

Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance

X. CERDÁ,*† J. RETANA* and S. CROS*

**Unidad de Ecología y CREAM, Facultad de Ciencias, Universidad Autónoma de Barcelona, E-08193*

Bellaterra (Barcelona), Spain and †Unidad de Ecología Evolutiva, Estación Biológica de Doñana, CSIC, Apdo 1056, E-41080 Sevilla, Spain

Summary

1. In Mediterranean ant communities, a close relationship has been found between activity rhythm in the period of maximum activity and position in the dominance hierarchy: subordinate species are active during the day, when conditions are more severe, while dominants are active during the afternoon and the night.
2. Results obtained in this study confirmed that the species foraging at higher temperatures were closer to their critical thermal limits than the species foraging at lower temperatures.
3. This enabled two extreme strategies of foraging in relation to temperature to be distinguished: (1) heat-intolerant ant species behaved as risk-averse species, foraging at temperatures very far from their critical thermal limits; and (2) heat-tolerant ant species behaved as risk-prone species, foraging very near their critical thermal limits and running a high heat mortality risk.
4. Heat-tolerant species benefited from this strategy by having better foraging performance at high temperatures.
5. This wide range of thermal niches may be one reason why Mediterranean ant faunas are so diverse in the face of limited diversity in vegetation and habitat structure: the daily range of temperature may be sufficiently great to meet the requirement both of heat-adapted and cold-adapted species as well as a spectrum of intermediate forms.

Key-words: Foraging activity, Mediterranean communities, risk temperature, thermal tolerance

Introduction

Temporal differences in foraging rhythms, at both daily and seasonal levels, are common among sympatric ant species (Lynch, Balinsky & Vail 1980; Lynch 1981; Herbers 1985, 1989; Lynch, Johnson & Balinsky 1988; Marsh 1988; Fellers 1989; Samways 1990). Although the temporal partition of interspecific foraging shifts is considered to be 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). Differential abilities of species to resist water loss by evaporation and high temperatures may influence the time of the day at which they are active. 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. Dreisig (1985) considers that the lower limit of the activity

range is determined by the costs and benefits of foraging, but it is not a tolerance limit, and activity is possible below it; on the other hand, the upper limit of the activity range is thought to be a tolerance limit determined by the impairment of physiological functions. A number of studies (Marsh 1985a; Cokendolpher & Phillips 1990; Wehner, Marsh & Wehner 1992) have demonstrated that environmental temperatures experienced by worker ants often result in body temperatures that exceed some critical thermal maximum, defined as the temperature at which locomotor ability 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 movement and foraging activity (O'Neill & Kemp 1990).

What are the benefits and costs of foraging at different temperatures? The problem for ectotherms is that, on the one hand, certain temperature levels are necessary for their activation and survival, but, on the other hand, critical temperatures can also be dangerous and

even lethal for them. It has been suggested that the maximal performance of ectotherms with high optimal temperatures should be greater than that of those with low optimal temperatures (see Huey & Kingsolver 1989). But, as Abrams (1991) points out, the act of obtaining food generally has costs, and for ants foraging at high temperatures the major cost is heat desiccation, which results in death. The term risk is usually applied to starvation (Caraco, Martindale & Whittam 1980; Real & Caraco 1986; Stephens & Krebs 1986; Caraco *et al.* 1990; Ha 1991; Krebs & Kacelnik 1991), predation (Lima, Valone & Caraco 1985; Hertz, Huey & Garland 1988; Lima & Dill 1990; Cartar 1991; Riechert 1991; Hughes, Ward & Perrin 1994) or both (Bednekoff & Houston 1994; McKillup & McKillup 1994). Nevertheless, mortality caused by environmental conditions during foraging can also represent an important risk for colonies of ants. Foraging activity 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). Although the optimum solution for colony yield is probably an intermediate one (López, Serrano & Acosta 1992), some ants run a high mortality risk by foraging at near-lethal temperatures, as happens with different genera from deserts and other dry areas (*Cataglyphis*, Wehner, Harkness & Schmid-Hempel 1983; Wehner *et al.* 1992; Cerdá & Retana 1997; *Ocymyrmex*, Marsh 1985a,b; *Melophorus*, Christian & Morton 1992).

Mediterranean regions are well known for their great range of temperature fluctuation. 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). In Mediterranean ant communities, activity rhythms of most species directly follow seasonal and daily changes in temperature (Cros, Retana & Cerdá 1997), and activity rhythm and position in the dominance hierarchy are closely related (Cerdá, Retana & Cros 1997). In the period of maximum activity (from late spring to late summer), subordinate species (i.e. species that are at the bottom of the dominance/aggression hierarchy) are active during the day, when conditions are more severe, and this leads them to avoid the competition from dominants (i.e. species that are at the top of the dominance/aggression hierarchy), which are active during the afternoon and the night. In ant communities, it is common to find no marked differences between dominants and subordinates, the foraging distribution of dominant species in relation to temperature being typical of that of other ants (Vepsäläinen & Savolainen 1990; Andersen 1992). Our hypothesis

is that, in Mediterranean communities, subordinates forage at temperatures closer to their critical thermal limits than do dominants. These subordinate species forage during the periods of the day when the risk of mortality is highest, but when they can exploit their main food resources more efficiently. Several questions related to being active at different temperatures are discussed in the present paper:

1. How different are the species of the same community in their foraging temperatures and critical thermal limits?
2. Is there any relationship between the thermal tolerance of each species and several factors, such as diet, body size or role as dominant or subordinate in the dominance hierarchy?
3. Do all species forage under a similar heat mortality risk, or are the species foraging at higher temperatures much closer to their critical thermal limits than the species foraging at lower temperatures?
4. What level of risk is incurred by each species and what are the benefits (measured as the exploitation of food resources) for the species of being active at risk temperatures?

Methods

STUDY SITE

This study was carried out in Canet de Mar (Barcelona, NE Spain) (41°3'N, 2°7'E) at 50 m above sea-level, 750 m from the coastline. It is a savannah-like grassland, one of the most disturbed communities of the original Holm Oak grove coastal ecosystem. Its main plant species are *Hyparrhenia hirta* (L.) and, to a lesser extent, *Foeniculum vulgare* Mill. and *Brachypodium retusum* (Pers.) Beauv. Only very scattered pines (*Pinus pinea* L.) are found in the overstorey stratum (3% of canopy cover). The total area sampled was 2000 m². The climate is of a Mediterranean type. The mean annual temperature within the study area is 16.1 °C, with mean monthly temperatures for January and July averaging 8.5 °C and 24.1 °C, respectively. Rainfall is concentrated in the winter half year (November to April). July and August are the driest months, although there is no severe drought in summer.

The ant community consisted of 13 species. A total of 11 species (two very rare species, *Leptothorax niger* Forel and *Diplorhoptrum* sp., were not included) were considered in this study, i.e. 99.8% of the total ant fauna. Their main biological characteristics are summarized in Table 1.

FIELD OBSERVATIONS

Daily foraging activity of each ant species was recorded, 1–3 days per month throughout the activity season (from March to November). Data were taken each hour for 24 h on every sampling day. Different

Table 1. Biological characteristics of the ant species studied. Worker size: *major workers; **minor workers. Main food resources are indicated in order of importance. Foraging activity rhythms: diurnal (D), twilight (T) and nocturnal (N); s, only diurnal in spring

Species	Worker body length (mm)	Main food resources	Activity rhythm			Month of maximum foraging activity
			D	T	N	
Dolichoderinae						
<i>Tapinoma nigerrimum</i> (Nylander)	2.8–5.1	honeydew, insects	s	+	+	May–June
Myrmicinae						
<i>Pheidole pallidula</i> (Nylander)	3.3–4.9*/1.2–2.6**	insects, seeds		+	+	September
<i>Tetramorium semilaeve</i> André	2.0–3.2	insects, seeds		+	+	June
<i>Messor bouvieri</i> (Bondroit)	4.0–8.5	seeds	+	+		September
<i>Messor capitatus</i> (Latreille)	3.8–13.0	seeds	+	+	+	October
<i>Aphaenogaster senilis</i> Mayr	6.4–7.7	insects, seeds	+			June–July
Formicinae						
<i>Camponotus sylvaticus</i> (Olivier)	5.3–13.2	honeydew, nectar		+	+	August
<i>Camponotus cruentatus</i> Latreille	6.0–14.0	honeydew, nectar	+	+	+	July
<i>Camponotus foreli</i> (Emery)	4.0–9.9	nectar, honeydew	+			July–August
<i>Cataglyphis cursor</i> (Fonscolombe)	4.3–7.2	insects, nectar	+			July
<i>Plagiolepis pygmaea</i> (Latreille)	1.1–2.0	nectar, insects	+			June

sampling methods were used to quantify the above-ground activity of the different species studied:

1. Activity at nest entrances. For species having conspicuous nest entrances (*Cataglyphis cursor* (Fonscolombe), *Camponotus foreli* (Emery), *Camponotus cruentatus* Latreille, *Camponotus sylvaticus* (Olivier), *Aphaenogaster senilis* Mayr, *capitatus* (Latreille)), foraging activity of two nests was monitored by counting, at the nest entrance, the number of workers leaving and entering the nest during the first 10 min of each hour. The sum of entries and exits of each period of time was taken as an activity index. Loaded and unloaded workers arriving at the nest were counted separately to calculate the efficiency of prey collection.
2. Activity at trails. For species forming permanent (*Tapinoma nigerrimum* (Nylander)) or temporary (*Messor bouvieri* (Bondroit)) trails, activity was measured by counting, for 3 min of each hour, the number of workers walking across a marked point at the trails of two colonies.
3. Activity at baits. Baits represent an exceptionally rich food source and were used to establish daily rhythms of species whose nest entrances were not visible (*Pheidole pallidula* (Nylander), *Tetramorium semilaeve* André, *Plagiolepis pygmaea* (Latreille)) because it has been observed that daily activity rhythms measured at the nest entry of various ant species of the study area (Cerdá *et al.* 1988, 1989; Retana *et al.* 1988; Cerdá & Retana 1994) mostly overlapped with those obtained at baits. Five series of six baits were laid randomly over the entire study area on the activity sampling days. Baits were plastic discs with different large food rewards (honey, ham, bacon, sausage, cheese and biscuit) that were attractive to ants and could not be transported in one piece

to the nest by foragers. Each hour, the number of ants of each species feeding at each bait was recorded. The overall number of workers counted each hour at all baits was used as a measurement of external activity of this species.

Together with the hourly measurements of activity, ground surface temperatures in the sun and in the shade were measured with glass-headed thermocouples connected to a Univolt DT-830 digital multimeter.

The position of each ant species in the dominance hierarchy has been determined by analysing interspecific interactions at baits, where species coexisting at the same periods of the day interacted actively. Three different types of interactions were distinguished: (1) expulsion, when one species drove another one away and occupied the bait; (2) escape, when one species was attacked and was forced to abandon the bait (the opposite behaviour of expulsion); and (3) coexistence, when workers of different species occupied the same bait without showing aggressive behaviour. To determine relative dominance, the dominance index of each species was calculated as the percentage of encounters won (i.e. it drove away another species) in all of its interspecific encounters. We are confident that the relationships observed are linear (or transitive) because a clear transitive dominance hierarchy has been suggested for these species in a previous paper (Cerdá *et al.* 1997).

To relate worker size of each species with its thermal tolerance, fresh samples of workers ($n = 50$) were collected. For estimating worker size, two measurements were taken in the laboratory under a stereoscopic microscope: (1) total body length was measured from frons to tip of gaster, with the ant in an extended position; and (2) maximum head width was measured at the interocular line.

LABORATORY TESTS

The critical thermal maximum (CTM) was measured at the laboratory by means of an electric Plactronic Selecta hot plate (J. P. Selecta, Barcelona, Spain) with a 5–200 °C temperature range and 1 °C accuracy. Only foragers of each species, i.e. workers collected outside the nest in the field, were used in these experiments. Twenty individuals of each species were placed on the surface of the hot plate in open containers with Fluon-painted inner walls which prevented ants escaping. Ants were exposed for 10 min to each temperature. The number of ants that began to have muscle spasms and died was noted (modified from Marsh 1985b; Christian & Morton 1992). The temperature of the hot plate was progressively raised at intervals of 2 °C, from 20 °C to 60 °C (depending on the thermal tolerance of each species). After each thermal treatment, individuals were changed to avoid thermal accumulation. The CTM of each species was considered to be the temperature at which at least 50% of workers died or lost muscular co-ordination after 10 min of exposure.

To investigate the relationship between temperature and exposure time in each species, 20 workers were exposed to the CTM and to temperatures 2 °C below and above it. The time each ant took to exhibit signs of muscle spasms and to die was noted. The lethal temperature (LT) of each species was defined as the temperature at which workers took, on average, less than 1 min to die.

DATA ANALYSIS

The relationship between ground surface temperature and external activity of each species was established by dividing the whole range of temperatures registered in the field into 2-°C classes. Considering together the data from all hours of all sampling days, the mean activity value of each species in each temperature class was calculated. The maximal activity temperature of each species was the temperature at which the mean activity value was greatest. The activity temperature range of each species was the difference between the highest and lowest temperatures at which it was active outside the nest. The thermal activity breadth (*sensu* Huey & Stevenson 1979; Huey & Kingsolver 1993), defined as the range of temperatures at which activity was greater than 50% of the activity registered at the maximal activity temperature, was also calculated for each species. In each curve of temperature vs foraging activity, the difference between the lowest and the maximal activity temperature vs the difference between the maximal activity and the highest temperature was recorded.

From the information on worker survival at different temperatures obtained with all species at the hot plate, the temperature at which a worker ant was subjected to mortality risk was defined as the CTM – 2 °C.

Another temperature interval (CTM – 4 °C) was also tested to confirm that the patterns of the analysis were robust. Then, the temperature range of each species was divided into: (1) risk temperatures, those \geq CTM – 2 °C (or CTM – 4 °C) and (2) non-risk temperatures, those $<$ CTM – 2 °C (or CTM – 4 °C). The percentage of foraging activity performed by each species at risk conditions was calculated, for each sampling day and for all sampling days considered together, as:

$$\text{Activity at risk} = (\text{Activity at risk temperatures} / \text{Total activity}) \times 100.$$

Since ants do not forage at 100% efficiency in all environmental conditions, each species should optimize its foraging strategy by balancing the intake of food and the risk of foraging in dangerous conditions. Then, species showing different risk levels are also expected to show different patterns of food exploitation at different environmental conditions (= different temperatures). To evaluate the potential benefits obtained by each species foraging at different temperatures, the foraging efficiency (FE) of each species each sampling hour was calculated, and compared with the surface temperature during each hour. According to the foraging strategy followed by the different ant species, FE was estimated by two different methods: (1) the FE of species that search and transport prey individually (e.g. *C. cursor* or *A. senilis*) was estimated as the percentage of loaded workers related to the total number of workers returning to the nest during this sampling period: FE = (number of loaded workers/total number of workers) \times 100; and (2) the FE of species that recruit large numbers of workers to food resources (e.g. *T. nigerrimum*, *T. semilaeve* or *P. pallidula*) was estimated each hour as the number of baits occupied by each species related to the maximum number of baits it occupied during any hour of this sampling day: FE = (number of occupied baits/maximum number of occupied baits) \times 100.

A comparative analysis by independent contrasts (CAIC, version 2.0.0; Purvis & Rambaut 1995) was performed in order to test the consistency of correlations among variables using individual species values and phylogenetically independent contrast values (Harvey & Pagel 1991; Harvey 1996; Ricklefs & Starck 1996). The 11 species studied are distributed among three subfamilies in the family Formicidae and only two genera were represented by more than one species (Table 1). A working phylogeny of these was reconstructed according to Baroni-Urbani, Bolton & Ward (1992). Because branch lengths in the Formicidae tree are unknown, Grafen's (1989) method was employed to assign arbitrary lengths to the branches of the tree (the 'age' of a node was taken as the number of branch tips descended from that node minus one). The correlations among contrasts were examined for CTM, maximum activity temperature

and difference between CTM and maximum activity temperature. Associations between standardized contrasts of variables were tested: correlation coefficients were computed between contrasts and all correlations were forced through the origin. Since all contrast correlations were statistically significant ($P < 0.05$) and consistent with those of original variables, species are accepted as independent points and therefore all reported correlation coefficients (r) and P -values refer hereafter to the original variables (see Ricklefs & Starck 1996 for other examples of consistent patterns among species values and contrast values).

Results

FORAGING ACTIVITY OF THE DIFFERENT ANT SPECIES RELATED TO TEMPERATURE

The species studied differed in their thermal features, both in maximal activity temperatures and in foraging temperature limits (Table 2). The maximal activity temperature varied from the 22 °C of *M. capitatus* and *P. pygmaea* to the 48 °C of *C. cursor*. Although lowest and highest foraging temperatures of each species were considerably different, the activity temperature range (difference between the highest and the lowest foraging temperature) was quite similar and, with the exception of some species (*C. sylvaticus*, *P. pygmaea*), ranged between 30 and 38 °C.

These interspecific differences were evident not only in the thermal limits, but also in the general shape of the specific curves of temperature vs foraging activity. Figure 1 shows two extreme curve shapes and an intermediate one. The species with a low maximal activity temperature (e.g. *T. semilaeve* in Fig. 1) showed steep increment to this value, and a slow decrease to the upper limit of the temperature range. On the other hand, the species with a high maximal activity temperature (e.g. *C. cursor* in Fig. 1) showed a slow increment to this value, and a steep decrease to the maximal foraging temperature. There were other

species with intermediate maximal activity temperatures, and also with intermediate-shaped curves (e.g. *M. bouvieri* in Fig. 1). A gradient of curve shapes was shown by the significant negative relationship ($r = 0.78$, $P = 0.005$) of the difference between the lowest and maximal activity temperature vs the difference between the maximal activity and the highest temperature of each species.

CRITICAL THERMAL LIMITS

CTM varied from 40 (*P. pallidula*, *T. semilaeve*, *P. pygmaea*) to 50 °C (*C. cursor*), a narrower range than that of the maximal activity temperature (which varied from 22 °C to 48 °C, Table 2). In most cases, the CTM was lower than the highest foraging temperature (column CTM – T_{high} of Table 2). *Camponotus sylvaticus* was the only exception because its activity rhythms were mainly conditioned by light levels: independently of the outside temperatures, workers of this species stayed at the nest entrance until night, when they started their foraging activity outside the nest. The presence of workers of the other species outside the nest at temperatures higher than their physiological limits can be explained by the existence in the field of partial thermal refuges: foragers avoided being exposed to critical temperatures for a long time by resting in the shade or by climbing on plants for a few seconds.

Lethal temperature (LT) of species foraging at low temperatures was 2 °C higher than CTM, but this difference increased to 4 °C and even 6 °C in species foraging at increasingly high temperatures (Table 2). In all species, the length of time required to produce a state of partial paralysis decreased with increases in temperature, following a significant exponential fit from CTM – 2 °C to CTM + 2 °C (Fig. 2). The slope of the regression line between temperature and mean time of survival (in log scale) decreased with CTM (slope = $-0.1 \times \text{CTM} + 6.0$, $r = 0.93$, $P = 0.001$). This

Table 2. Main thermal characteristics of the different ant species studied. MAT, maximal activity temperature of foraging. Activity temperature range: temperature limits (minimum temperature–maximum temperature) of foraging activity of each species. Thermal activity breadth: limits of temperature within which foraging activity is greater than 50% of the activity registered at the MAT. CTM, critical thermal maximum; LT, lethal temperature. T_{high} , highest temperature of foraging activity

Species	MAT (°C)	Thermal tolerance (°C)	Thermal activity breadth (°C)	CTM (°C)	LT (°C)	LT–CTM (°C)	CTM– T_{high} (°C)	CTM–MAT (°C)
<i>P. pygmaea</i>	22	10–36	14–28	40	42	2	4	18
<i>M. capitatus</i>	22	10–46	12–28	44	46	2	–2	22
<i>T. semilaeve</i>	24	12–46	16–30	40	42	2	–6	16
<i>T. nigerrimum</i>	24	10–46	14–36	42	44	2	–4	18
<i>P. pallidula</i>	24	10–46	14–32	40	42	2	–6	16
<i>C. sylvaticus</i>	28	12–36	16–32	46	48	2	10	18
<i>M. bouvieri</i>	30	14–46	24–40	44	46	2	–2	14
<i>C. cruentatus</i>	40	14–48	24–44	48	52	4	0	8
<i>A. senilis</i>	42	16–50	28–48	46	50	4	–4	4
<i>C. foreli</i>	44	16–52	32–46	48	52	4	–4	4
<i>C. cursor</i>	48	16–54	42–52	50	56	6	–4	2

means that the species that tolerated higher critical temperatures (e.g. *C. cursor* in Fig. 2) also resisted greater exposure times at these temperatures than less tolerant species (e.g. *T. nigerrimum* in Fig. 2).

A high negative correlation ($r = 0.96$, $P = 0.0001$) was obtained between the maximal activity temperature of each species and the difference between the CTM and the maximal activity temperature (Fig. 3): the species foraging at higher temperatures were closer to their critical thermal limits than the species

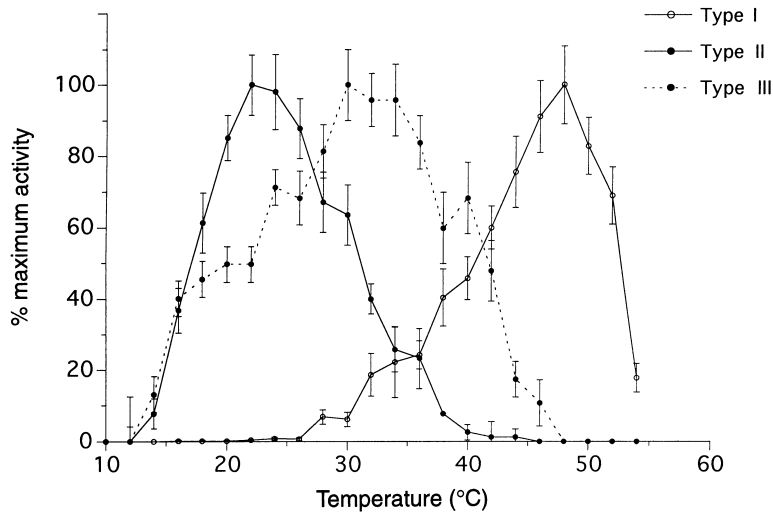


Fig. 1. Representative models of curve shape described for the relationship between ground surface temperature ($^{\circ}\text{C}$) and foraging activity: type I, *Tetramorium semi-laeve*; type II, *Cataglyphis cursor*; and type III, *Messor bouvieri*. Each point represents the mean (\pm SE) activity value of all cases with the same temperature (in 2°C classes) from all hours of all sampling days. Data of the different species have been standardized by defining the maximum mean activity value observed, which corresponds to the maximal activity temperature, as 100% of activity.

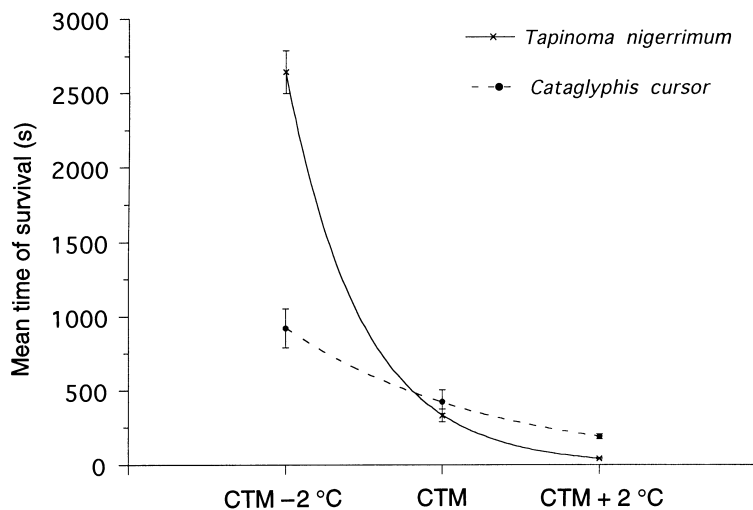


Fig. 2. Mean survival time (\pm SE) of workers of two studied species (*Tapinoma nigerrimum* and *Cataglyphis cursor*) at the critical thermal maximum (CTM) and at temperatures 2°C lower and higher than CTM. Data of each species have been fitted to an exponential function (broken line for *Tapinoma nigerrimum*: $y = 20\,690 \exp(-2.06x)$, Pearson's $r = 0.999$, $P = 0.001$; and unbroken line for *Cataglyphis cursor* $y = 2034.2 \exp(-0.79x)$, $r = 0.999$, $P = 0.001$).

foraging at lower temperatures. A significant relationship did not exist between the mean worker size of each species and either the maximal activity temperature or the highest temperature of foraging (Pearson's r coefficient not significant, $P > 0.15$ and $P > 0.60$, respectively). Nevertheless, there was a significant positive relationship between the mean size of each species and the CTM it tolerated ($\text{CTM} = 0.9 \times \text{Size} + 39.1$, $r = 0.75$, $P = 0.008$).

FORAGING ACTIVITY AT RISK TEMPERATURES

To evaluate the risk conditions assumed by foragers in the field when searching for and carrying food to the nest at different hourly temperatures, the relationship between ecological (foraging activity) and physiological (critical thermal limits) features of each ant species was determined. The risk of mortality of each species (i.e. the percentage of its foraging activity performed at temperatures higher than the $\text{CTM} - 2^{\circ}\text{C}$, see Methods) for all sampling days considered together is represented in Fig. 4. Only three species (all of them subordinate species, see Table 3) had an overall value of activity at risk conditions higher than 10% of their total foraging activity (the same pattern was obtained when $\text{CTM} - 4^{\circ}\text{C}$ was used as risk temperature: the same three subordinate species had risk values greater than 25%, and the remainder had values lower than 10%). Results were even more remarkable when daily values were considered: the already-mentioned species that foraged at risk conditions showed maximum values of risk activity over 50% of total activity, on some days these values accounting for up to 70% and 80% (*A. senilis* and *C. cursor*, respectively). There was a significant negative correlation between the dominance index (DI) of each species and the percentage of foraging activity it performed at risk conditions ($\text{Risk activity} = -0.3 \times \text{DI} + 18.4$, $r = 0.66$, $P = 0.027$).

CHANGES IN THE FORAGING PERFORMANCE OF ANTS AT DIFFERENT TEMPERATURES

Among species studied, the relationship between temperature and foraging efficiency did not follow a single pattern, but rather two very opposite ones:

1. One pattern was observed in subordinate species in the dominance hierarchy, which usually foraged at temperatures close to their physiological thermal limits (type II curve, see Fig. 1 and Table 2). These species, represented by *A. senilis* (Fig. 5a) and *C. cursor* (Fig. 5b), increased their foraging efficiency (FE) with ground temperature (T) (linear regression, $\text{FE} = 0.48 \times T + 15.88$, $r = 0.73$, and $\text{FE} = 0.66 \times T - 10.96$, $r = 0.78$, respectively; $P < 0.0005$ in both cases), i.e. there was a greater percentage of loaded foragers returning to the nest at higher temperatures than at lower ones.

2. A different pattern was observed in dominant species in the dominance hierarchy, whose foraging strategy was mainly based on the recruitment of large numbers of workers and aggressive defence of food resources at temperatures far from their physiological thermal limits (type I curve, see Fig. 1 and Table 2). For these species, represented by *T. nigerimum* (Fig. 5c) and *P. pallidula* (Fig. 5d), and after an initial more or less evident increase according to the species, foraging efficiency decreased when temperature increased.

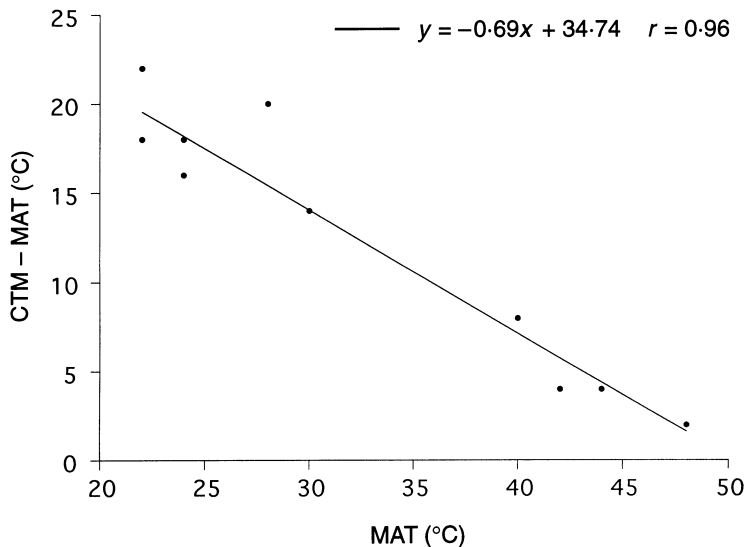


Fig. 3. Relationship between the maximal activity temperature (MAT, °C) of each species and the difference between its critical thermal maximum (CTM) and its MAT (°C).

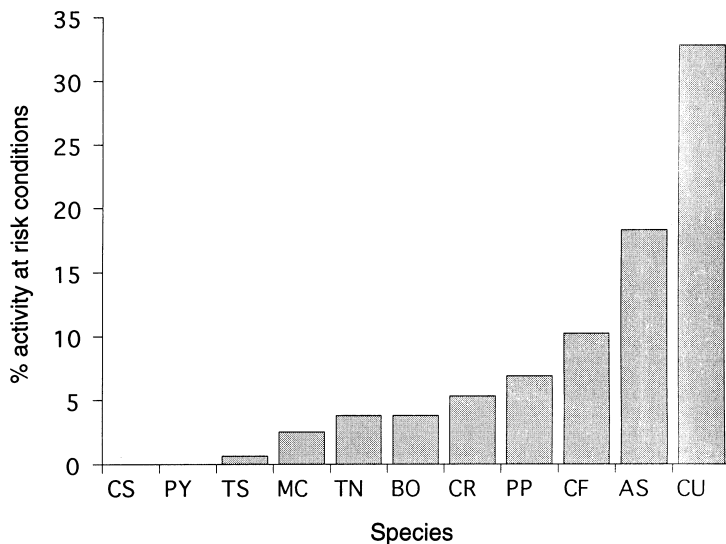


Fig. 4. Percentage of the foraging activity of each species performed at risk conditions (i.e. at temperatures higher than the CTM - 2 °C), calculated as: Activity at risk = (Activity at risk temperatures/Total activity) × 100. Each bar represents the overall value of each species for all sampling days considered together. Abbreviations of species are as follows: CS, *Camponotus sylvaticus*; PY, *Plagiolepis pygmaea*; TS, *Tetramorium semilaeve*; MC, *Messor capitatus*; TN, *Tapinoma nigerrimum*; BO, *Messor bouvieri*; CR, *Camponotus cruentatus*; PP, *Pheidole pallidula*; CF, *Camponotus foreli*; AS, *Aphaenogaster senilis*; CU: *Cataglyphis cursor*.

Discussion

Temperature extremes are considered to be the most serious form of environmental stress to ant species in dry regions (Whitford, Kay & Schumaker 1975; Whitford, Deprée & Johnson 1980; MacKay *et al.* 1986; Cloudsley-Thompson 1989; Lighton & Feener 1989). In the studied Mediterranean communities, activity of ant species is strongly affected by temperature. However, important differences in the temperatures at which each species starts, peaks and stops above-ground activity have been found. The shape of the curve of temperature–foraging activity shows clearly different patterns between heat-intolerant and heat-tolerant species, and leads us to distinguish two extreme foraging strategies in relation to temperature for Mediterranean ant species:

1. Heat-intolerant ant species are generally active during the daytime in early spring and autumn, nocturnal from late spring to late summer, and crepuscular during seasonal transitions. These nocturnally active species adopt a strategy of ‘minithermy’ by foraging when temperatures are much lower than their CTM. They have low maximal activity temperatures and display a type I curve (Fig. 1), with a steep increase and a slow decrease from this value.

2. On the other hand, heat-tolerant ant species of these communities are active during the daytime in all seasons, showing the highest activity peak in summer, when few other species are able to forage during the daytime. These diurnally active species adopt a strategy of ‘maxithermy’ by foraging when temperatures are closer to their CTM. They have high maximal activity temperatures and display a type II curve (Fig. 1), with a slow increase and a steep decrease from this value.

These two strategies, with a gradient of intermediate situations (represented by the type III curve of Fig. 1), have been intuitively suggested by other authors when describing thermal behaviour and activity patterns of sympatric ant species in other arid areas: Heatwole & Muir (1989) and Heatwole & Harrington (1989) observe these two extremes in the pre-Saharan steppe of Tunisia, with two *Cataglyphis* species foraging at the highest temperatures available, even in summer, and other species (*Camponotus martensi*, *Pheidole megacephala* and *Monomorium salomonis*, among others) which always operate near the lower range of available environmental temperatures. Each of these strategies, in terms of mortality risk, can be ascribed to each of the two usual risk strategies described in the optimal foraging literature (Caraco *et al.* 1980, 1990; Stephens & Krebs 1986). Heat-intolerant species behave as risk-averse species (*sensu* Stephens & Krebs 1986), foraging at temperatures very far from their critical thermal limits and avoiding the risk of mortality by heat. On the other hand, heat-tolerant species behave as risk-prone species (*sensu* Stephens

1. & Krebs 1986), foraging very near their critical thermal limits and assuming a high heat mortality risk.

What do these species that assume high mortality risks have in common? From the review of the literature related to these topics, four possible factors affecting the thermal tolerance range of ant species would appear to be the most relevant: phylogeny, dietary spectrum, worker size and position in the dominance hierarchy of the community.

Table 3. Dominance indices of ant species at food resources. Those species that are not significantly different, based on χ^2 contingency tests using all the observations of expulsion vs coexistence + escape interactions for each species, share a common letter

Species	Number of interactions	Dominance index
<i>Tetramorium semilaeve</i>	78	60.2 ^a
<i>Camponotus sylvaticus</i>	82	56.1 ^a
<i>Camponotus cruentatus</i>	50	56.0 ^{ab}
<i>Pheidole pallidula</i>	523	48.2 ^{ab}
<i>Tapinoma nigerrimum</i>	240	41.1 ^{bc}
<i>Messor capitatus</i>	125	40.8 ^{bc}
<i>Messor bouvieri</i>	73	28.8 ^{cd}
<i>Camponotus foreli</i>	115	26.1 ^{de}
<i>Aphaenogaster senilis</i>	637	18.5 ^e
<i>Plagiolepis pygmaea</i>	88	2.3 ^f
<i>Cataglyphis cursor</i>	111	0.0 ^f

The first option is that the differences in the thermal traits of ant species fall along phylogenetic lines. A common phylogeny would lead to similar physiological features and therefore to a similar thermal biology. Nevertheless, foraging temperatures and critical thermal limits are not linked to phylogenetic relationships, as it has been shown in the Methods section. Heat-tolerant species include both formicine (*C. cursor*; *C. foreli*, *C. cruentatus*) and myrmicine species (*A. senilis*), while heat-intolerant species also include species from different subfamilies: formicines (*P. pygmaea*), myrmicines (*P. pallidula*, *T. semilaeve*) and dolichoderines (*T. nigerrimum*).

Secondly, since heat tolerance has evolved in very specialized genera from hot deserts (Marsh 1985a,b; Christian & Morton 1992; Wehner *et al.* 1992), different authors (Wehner 1987; Heinrich 1993) suggest that the reason diverse ants choose to be active under what appear to be dangerous conditions (many of the thermophilic species forage at soil surface temperatures of up to 70°C) is related to diet: they are all scavengers feeding on arthropods that have died from heat and desiccation (this idea of maximizing prey availability by foraging at high temperatures has also been suggested for other insects, such as predatory tiger beetles; see Dreisig 1980). This is probably true

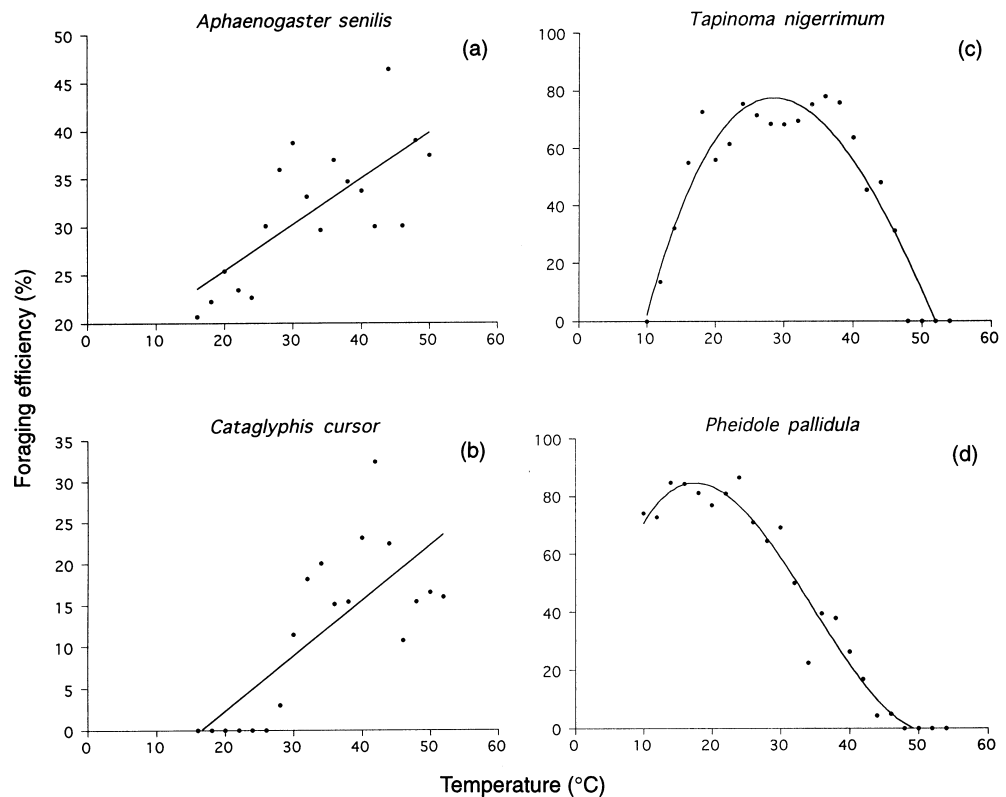


Fig. 5. Relationship between ground surface temperature and foraging efficiency of: (a) *Aphaenogaster senilis*; (b) *Cataglyphis cursor*; (c) *Tapinoma nigerrimum*; and (d) *Pheidole pallidula*. The foraging efficiency of *C. cursor* and *A. senilis* has been estimated as the percentage of loaded workers related to the total number of workers returning to the nest. The foraging efficiency of *T. nigerrimum* and *P. pallidula* has been estimated each hour as the percentage of baits occupied by each species related to the maximum number of baits it occupied during any hour of that sampling day. Each dot represents the mean of all cases with the same temperature (in 2-°C classes) from all hours of all sampling days.

for the most specialized heat-resistant ant genera, but not when the whole community is analysed: in this study we demonstrate that there is a gradient of heat-tolerance among ant species of the same community, and that the most resistant ones are scavenger (*C. cursor*), omnivorous (*A. senilis*) and nectar- and honeydew-eating species (*C. foreli*, *C. cruentatus*).

Thirdly, other studies (see review in Kaspari 1993) state that in ants heat tolerance is related to body size: desiccation (Hood & Tschinkel 1990; Kaspari 1993), maximum foraging time (Lighton & Feener 1989) and foraging temperature (Rissing & Pollock 1984) increase with body size of species. In this study, a conclusive relationship between worker size and foraging temperatures has not been found: a positive relationship between mean specific body size and CTM has been obtained, although a similar relationship between body size and maximal activity temperature is not significant, i.e. the largest ants are more resistant, but they do not necessarily forage during the hottest periods of the day.

Finally, other authors (Fellers 1989; Cros *et al.* 1997) have suggested that species forage at different temperatures according to their position in the dominance rank, with dominant species being limited by temperature, while subordinate species show a wider tolerance. In this study, there was a negative relationship between the dominance index and the percentage of activity performed at risk conditions: dominant species (such as *P. pallidula*, *T. semilaeve* or *T. nigerimum*) forage at low temperatures quite distant from their critical thermal limits, while most subordinate species (such as *C. cursor*, *A. senilis* or *C. foreli*) foraged at high temperatures very close to their physiological thermal limits.

These ideas lead us to discuss the optimization of the risk level assumed by each species. Why do risk-prone species forage at temperatures far from their CTM while risk-averse species forage at temperatures close to it? Until now, the optimization of risk in ants has been related almost exclusively to predation (Nonacs & Dill 1988, 1990; Fewell 1990; Nonacs 1990). Mortality rates of foragers are unlikely to be homogeneously distributed in space and time because some areas and some periods of the day should be safer than others. Although the ability to reduce mortality risk while foraging may be a factor that favours insect sociality in general (Nonacs & Dill 1990), in certain cases risk is ignored or at least tolerated when food is good, probably because the potential colony growth gains offset the loss of a few foragers (Nonacs 1990; Nonacs & Dill 1990). 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 & Dill 1990). There may be situations in nature in which it is advantageous to risk near-lethal

temperatures to maximize foraging success. In the Mediterranean communities studied, dominant species forage very rarely at temperatures close to their critical thermal limits, while subordinate species forage more frequently at risk temperatures. Subordinate, heat-tolerant ant species follow a risk-prone strategy by foraging at nearly lethal environmental conditions, but they benefit from this strategy by having a better foraging performance. The foraging efficiency of subordinates increases when temperature increases (see Fig. 5; also Marsh 1985a), while that of dominants decreases with temperature. The wide range of thermal niches found, on a daily basis, in Mediterranean habitats may be one reason why Mediterranean ant faunas can be so diverse in the face of limited diversity in vegetation and habitat structure. That is, more species can be packed into a long thermal axis than into a shorter one. As Heatwole & Muir (1989) point out, there may be room for thermophilic, thermotolerant and cryophilic species in the same habitat.

Acknowledgements

We are very grateful to Profs Rüdiger Wehner and Raymond Huey for their helpful comments on an earlier draft of the manuscript, to Dr Pedro Jordano for his encouragement, ideas and helpful discussions on comparative methods, to Valentín Cavia ('Looking-valleys') and Nicole Salini for their help in laboratory measurements, to Fernandito García del Pino for allowing us to use the hot plate, to Jordi Bosch and Dolors Company for their help in the field work, to Paqui Ruano and Alberto Tinaut for providing us with some references and the ant phylogeny tree, and to Rocio Requerey for bibliographic assistance. This research was partly funded by DGICYT project PB91-0114 to Xim Cerdá.

References

- Abrams, P.A. (1991) Life history and the relationship between food availability and foraging effort. *Ecology* **72**, 1242–1252.
- Andersen, A.N. (1992) Regulation of 'momentary' diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. *American Naturalist* **140**, 401–420.
- Baroni-Urbani, C., Bolton, B. & Ward, P. (1992) The internal phylogeny of ants (Hymenoptera: Formicidae). *Systematic Entomology* **17**, 301–329.
- Bednekoff, P.A. & Houston, A.I. (1994) Dynamic models of mass-dependent predation, risk-sensitive foraging, and premigratory fattening in birds. *Ecology* **75**, 1131–1140.
- Briese, D.T. & Macauley, B.J. (1980) Temporal structure of an ant community in semi-arid Australia. *Australian Journal of Ecology* **5**, 121–134.
- Caraco, T., Martindale, S. & Whittam, T.S. (1980) An empirical demonstration of risk-sensitive foraging preferences. *Animal Behaviour* **28**, 820–831.
- Caraco, T., Blanckenhorn, W.U., Gregory, G.M., Newman, J.A., Recer, G.M. & Zwicker, S.M. (1990) Risk-sensitivity: ambient temperature affects foraging choice. *Animal Behaviour* **39**, 338–345.

- Cartar, R.W. (1991) Colony energy requirements affect response to predation risk in foraging bumble bees. *Ethology* **87**, 90–96.
- Cerdá, X., Bosch, J., Alsina, A. & Retana, J. (1988) Dietary spectrum and activity patterns of *Aphaenogaster senilis* (Hymenoptera: Formicidae). *Annales de la Société entomologique de France* **24**, 69–75.
- Cerdá, X. & Retana, J. (1994) Food exploitation patterns of two sympatric seed-harvesting ants *Messor bouvieri* (Bond.) and *Messor capitatus* (Latr.) (Hymenoptera: Formicidae) from Spain. *Journal of Applied Entomology* **117**, 268–277.
- Cerdá, X. & Retana, J. (1997) Links between worker polymorphism and thermal biology in a thermophilic ant species. *Oikos* **78**, 467–474.
- Cerdá, X., Retana, J., Bosch, J. & Alsina, A. (1989) Daily foraging activity and food collection of the thermophilic ant *Cataglyphis cursor* (Hymenoptera, Formicidae). *Vie et Milieu* **39**, 207–212.
- Cerdá, X., Retana, J. & Cros, S. (1997) Thermal disruption of transitive hierarchies in Mediterranean ant communities. *Journal of Animal Ecology* **66**, 363–374.
- Christian, K.A. & Morton, S.R. (1992) Extreme thermophilia in a Central Australian ant, *Melophorus bagoti*. *Physiological Zoology* **65**, 885–905.
- Cloudsley-Thompson, J.L. (1989) Temperature and activity of ants and other insects in Central Australia. *Journal of Arid Environments* **16**, 185–192.
- Cokendolpher, J.C. & Phillips, S.A. Jr. (1990) Critical thermal limits and locomotor activity of the red imported fire ant (Hymenoptera: Formicidae). *Environmental Entomology* **19**, 878–881.
- Cros, S., Retana, J. & Cerdá, X. (1997) Spatial and temporal variations in the activity patterns of Mediterranean ant communities. *Ecoscience* **4**, 269–278.
- De Bie, G. & Hewitt, P.H. (1990) Thermal responses of the semi-arid zone ants *Ocymyrmex weitzackeri* (Emery) and *Anoplolepis custodiens* (Smith). *Journal of the Entomological Society of South Africa* **53**, 65–73.
- Dreising, H. (1980) Daily activity, thermoregulation and water loss in the tiger beetle *Cicindela hybrida*. *Oecologia* **44**, 376–389.
- Dreising, H. (1985) A time budget model of thermoregulation in shuttling ectotherms. *Journal of Arid Environments* **8**, 191–205.
- Fellers, J.H. (1989) Daily and seasonal activity in woodland ants. *Oecologia* **78**, 69–76.
- Fewell, J.H. (1990) Directional fidelity as a foraging constraint in the western harvester ant, *Pogonomyrmex occidentalis*. *Oecologia* **82**, 45–51.
- Grafen, A. (1989) The phylogenetic regression. *Philosophical Transactions of the Royal Society of London (Biology)* **326**, 119–156.
- Ha, J.C. (1991) Risk-sensitive foraging: the role of ambient temperature and foraging time. *Animal Behaviour* **41**, 528–529.
- Harvey, P.H. (1996) Phylogenies for ecologists. *Journal of Animal Ecology* **65**, 255–263.
- Harvey, P.H. & Pagel, M.D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- Heatwole, H. & Harrington, S. (1989) Heat tolerances of some ants and beetles from the pre-Saharan steppe of Tunisia. *Journal of Arid Environments* **16**, 69–77.
- Heatwole, H. & Muir, R. (1989) Seasonal and daily activity of ants in the pre-Saharan steppe of Tunisia. *Journal of Arid Environments* **16**, 49–67.
- Heinrich, B. (1993) *The Hot-blooded Insects. Strategies and Mechanisms of Thermoregulation*. Springer Verlag, Berlin.
- Herbers, J.M. (1985) Seasonal structuring of a north temperate ant community. *Insectes Sociaux* **32**, 224–240.
- Herbers, J.M. (1989) Community structure in north temperate ants: temporal and spatial variation. *Oecologia* **81**, 201–211.
- Hertz, P.E., Huey, R.B. & Garland, T. Jr. (1988) Time budgets, thermoregulation, and maximal locomotor performance: are reptiles olympians or boy scouts? *American Zoologist* **28**, 927–938.
- Hood, W.G. & Tschinkel, W.R. (1990) Desiccation resistance in arboreal and terrestrial ants. *Physiological Entomology* **15**, 23–35.
- Huey, R.B. & Kingsolver, J.G. (1989) Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology and Evolution* **4**, 131–135.
- Huey, R.B. & Kingsolver, J.G. (1993) Evolution of resistance to high temperature in ectotherms. *American Naturalist* **142**, S21–S46.
- Huey, R.B. & Stevenson, R.D. (1979) Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *American Zoologist* **19**, 357–366.
- Hughes, J.J., Ward, D. & Perrin, M.R. (1994) Predation risk and competition affect habitat selection and activity of Namib desert gerbils. *Ecology* **75**, 1397–1405.
- Kaspari, M. (1993) Body size and microclimate use in neotropical granivorous ants. *Oecologia* **96**, 500–507.
- Krebs, J.R. & Kacelnik, A. (1991) Decision-making. *Behavioural ecology: an evolutionary approach* (eds J. R. Krebs & N. B. Davis), pp. 105–136. Blackwell Scientific Publications, Oxford.
- Lighton, J.R.B. & Feener, D.H. Jr. (1989) Water-loss rate and cuticular permeability in foragers of the desert ant *Pogonomyrmex rugosus*. *Physiological Zoology* **62**, 1232–1256.
- Lima, S.L. & Dill, L.M. (1990) Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**, 619–640.
- Lima, S.L., Valone, T.J. & Caraco, T. (1985) Foraging-efficiency-predation-risk tradeoff in the grey squirrel. *Animal Behaviour* **33**, 155–165.
- López, F., Serrano, J.M. & Acosta, F. (1992) Temperature-vegetation structure interaction: The effect on the activity of the ant. *Messor barbarus* L. *Vegetatio* **99–100**, 119–128.
- Lynch, J.F. (1981) Seasonal, successional and segregation in a Maryland ant community. *Oikos* **37**, 183–198.
- Lynch, J.F., Balinsky, E.C. & Vail, S.G. (1980) Foraging patterns in three sympatric forest ant species, *Prenolepis imparis*, *Paratrechina melanderi*, and *Aphaenogaster rudis* (Hymenoptera: Formicidae). *Ecological Entomology* **5**, 353–371.
- Lynch, J.F., Johnson, A.K. & Balinsky, E.C. (1988) Spatial and temporal variation in the abundance and diversity of ants (Hymenoptera Formicidae) in the soil and litter layers of a Maryland forest. *American Midland Naturalist* **119**, 31–44.
- MacKay, W.P., Silva, S., Lightfoot, D.C., Inez-Pagani, M., Whitford, W.G. (1986) Effect of increased soil moisture and reduced soil temperature on a desert soil arthropod community. *American Midland Naturalist* **116**, 45–56.
- Marsh, A.C. (1985a) Microclimatic factors influencing foraging patterns and success of the thermophilic desert ant, *Ocymyrmex barbiger*. *Insectes Sociaux* **32**, 286–296.
- Marsh, A.C. (1985b) Thermal responses and temperature tolerance in a diurnal desert ant, *Ocymyrmex barbiger*. *Physiological Zoology* **58**, 629–636.
- Marsh, A.C. (1988) Activity patterns of some Namib desert ants. *Journal of Arid Environments* **14**, 61–73.
- McKillup, S.C. & McKillup, R.V. (1994) The decision to

- feed by a scavenger in relation to the risks of predation and starvation. *Oecologia* **97**, 41–48.
- Nonacs, P. (1990) Death in the distance: mortality risk as information for foraging ants. *Behaviour* **112**, 23–35.
- Nonacs, P. & Dill, L.M. (1988) Foraging response of the ant *Lasius pallitarsis* to food sources with associated mortality risk. *Insectes Sociaux* **35**, 293–303.
- Nonacs, P. & Dill, L.M. (1990) Mortality risk vs. food quality trade-off in a common currency: ant patch preferences. *Ecology* **71**, 1886–1892.
- O'Neill, K.M. & Kemp, W.P. (1990) Worker response to thermal constraints in the ant *Formica obscuripes* (Hymenoptera: Formicidae). *Journal of Thermal Biology* **15**, 133–140.
- Purvis, A. & Rambaut, A. (1995) Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer Applications in the Biosciences* **11**, 247–251.
- Real, L.A. & Caraco, T. (1986) Risk and foraging in stochastic environments: theory and evidence. *Annual Review of Ecology and Systematics* **17**, 371–390.
- Retana, J., Cerdá, X., Alsina, A. & Bosch, J. (1988) Field observations of the ant *Camponotus sylvaticus* (Hym: Formicidae): diet and activity patterns. *Acta Oecologica Oecologia Generalis* **9**, 101–109.
- Ricklefs, R.E. & Starck, J.M. (1996) Applications of phylogenetically independent contrasts: a mixed progress report. *Oikos* **77**, 167–172.
- Riechert, S.E. (1991) Prey abundance vs. diet breadth in a spider test system. *Evolutionary Ecology* **5**, 327–338.
- Rissing, S.W. & Pollock, G.B. (1984) Worker size variability and foraging efficiency in *Veromessor pergandei* (Hym.: Formicidae). *Behavioural Ecology and Sociobiology* **15**, 121–126.
- Samways, M.J. (1990) Species temporal variability: epigeic ant assemblages and management for abundance and scarcity. *Oecologia* **84**, 482–490.
- Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton.
- Vepsäläinen, K. & Savolainen, R. (1990) The effect of interference by formicine ants on the foraging of *Myrmica*. *Journal of Animal Ecology* **59**, 327–335.
- Wehner, R. (1987) Spatial organization of foraging behavior in individually searching desert ants, *Cataglyphis* (Sahara desert) and *Ocymyrmex* (Namibia desert). *From Individual to Collective Behavior in Social Insects* (eds J. M. Pasteels & J. L. Deneubourg), pp. 15–42. Birkhäuser Verlag, Basel.
- Wehner, R., Harkness, R.D. & Schmid-Hempel, P. (1983) *Foraging Strategies in Individually Searching Ants, Cataglyphis bicolor* (Hymenoptera: Formicidae). Gustav Fischer Verlag, Stuttgart.
- Wehner, R., Marsh, A.C. & Wehner, S. (1992) Desert ants on a thermal tightrope. *Nature* **357**, 586–587.
- Whitford, W.G., Kay, C.A. & Schumaker, A.M. (1975) Water loss in Chihuahuan desert ants. *Physiological Zoology* **48**, 390–397.
- Whitford, W.G., Deprée, E. & Johnson, P. (1980) Foraging ecology of two Chihuahuan desert ant species: *Novomessor cockerelli* and *Novomessor albisetosus*. *Insectes Sociaux* **27**, 148–156.