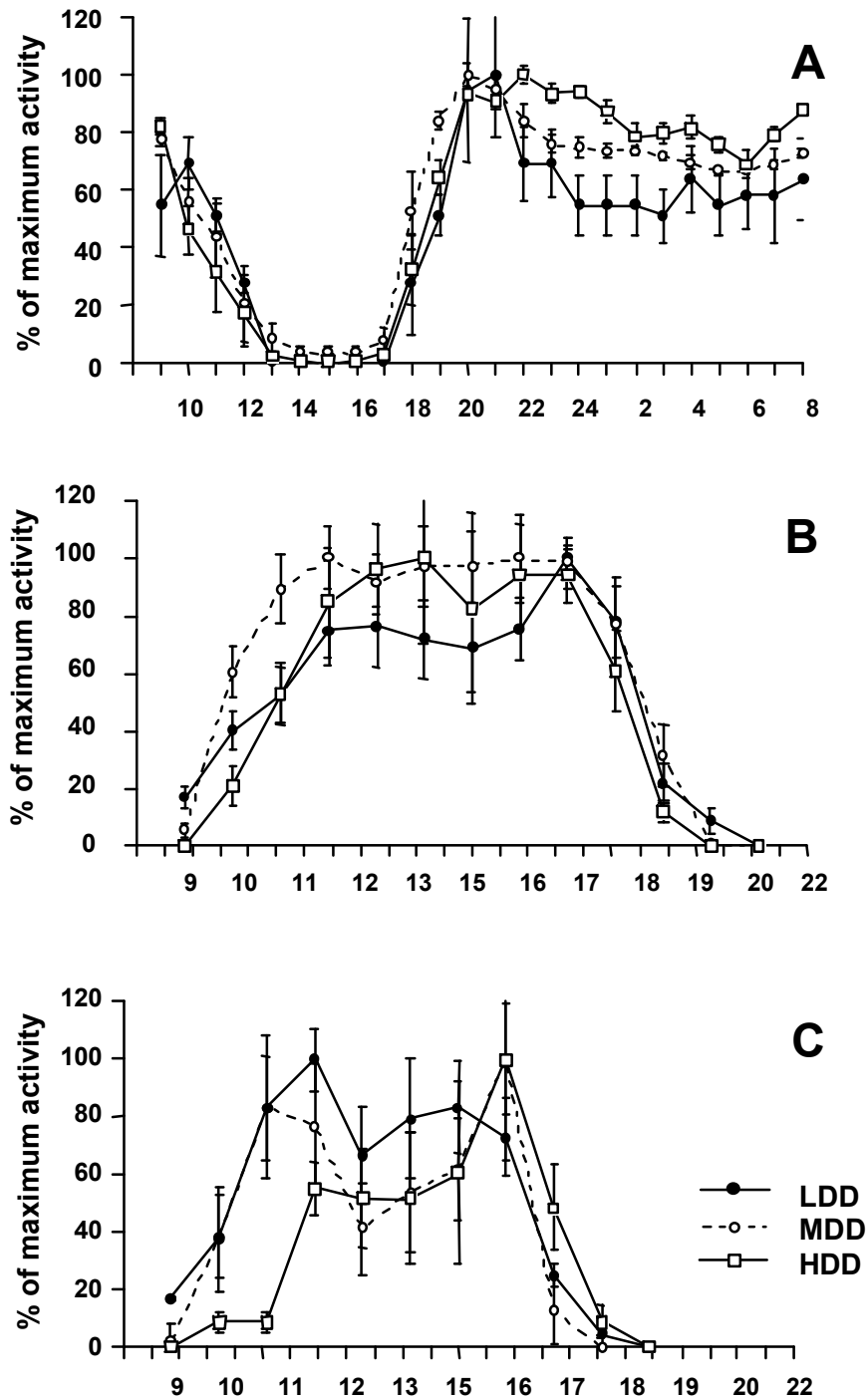
Figure 3. Daily activity rhythms of A) dominant ant species (*Tetramorium semilaeve*, *Pheidole pallidula* and *Tapinoma nigerrimum*); B) *Cataglyphis velox*; and C*) Cataglyphis rosenhaueri*, in Palomares site (Sierra Sur de Jaén, SE Spain) in summer. Data (mean±SE) have been standardized by defining the maximum hourly activity value for each species as its 100% of activity. (Modified from Cerdá et al., 1998b)

exclusion, when observed, seems just the result of different circadian activities and physiological traits. Differences in the response to temperature might explain the reduced effect of interspecific competition in structuring these fluctuating systems, where climatic axes appear to have a primary role in community structure, and resistance to physical factors reduces the occurrence of competition (Schoener 1986).

Thermophilic ants don't have the same size or the same behaviour: the case of *Cataglyphis velox* and *C. rosenhaueri*

In the previous sections it has been shown how thermophilic subordinate are able to coexist, compete and, sometimes, "win" (having greater foraging efficiency) with dominant ant species in the framework

Table 4. F-values from repeated-measures ANOVA test of effects of density of dominants (DD) as independent variable, and days (time, T) as repeated measures on the four variables describing the foraging of *Cataglyphis* species in Palomares site (Sierra Sur de Jaén, SE Spain). To remove the effect of the temperature, the residuals of the regressions of the different variables against temperature were employed in the ANOVA instead the of the original values. The effect of temperature is shown as the correlation coefficient (Pearson's *r*) between mean daily temperature and the four dependent variables. Significant coefficients of F and *r* (at α=0.05 when the sequential Bonferroni method is employed) are indicated in bold. (Table modified from Cerdá et al., 1998b).

Variable	Source of variation	*C. velox*	*C. rosenhaueri*
Baits occupied/day	Density of dominants (DD)	**65.47**	1.36
	Time (T)	5.35	0.90
	DDxT	2.44	2.16
	[Temperature (Pearson's *r*)	**0.507**	**0.419**]
Number of workers/bait	Density of dominants (DD)	5.89	2.84
	Time (T)	2.10	3.15
	DDxT	0.80	3.34
	[Temperature (Pearson's *r*)	**0.548**	**0.399**]
Foraging efficiency	Density of dominants (DD)	1.02	2.10
	Time (T)	0.97	0.46
	DDxT	1.17	0.73
	[Temperature (Pearson's *r*)	0.063	0.182]
Number of foragers in traps	Density of dominants (DD)	**14.93**	0.07
	Time (T)	5.89	4.04
	DDxT	4.01	4.04
	[Temperature (Pearson's *r*)	0.187	0.227]

Table 5. Proportion of workers of different sizes of *Cataglyphis velox* and *C. rosenhaueri* foraging outside the nests (outside) and in the entire excavated nests (nest) in Palomares (Sierra Sur de Jaén, SE Spain). (Data from Cerdá & Retana, 2000).

	C. velox		*C. rosenhaueri*	
Worker size	outside	nest	outside	nest
very small	3.6	23.4	52.1	57.4
small	16.2	30.0	47.9	42.6
medium	39.3	35.6		
large	40.9	11.0		
	χ^2=541, p=0.001		χ^2=2.13, p=0.16	

of Mediterranean communities. In any case, it seems that thermophily provides an ecological advantage. How have these thermophilic ants been able to penetrate into this dangerously hot environment? Which are the mechanism that subordinate species have developed to do it? Is it possible that the adaptation to extreme heat conditions may have followed different evolutionary routes? To answer these questions (or to try to answer them) we will analyse the case of two well-known (from the previous sections) subordinate species: *Cataglyphis velox* and *C. rosenhaueri*.

The first topic deals with worker size. Species with very different degrees of worker polymorphism are found within *Cataglyphis* genus, from monomorphic (Cerdá et al., 1996) to very polymorphic species (Cerdá & Retana, 1997), with all intermediate levels of polymorphism within them (Wehner, 1983; Agosti, 1990). *Cataglyphis* is one of the rare ant genera that display this striking variation in the degree of worker polymorphism (only 4% of all ant genera, 11 out of 297, are known to contain both monomorphic and polymorphic species, Frumhoff & Ward [1992]).
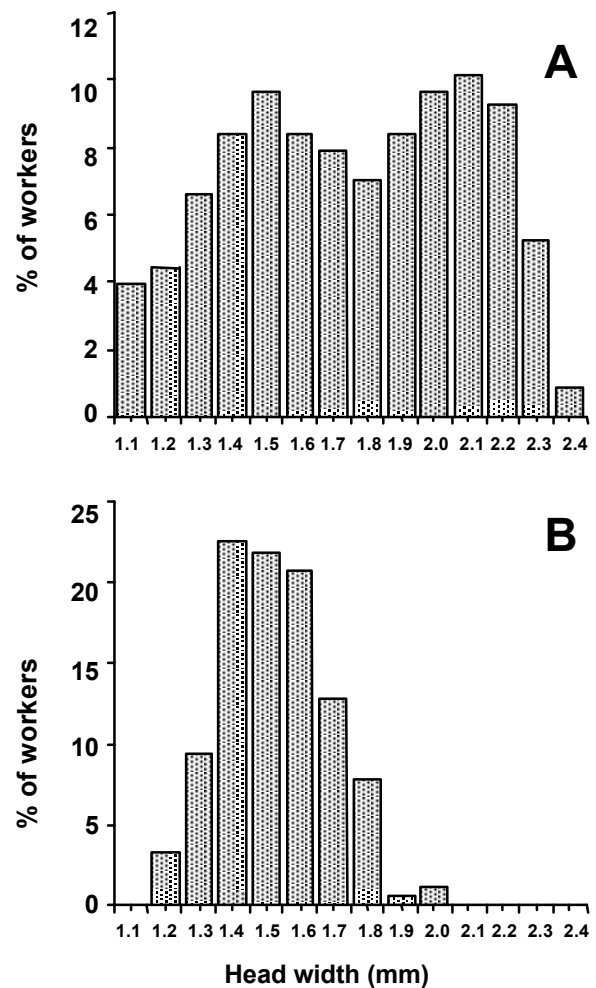
Figure 4. Head width (mm) distributions of workers of A) *Cataglyphis velox*, and B) *Cataglyphis rosenhaueri*. (J. Retana, & X. Cerdá, unpublished data).
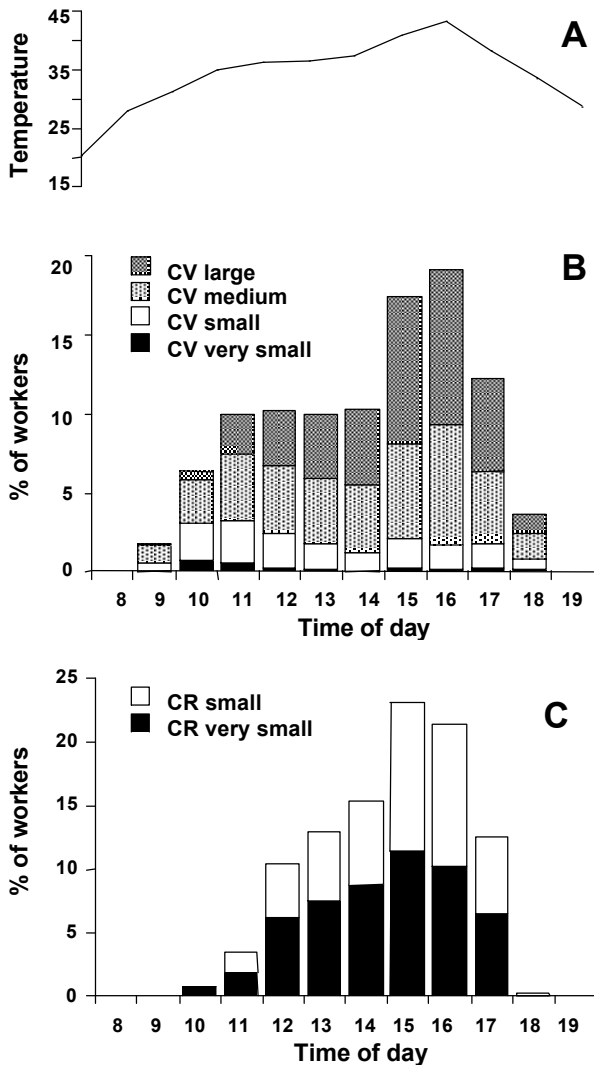
Figure 5. Diel patterns of ground soil temperature (A) and proportion of different-sized workers of *Cataglyphis velox* (B), and *Cataglyphis rosenhaueri* (C) in a summer day in Palomares (Sierra Sur de Jaén, SE Spain). The proportion of each worker size has been calculated by dividing all values by the total number of workers registered in all sizes categories during the whole day in each nest (data are mean values of four nests). (Modified from Cerdá & Retana, 2000).

Figure 6. Mean values (±SE) of variables describing the physiological traits of the different-sized worker of *Cataglyphis rosenhaueri* (CR) and *C. velox* (CV). A) Percentage of transcuticular passive water loss after 24 h. B) Cuticular transpiration rate, calculated as the negative slope of the relation between ln (M_t/M_o) and elapsed time, where M_o is the initial mass and M_t is mass at time t. C) Oxygen consumption rate, measured 4 h after the ants were placed in a Warburg respirometer. The results of the one-way ANOVAs used to investigate differences among worker types for the different variables examined are given. Those groups of workers that were not significantly different (p>0.05) based on Fisher's protected LSD *post-hoc* test share a common letter. Data of percentage of water loss were arcsin transformed, and data of cuticular transpiration rate were log transformed previously to perform the ANOVA tests. n=5 for the metabolic rate and n=10 for the other variables. (Modified from Cerdá & Retana, 2000).

C. velox is one of the most polymorphic *Cataglyphis* species (Figure 4a) in the Iberian Peninsula, with a worker length range of 4.5-12 mm (Cerdá & Retana, 1997). On the other hand, *C. rosenhaueri* shows a rather lower worker polymorphism (Figure 4b), with a worker length between 4.5-7.5 mm. Following Cerdá & Retana (1997, 2000), workers of both species can be categorized according to total body length as either very small (<6 mm), small (6-8 mm), medium (8-10 mm) or large (>10 mm). The last two categories are only present in *C. velox* colonies. If the worker caste has indeed been shaped by strong colony-level selection (Oster & Wilson, 1978; Frumhoff & Ward, 1992), and the species face a common problem, in this case to forage at high temperatures, we can reasonably infer that the size-frequency distributions of workers are adaptive. The addition of large castes (a generalization applied to ants
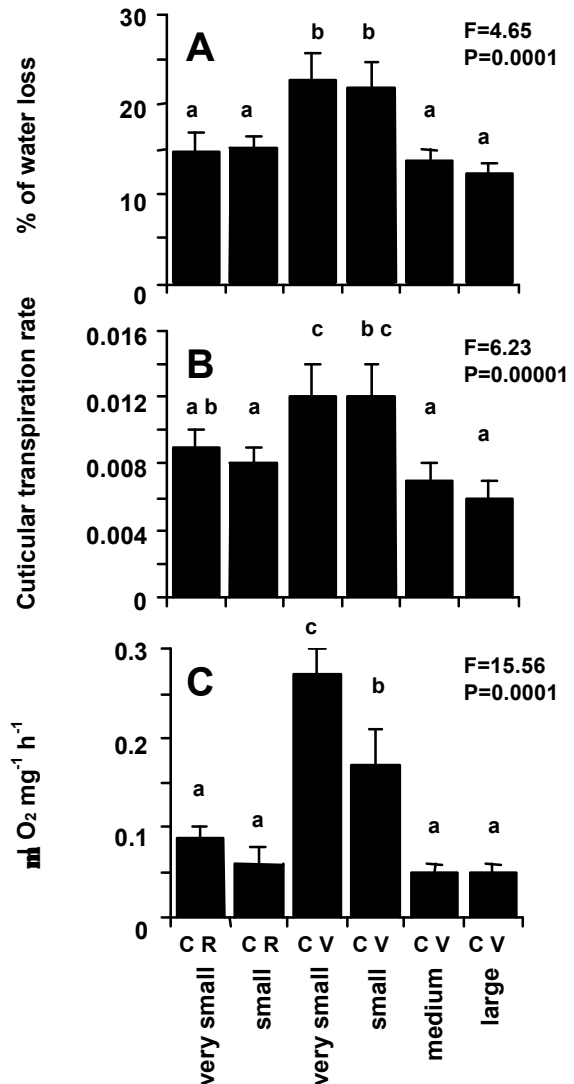
is that physical polymorphism has usually been created by the addition of a major caste, Oster & Wilson [1978]) may be limited by both developmental (high energy costs of manufacture and maintenance) and ecological factors (decreased flexibility in response to environmental and demographic variability). For this reason, in certain cases ant colonies follow strategies other than the production of major workers to face these selective pressures.

Foraging activity diel patterns of the two *Cataglyphis* species considered were very similar (Fig.

5). Nevertheless, there were important differences in the proportion of different-sized workers of the two species at different times of the day, i.e. at different surface temperatures. Very small and small workers of *C. rosenhaueri* were outside the nest during the whole day, especially at midday, when temperatures were at their hottest. *C. velox* colonies, on the other hand, showed a very clear diel pattern of forager size, with very small and small workers foraging preferentially in the morning hours and decreasing their relative proportion at midday, while the greatest foraging force at midday was mainly composed by medium and large workers (Fig. 5b). Moreover, the proportion of workers of different sizes foraging outside the nests and in the entire excavated nests differs statistically in *C. velox* ($\chi^2 = 540.9$, p=0.0001), but not in *C. rosenhaueri* ($\chi^2 = 2.13$ p=0.16) (Table 5). Thus, the proportions of very small and small *C. rosenhaueri* workers outside the nests were similar to those in the entire nests, but the proportion of very small and small *C. velox* foragers was lower than in the entire nests. Small *C. rosenhaueri* workers may withstand extreme heat conditions in a similar way to large *C. velox* workers, and much better than small *C. velox* workers. But the CTM depended on size class but not on species: CTM of very small workers of both species was 50°C, that of small workers was 52°C, while that of medium and large was, respectively, 54 and 56°C.

In Cerdá & Retana (2000) three physiological variables were calculated to evaluate cuticular transpiration in the different-sized groups of workers: percentage of transpiratory water loss, cuticular transpiration rate and metabolic rate (oxygen consumption rate). These variables showed a different pattern for each worker size, but a similar pattern among variables (Figure 6): water loss across the cuticle was higher and quicker in very small and small *C. velox* foragers, and lower and slower in the other worker groups, including very small and small *C. rosenhaueri* ants; similarly, very small and small *C. velox* workers respired more quickly per mg of tissue than medium and large *C. velox* workers and also very small and small *C. rosenhaueri* workers (which did not show significant differences in their metabolic rates compared with the larger *C. velox* ants). Thus, from the point of view of water loss, the behaviour of very small and small *C. rosenhaueri* workers was completely different from that of their equivalents in size of *C. velox*, but very similar to that of medium and large workers of the latter species.

Behavioural variables measured during the foraging trips showed several differences among worker types (Figure 7). ANOVA and post hoc tests showed that the maximum distance travelled and speed varied with worker size. There were two-fold or even three-fold differences between medium and large *C. velox* workers and small workers of the two species. The maximum distance an ant went from the nest on a search was 60.1 m in *C. velox* and 21.1 m in *C. rosenhaueri*, while the maximum duration of a foraging
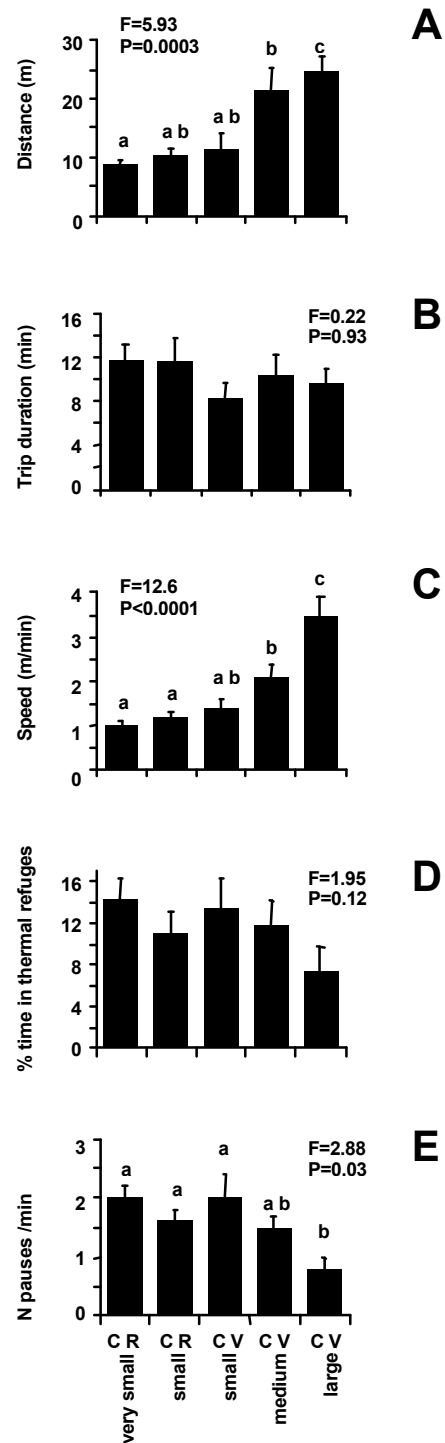

Figure 7. Mean values (±SE) of variables describing the foraging trips of the different-sized workers of *Cataglyphis rosenhaueri* (CR) and *C. velox* (CV). A) Maximum distance traveled (in m), *n*=20. B) Trip duration (in min) to reach the maximum distance, *n*=20. C) Speed (in m/min), calculated as a quotient between maximum distance traveled and duration time, *n*=20. D) % of foraging time spent in a thermal refuge (pausing in the shade or climbing up grass stalks), *n*=10. E) Frequency of pauses (number of pauses/min) at thermal refuges during foraging trips, *n*=10. The results of the one-way ANOVAs used to investigate differences among worker types for the different variables examined are given. Those groups of workers that were not significantly different (*p*>0.05) based on Fisher's protected LSD *post-hoc* test share a common letter. Data of maximum distance traveled and trip duration were log transformed, while data of percentage of time in thermal refuges were arcsin transformed previously to perform the ANOVA tests. Since all foraging trips were monitored at midday, and very small *C. velox* were not found outside the nests during this period of the day, no data for this group are available. (Modified from Cerdá & Retana, 2000).
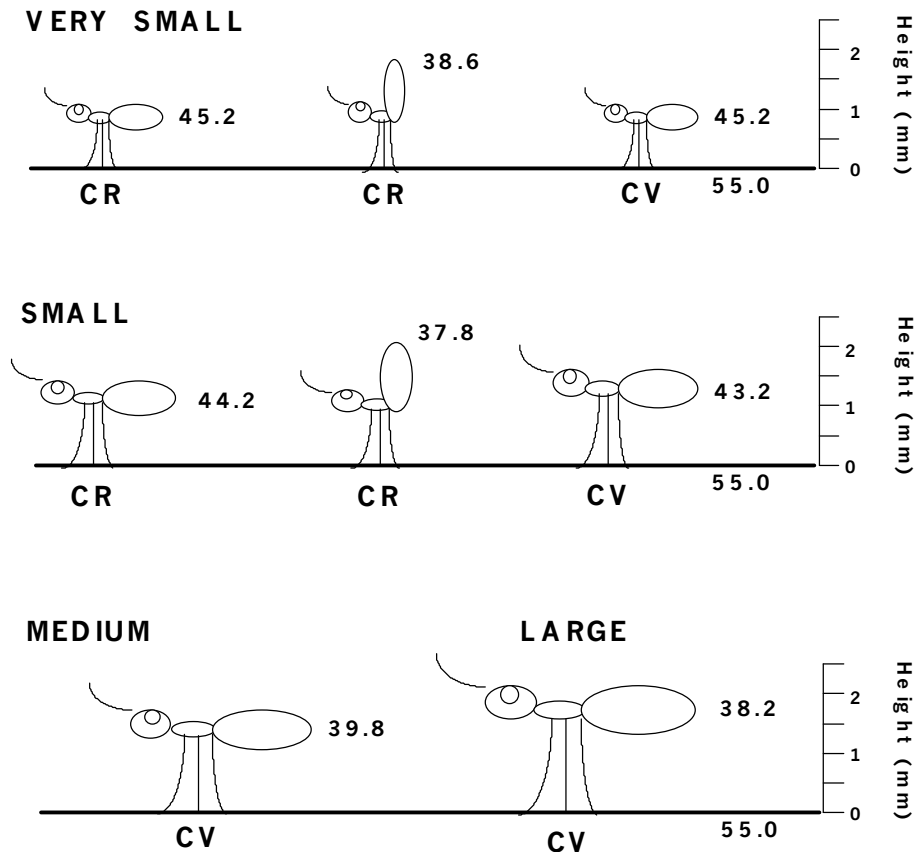
VERY SMALL

SMALL

MEDIUM   **LARGE**

Figure 8. Schematic view of temperature values (in ºC) of gaster at different height levels (height, in mm) of the different-sized workers of *Cataglyphis rosenhaueri* (CR) and *C. velox* (CV) when temperature was 55ºC at ground level. For *C. rosenhauri* workers, measures were taken with the gaster in an extended (a comparable measure as the one taken in *C. velox*) and in an elevated position (the natural position for this species when temperatures are hot). (Modified from Cerdá & Retana, 2000).

trip was 32 min in *C. velox* and 42 min in *C. rosenhaueri*. There were no significant differences among types of workers in the percentage of time spent at thermal refuges. There were only slight significant differences in the frequency of thermal respites, which varied from 0.8 pauses/min in large *C. velox* workers to 2.0 pauses/min in very small *C. rosenhaueri* and small *C. velox* workers (Table 2).

The different types of workers did, however, show considerable morphological differences concerning leg length, an important feature because long legs allow the ants to stilt above the hot substrate and to achieve a high running speed and thus short foraging. Thus, tibia length was greater in large (mean±SE: 4.22±0.04 mm, *n*=15) and medium (3.77±0.11 mm, *n*=15) *C. velox* foragers, than in very small and small workers of both species (for *C. velox*: 2.62±0.08 and 1.98±0.08 mm, and for *C. rosenhaueri*: 2.42±0.05 and 2.18±0.05 mm, for small and very small workers, respectively; *n*=15 in all cases). Large *C. velox* workers considerably raised their body over the ground due to their longer legs Nevertheless, there were differences between workers of similar size of the two species: *C. velox* displayed their body in a horizontal position, with head and gaster at low height over the ground surface; on the contrary, *C. rosenhaueri* workers

raised both head and gaster 0.2-0.4 mm compared to *C. velox* individuals of similar size (Figure 8). This led to 4-6ºC lower temperatures experienced at gaster by *C. rosenhaueri* workers compared to *C. velox* ones. *C. rosenhaueri* workers raise their abdomen from 1.0-1.1 to 1.9-2.1 mm when temperatures are hot, and this mechanism allows them to protect the vital organs contained in the gaster from high temperatures. With this behavioural mechanism, *C. rosenhaueri* foragers substitute the long legs of large *C. velox* workers, and place their gaster at a similar (and ever higher) height above the ground. As evidence of the advantage of this behaviour for *C. rosenhaueri* workers, for a ground surface temperature of 55ºC, the difference in temperature of the gaster placed in a horizontal or a vertical position was 6.4-6.6ºC for small and very small workers, respectively (Figure 8).

These species have developed two alternative mechanisms facing extreme heat. Although the results obtained for *C. velox* suggest that worker polymorphism may represent an adaptive way of achieving better exploitation of external environmental conditions by thermophilic ants, it is obvious that this is not the case of *C. rosenhaueri*. In *C. velox*, foraging at high surface temperatures is clearly dependent on size: large *C. velox* workers forage at midday and are able to

withstand higher temperatures than small workers. On the other hand, *C. rosenhaueri* has not developed great physical specialization, but the workers of this species have achieved physiological (such as low cuticular transpiration and metabolic rate), and behavioural adaptations (such as raising their abdomen to protect the vital organs contained in it from high temperatures) to tolerate thermal stress. The result is that small *C. rosenhaueri* workers may withstand extreme heat conditions in a similar way to large *C. velox* workers, and much better than small *C. velox* workers. Tolerance to extreme heat conditions has been well achieved in the two species, but probably following different evolutionary ways. In some situations, selection may act to promote a relatively narrow size range of adult workers, all of them able to withstand thermal extremes, while in others it may act by producing different worker sizes with different tolerance to environmental conditions (Cerdá & Retana, 2000).

Conclusion

During the course of evolution, thermophilic ants have developed alternative mechanisms to ensure that metabolism occurs at acceptable levels over the range of environmental temperatures. The most obvious one is a large size: different studies state that variables such as desiccation (Hood & Tschinkel, 1990; Kaspari, 1993), respiratory rate (Lighton et al., 1987; Bartholomew et al., 1988; Cerdá & Retana, 2000), running speed (Bartholomew et al., 1988; Cerdá & Retana, 2000), maximum foraging time (Lighton & Feener, 1989) and foraging temperature (Rissing & Pollock, 1984; Porter & Tschinkel, 1987; but see Christian and Morton, 1992) vary with body size. Other mechanisms to tolerate high temperatures and to conserve body water include both physiological (Lighton & Bartholomew, 1988; Lighton & Feener, 1989, Lighton et al. 1993), biochemical (Gilby, 1980; Gehring & Wehner, 1995) or behavioural adaptations, with responses such as making frequent pauses at thermal refuges (Marsh, 1985; Christian & Morton, 1992; Wehner et al., 1992; Cerdá & Retana, 2000), or raising the abdomen over the hot substrate (Wehner, 1983, 1989; Cerdá & Retana, 2000).

The generality of these patterns could be tested in future studies that should compare additional species of this and other genus. Thermophilic ant species, inhabiting in open-habitats ant communities, have a world-wide distribution. They have been identified in unrelated taxa as *Forelius* in subtropical South America (Bestelmeyer, 1997, 2000), *Melophorus* in tropical (Hoffmann, 1998) and temperate Australia (Briese & Macauley, 1980; Christian & Morton, 1992), *Ocymyrmex* in Namib Desert (Marsh, 1985), *Proformica* in Mediterranean high-mountains (Fernández-Escudero & Tinaut, 1998), and *Cataglyphis* in Mediterranean mountains (Cerdá et al., 1998b), coastal areas (Wehner et al., 1983; Cerdá et al., 1989, 1997), pre-Saharan African steppe (Heatwole & Muir, 1989), Anatolian

steppe (Baroni-Urbani & Aktaç, 1981) and Tunisian desert (Wehner et al., 1983, 1992). A multispecies and multigenus, explicitly phylogenetic approach which included more or less closely related species (*C. velox* and *C. rosenhaueri* belong to two different species-groups which are placed quite distant in the *Cataglyphis* cladogram, Agosti [1990]) and also other genus, would lead to the detection of rates and directions of evolutionary change in both thermal biology and worker polymorphism (Cerdá & Retana, 2000), important questions not only for ant evolutionary or behavioural ecology but also for ant community ecology.

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