# ORIGINAL ARTICLE

Ignacio Fernández-Escudero · Alberto Tinaut

# Heat-cold dialectic in the activity of *Proformica longiseta*, a thermophilous ant inhabiting a high mountain (Sierra Nevada, Spain)

**Abstract** The activity of the thermophilous ant *Proformica longiseta* has been studied in a Mediterranean high-mountain environment. An analysis has been made of the biotic and abiotic variables involved, the location of and conditions surrounding the activity, as well as the strategies used by the ant to remain active at high temperatures. The results of this study indicate that the maximum activity occurs during the middle hours of the day and that the variable which most influences daily activity is temperature, especially at the soil surface. With respect to the biotic variables, the availability of food and the demand for food by the larvae strongly correlate with activity. The time outside the nest is usually spent in vegetation searching for food. This activity continues even when the temperature of the soil surface exceeds 58°C. To tolerate these temperatures, the ant not only has a high resistance to heat (critical thermal maximum = 51.1°C), but also increases the speed of its movements and resorts to thermal refuges. The present work contributes data on the biology of this highly thermophilous species, which is also capable of tolerating a long, hard winter and then developing within a short vegetative period.

**Key words** High mountain · Activity · Temperature · Resistance to heat · Ants

## Introduction

The activity pattern of ant species arises from the interaction of various factors (Heatwole and Muir 1989). In some cases, "ambient conditions" are held to be the general factors responsible for this pattern (Ayre 1958;

I. Fernández-Escudero (✉)[1] · A. Tinaut
Departamento de Biología Animal y Ecología,
Facultad de Ciencias, Universidad de Granada, E-18071 Granada,
Spain

*Present address*:
[1] Department of Genetics, Uppsala Genetic Center,
University of Uppsala, Box 7003, S-75007 Uppsala, Sweden

Cerdá and Retana 1988; Fellers 1989; North 1993) and, in other cases, temperature (Harkness 1977; Hölldobler and Taylor 1983; Curtis 1984a; Cloudsley-Thompson 1989) or light intensity (Gano and Rogers 1983; Rosengren and Fortelius 1986; Cerdá and Retana 1989). Besides these factors, which might be the most obvious ones, biotic factors may emerge, superimposed over them, which may control the rhythm of the activity. These latter factors include: fluctuation in food availability (Whittford and Etterschank 1975; Cros et al. 1992); biological cycle and larval presence (Bosch et al. 1987; Cros et al. 1992); competition or conflict with simultaneously foraging species (Bernstein 1979; Retana et al. 1988); interference of myrmecophagous (anteaters) species (Mehlop and Scott 1983); and compromises between predator pressure and heat stress (Wehner et al. 1992).

Most of these studies have focused on arid or desert areas but not at high altitude, as in the present paper. Mountain biotopes differ markedly from low arid or desert areas, primarily because sharp decreases in atmospheric pressure set in motion a series of peculiarities. The principal characteristic, the reduction in dust and haze particles, results in lower air humidity and therefore increased insulation and radiation. All of these factors exert considerable impact on the ecology, morphology and physiology of alpine fauna, particularly arthropods (Mani 1990; Sømme and Block 1991).

The Mediterranean mountain is unique among high-altitude biotopes because its latitudinal position increases total radiation and decreases air humidity as well as rainfall. This creates a cold, arid environment with special characteristics (Table 1) such as: (1) a range of daily temperature variations exceeding that of more northerly and wetter mountains (the Alps); (2) a rainfall rate during the vegetative period (May–September) similar to that of arid environments. Furthermore, the Sierra Nevada, although arid, differs from deserts, at least hot deserts, in having: (1) a thermal contrast between the soil surface and the air which is more extreme than in deserts; (2) low night-time temperatures, even in summer. All these characteristics make the Sierra Nevada more

**Table 1** Climatic data for desert areas and high mountain

| Place | Average temperature (°C) January | Average temperature (°C) July | Annual average temperature (°C) | Annual precipitation (mm) |
|---|---|---|---|---|
| Turanico[a] | −6.9 to 4.8 | 27.1–32.3 | 11.0–17.1 | 82–244 |
| Kazahjastan[a] | −13.6 to 6.0 | 25.1–28.6 | 7.5–12.1 | 103–184 |
| Dzungaria[a] | −22.0 to −15.2 | 23.9–25.4 | 4.3–6.8 | 96–247 |
| Gobi[a] | −18.1 | 23.3 | 3.8 | 107 |
| Pei-Shan[a] | −15.6 to −9.8 | 22.6–24.6 | 4.3–9.6 | 42–74 |
| Deserts of Tibet and Pamir[a] | −20.0 | 8.0–12.0 | – | 103 |
| Great Basin[a] | −2.0 | 20.4 | 7.8–13.2 | 158–419 |
| Chihuahua[b] | 12.2 | 26.6 | 21.1 | 204.3 |
| Sahara[c] | 11.8 | 35.1 | 22.8 | 32.1 |
| Sierra Nevada (2500 m)[d] | −2.5 | 14.0 | 3.3 | In summer 142 |
| Alps (2500 m)[e] | −9.5 | 5.2 | −2.7 | 1552 |
| Pyrenees (1714 m)[f] | −1.6 | 13.4 | 5.2 | In summer 635 |

| Place | Average diurnal range (°C) | Difference air temperature-ground temperature (°C) | Lowest temperature in July (°C) |
|---|---|---|---|
| Sierra Nevada (2500 m)[d] | 7.7 | 40 | 5 |
| Alps (2500 m)[e] | 5 | – | 6 |
| Sahara[g] | – | 18 | 15.5 |
| Tunisia[h] | – | 21 | 15 |

[a] West 1983, Orlovsky 1994
[b] Morafka et al. 1981
[c] Delye 1968
[d] Tinaut 1979, Prieto 1983
[e] Mani 1968, 1990
[f] Font Tullot 1983
[g] Wehner 1989
[h] Heatwole and Muir 1979

similar to a cold desert than to other European high mountains or other arid zones.

Under these conditions, it might be expected that the rhythms of biological activity, as well as habitat use, would contrast clearly with those in arid or hot zones; that is, while one of the prime aims of animals in arid zones is heat loss, in the high mountain it is heat gain.

Thus, in arid and hot areas, some ant species change their daily activity patterns over the year, becoming nocturnal during the summer, e.g. *Tapinoma nigerrimum* in the Mediterranean area (Cerdá and Retana 1988) or *Messor arenarius* in the pre-Sahara steppe (Heatwole and Muir 1989). In addition, two groups of species, diurnal (heat-adapted) and nocturnal (cold-adapted), inhabit most deserts, as in Anatolia (Baroni-Urbani and Aktac 1981) or the Sahara (Heatwole and Muir 1989; Heatwole 1991).

On the other hand, Somme and Block (1991) stated that in alpine habitats arthropod activity can be nocturnal, a situation that these authors assumed to represent an adaptive advantage, perhaps by reducing the risk of overheating in melanistic species, or by maintaining a corporal water balance or avoiding predators. In a high Mediterranean mountain the temperature difference between the day and night or between the presence or absence of sun is higher than in an alpine mountain; therefore, the compromise is between the heat gain during the night or sun absence and heat loss during the middle of the day.

However, despite the importance of the ants in these mountainous habitats (Pisarski 1978; Gómez and Zamora 1992), few studies have focused on how these insects manage to thrive under such harsh climatic conditions (Heinze and Hölldobler 1994) and virtually nothing is known about the activity pattern of high-mountain ants. In addition, the high mountain probably does not have the broad spectrum of ant species found in the hot desert.

The objective of this investigation was to study the activity pattern of a Mediterranean high-mountain ant species and its relation to abiotic and biotic factors, in an attempt to resolve the apparent contradiction of a thermophilic ant inhabiting a cold environment.

## Materials and methods

### Natural history of *Proformica longiseta*

*P. longiseta* Collingwood, a small [3.3 (SEM 5) mm; $n = 30$] allometric and polymorphic ant (Fernández-Escudero et al. 1994), is endemic to the Sierra Nevada and neighbouring mountains between 1900 m and 2800 m in altitude. The nests are found under stones which serve as an efficient heat source (Fernández-Escudero et al. 1993; Tinaut and Fernández-Escudero 1993). The *P. longiseta* populations typically lodge between 155 and 1200 individuals. This ant feeds mainly on nectar and occasionally on dead insects (Fernández-Escudero and Tinaut, in press a). It inhabits the driest areas of these mountains, where it is the most abundant ant (83.16%; Tinaut 1979). The other ant species sharing the area include *Tetramorium caespitum* L., *Tapinoma nigerrimum* Nyl., *Leptothorax tristis* Bondroit, *L. tuberum* Fabricius and *Formica lemani* Bondroit.

The genus *Proformica* inhabits arid steppes from Central Asia to the Iberian Peninsula and thus occupies cold as well as hot places. In the Iberian Peninsula, two other species, *P. ferreri* Bondroit and *P. nasuta* Nylander, live in a savannah-like grassland but only at altitudes of no more than 1000 m (Tinaut 1981; Cros 1986).

### Study area

The present study was carried out at the head of the San Juan River (2400 m in altitude) in the Sierra Nevada (Granada, Spain). The study area covers the dry places in this valley, where the most representative vegetation includes *Genista versicolor* Boiss., *Juniperus communis* subp. *alpina* (Suker) Celak, *Hormatophylla spinosa* (L.) Kupler and *Thymus serpilloides* Bory. Of the vegetal cover, roughly 16% is shrub, 27% grass, while 57% is bare ground. The soil is very poor and siliceous. This zone belongs climatically to the Atlantic domain (Jimenez Olivencia 1991); the annual precipitation

amounts to 926 mm, mostly during the winter, and is thus principally snow with only scattered torrential rainfalls during the vegetative period (May–September), measuring less than 142 mm. The average number of rainy days per year is around 50. Temperatures at 2,500 m fluctuate over the year between 27°C maximum and –14°C minimum, with a monthly average of between –4.3°C and 18.4°C. The potential evapo-transpiration reaches 100 mm in August, causing a water deficit from May to September (Tinaut 1979, Prieto 1983).

Activity

The pattern of daily activity was studied at two nests 1.1 m apart, by counting the number of nest entries (the times any ant entered) and exits (the times any ant ventured outside a circle of 15 cm radius from the entrance). The counts started when nest activity began in the morning until the nest was closed and there were no more entries or exits. The census lasted for 10 min every hour. Activity was noted for 8 days, from the end of May until mid-September. At the end of the experiment the nests were exposed and their respective populations counted.

At the same time, different environmental factors were monitored to determine which abiotic factors were most responsible for the variation in activity. These were:

1. Environmental temperature in the shade at 1 m from the soil surface
2. Vegetation temperature at 15 cm from the soil surface
3. Soil-surface temperature
4. Temperature beneath the stone belonging to nest A, which had a size similar to that of the first stone of nest B – a surface area of 182 cm$^2$ and a thickness of 3.5 cm
5. Temperatures 3 cm, 15 cm and 50 cm deep in the soil. The temperatures were measured with T-P.6 (*Physitemp*, USA) thermocouples connected to a Datataker DT 500 data-logger (Data Electronics, Australia), which automatically logged the information from the different sensors. In the case of deep soil temperatures, the sensors were placed between the nests, as it was not feasible to place them inside; thus these measurements served as the inferred temperature of the interior of the nest. The depths were chosen based on the structure of 17 previously studied nests (Tinaut and Fernández-Escudero 1993). With these measurements, we hoped to determine whether interior soil temperature influenced external activity.
6. Light intensity, measured with a Neurtek H D 8366 (Delta OHM, Italy) light meter which could register the light reflected 90 cm from a sheet of white paper on the ground.
7. Wind at ground level, measured with a Turbo-Meter anemometer (Davis Instruments, USA).
8. Relative air humidity at 1.5 m, recorded using a digital hydrometer Rotronic (Hygroskop Gt, Switzerland)

All variables were measured every hour from 0630 hours to 1830 hours, in order to determine the environmental conditions before and after nest activity. To show the relationships between the variables, and to avoid the problem of introducing into the regression analysis variables that behaved similarly, we first applied a principal components analysis (PCA). This expresses covariation in terms of factors that explain a large part of the variance and covariance of the original variables. We used the factors thus obtained as independent variables in the stepwise regression analysis, with activity being the dependent variable. PCA factors were rotated by a varimax/normalized method. Some variables were log transformed to approximate a normal distribution (Sokal and Rohlf 1995). The programme Statview TM.2 was used for the statistical analysis.

A complementary study was conducted to discover where foraging took place, to ascertain the conditions that the ant encounters outside the nest, and thereby to understand more fully the influence of certain variables on the activity. In observation intervals set at 5 min, records were kept of the time during which workers were on the ground and in the vegetation. In addition, the temperature of the soil surface and the vegetation at 2 cm and at 7 cm (where the ant rested) were measured every 30 min. These observations were made when the temperatures were highest in order to understand worker behaviour under extreme conditions. Furthermore, to determine whether the great amount of time that the worker spent in the vegetation was due to the vegetal abundance, we calculated the vegetal cover in the zone, using five parallel transects 10 m long and 2 m apart, in which the cover of every type of vegetation (grass, shrubs, etc.) was counted.

In addition, we analysed two biological factors, food demand and availability, in relation to pattern shifts in daily activity over the entire active period. The demand was extrapolated from the presence of ant larvae in the nest, unearthing 36 nests between May and November (1990–1995), the populations of which were counted. Larval abundance in the nest was made relative by giving a value of 10 to the point of greatest larval presence in the entire ant nest, which we considered the point of maximum food requirement in the nest. This became the reference value for the other periods, within a range of 0–10. Due to the marked floral preference in this species, being one of the most abundant floral visitors in this zone (Gomez and Zamora 1992), and given that nectar is the major dietary component of this ant (Fernández-Escudero and Tinaut, in press a), we estimated the availability of food as the number of flowers per square metre among the species visited by *P. longiseta* (*Arenaria tetraquetra* subp. *imbricata* Lug. ex Rodr. *Thymus serpilloides*, *Genista versicolor*) found in an area of 200 m$^2$ surrounding the nests studied. This manner of estimating the food availability is only approximate, and was treated as such in analysing the results obtained.

Food demand and availability were used in this work only as variables which can influence activity, since a thorough examination of the biological cycle and feeding habits of *P. longiseta* is discussed in other studies (Fernández-Escudero and Tinaut, in press a, b).

The relationship of these two variables and soil temperature with activity was analysed using the Pearson correlation index, for which the active period was divided into eight sections of 15 days each. The activity value considered was the sum of the entries and exits of the sampling day in that 15-day period, the day when the number of flowers per square metre was counted and when the soil temperature was measured. The presence of larvae refers to the number of nests exposed during this same period.

Critical thermal maximum

For a better understanding of the results, we calculated the heat resistance of *P. longiseta*, considering the temperature at which the workers remained immobile to be more ecologically significant than lethal temperatures. The critical thermal maximum (CTM) is defined by Whitford and Ettershank (1975) as the statistical mean of the temperature at which individuals become immobile and cannot escape potentially lethal conditions. Following the measurements used by these authors, we determined the CTM by introducing six to seven workers into a receptacle with an Erlenmeyer flask containing 2 cm sand at the bottom. Water was added to this receptacle and heated with an electrical resistor. The temperature increased at 1°C min$^{-1}$, monitored by a sensor 2 mm from the sand surface. Before the experiment, all the ants were kept for more than 24 h at 20°C for acclimatization. As a reference measurement, a calculation was made of the CTM of *P. ferreri*, a member of the same genus also found in the Sierra Nevada, but at an altitude of less than 900 m.

# Results

Activity

*P. longiseta* foraged only during daylight, and displayed a unimodal activity pattern with maximum activity at midday (Fig. 1). The duration of activity (Fig. 2) varied
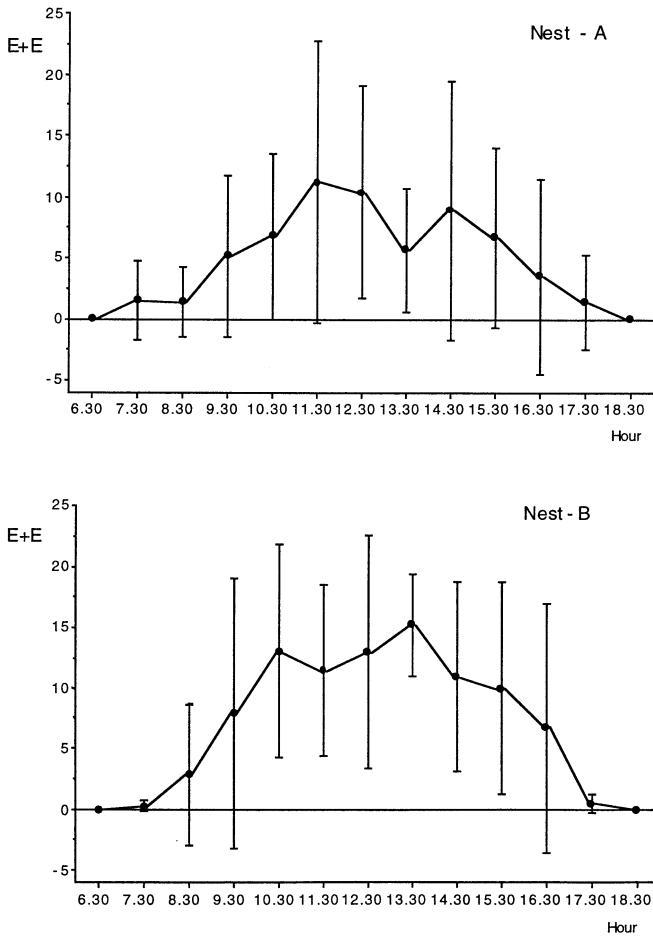
**Fig. 1** Mean values of the daily activity, entries + exits ($E + E$), of the two nests ($n = 8$). *Bars* represent standard deviation



**Fig. 2** Opening and closing hours of nest A and B of *Proformica longiseta*, and sum of the exits and entrances (*left*) during the sample days (date on the *right*)



**Fig. 3** Maximum, minimum and average soil-surface temperatures each hour during the active period of *P. longiseta* ($n = 8$)

between 4 and 11 h for both nest A (14 September 1993 and 23 July 1993, respectively) and nest B (14 September 1993 and 10 July 1993, respectively). The mean duration was 7.3 (SEM 2.5) h.

The daily activity of *P. longiseta* began after dawn between 0730 hours and 1030 hours when the sun was over the nest. At that time, the activity was scant but this clearly increased, reaching a maximum between 1230 hours and 1430 hours. The maximum activity remained stable for about 1 h, after which activity began to decline until it stopped between 1630 hours and 1830 hours. (Fig. 1). Although this was the norm, sometimes at midday there was a slight variation in activity that did not correspond to any of the variables studied.

Activity took place mainly between 30°C and 50°C (soil-surface temperature), while the most extreme conditions under which ant activity occurred involved a daily soil-surface temperature range of 17–53.4°C (Fig. 3). However, in other observations in the study area, some workers were found to be active at surface temperatures of 10.4°C and 58.8°C, the maximum observed in the zone. With respect to light intensity, foraging (invariably diurnal) was never observed below 4310 lx on sunny days, a value that coincided with sunset. With the ap-
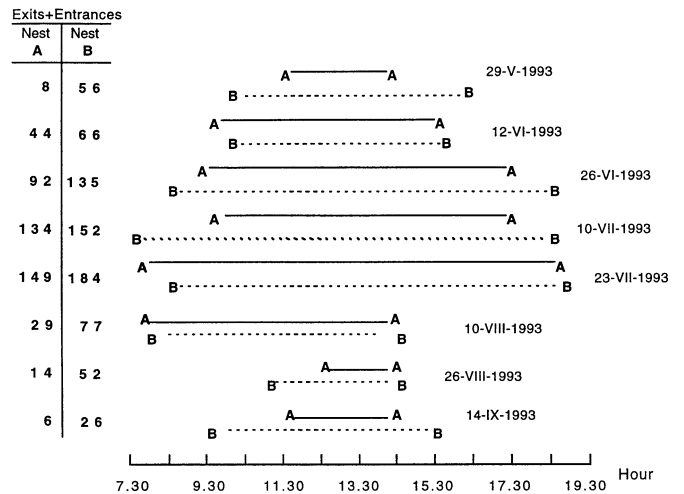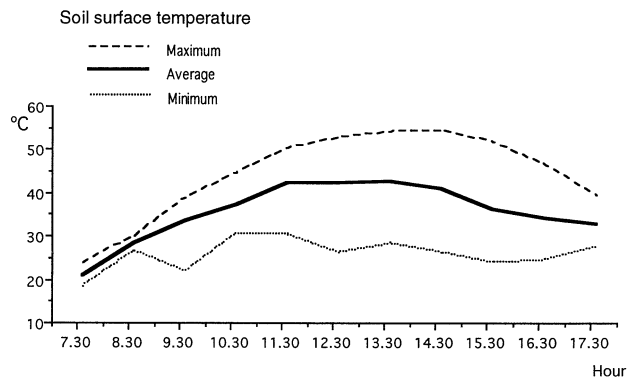
pearance of clouds, activity dropped appreciably and, when the day remained cloudy, activity stopped. The maximum light intensity of the sampling days, 17 290 lx, did not disturb nest activity.

The workers also remained active in high winds (6.9 m/s at ground level), although on these occasions the workers were sometimes carried away by the wind. The humidity values when the ants were active were low, averaging 35.4 (SEM 2)%, with a maximum of 62.2% and a minimum of 5.8%. Rain was the factor most likely to stop activity – we noted five occasions on which rain completely halted activity.

With respect to the influence of these variables on the activity of *P. longiseta*, the PCA grouped the variables into four factors (Table 2), the first being light intensity and all the temperatures except those referring to soil depth. Soil-surface temperatures proved to be the factors with the most weight, followed by the temperature at 3 cm below the soil surface and beneath the stone. The second grouping was clearly characterized by soil temperatures, with light intensity notably negative yet high, indicating an inverse relationship between these factors. This inverse

**Table 2** Results of principal components analysis. Rotated by varimax/normalized method. Eigenvalue: degree of variance explained by each factor. Values express the weight of the variables for each factor (for further details see Materials and methods)

| | Factor 1 | Factor 2 | Factor 3 | Factor 4 |
|---|---|---|---|---|
| Environmental temperature | 0.065 | 0.233 | −0.650 | −0.084 |
| Soil-surface temperature | 0.931 | −0.196 | 0.225 | −0.042 |
| Vegetation temperature | 0.538 | −0.170 | −0.408 | −0.132 |
| −3 cm temperature | 0.724 | 0.001 | −0.113 | −0.029 |
| −15 cm temperature | 0.084 | 0.876 | −0.045 | 0.070 |
| −50 cm temperature | −0.013 | 0.901 | 0.293 | −0.134 |
| Stone temperature | 0.694 | 0.256 | 0.001 | 0.227 |
| Light intensity | 0.626 | −0.670 | 0.454 | −0.097 |
| Humidity | 0.039 | −0.023 | 0.024 | 0.980 |
| Wind 0 m | 0.107 | 0.172 | 0.763 | −0.039 |
| Eigenvalue | 3.901 | 2.408 | 1.282 | 1.059 |
| Variance | 0.39 | 0.630 | 0.759 | 0.865 |

**Table 3** Factors with significant influence on activity in nest A and B according to stepwise regression analysis

| | Variable | Intercept | SE | Std. coeff. | F to remove |
|---|---|---|---|---|---|
| Nest A | Factor 1 | 0.693 | 0.047 | 0.637 | 44.46 |
| Nest B | Factor 1 | 10.985 | 0.834 | 0.607 | 37.95 |

relationship is due to the fact that deep in the soil, there is a 12-h lag between temperature increases and decreases with respect to light intensity (Tinaut and Fernández-Escudero 1993). In the third group, wind had the highest positive value, with environmental temperature being negative. The final group was characterized by humidity.

The application of multiple stepwise regression showed that the first group was the only one that significantly influenced *P. longiseta* activity outside the nest (Table 3). This implies that the most influential variables were environmental temperatures surrounding the ant, chiefly soil-surface temperature.

On the other hand, soil-depth temperature, wind and humidity did not significantly explain this activity. The influence of light intensity was primarily a limiting factor, given that there was no activity below 4310 lx (at sunset), even though soil surface temperature was greater than 35°C on some days.

The dynamics of the biotic factors analysed, food availability and demand (larvae in the nest), over the vegetative period, closely matched the dynamics of *P. longiseta* activity (Fig. 4), as we confirmed by the correlation results (Table 4). These two factors had low values at the beginning of the vegetative period, rose to maximum values in July and then fell towards the end of August as the flowers and almost all of the larvae disappeared. At a seasonal level, soil-surface temperature also correlated closely with activity and, although lacking values as low as the previous variables at the beginning and end of the activity period, the dynamics were in many ways parallel (Fig. 4).
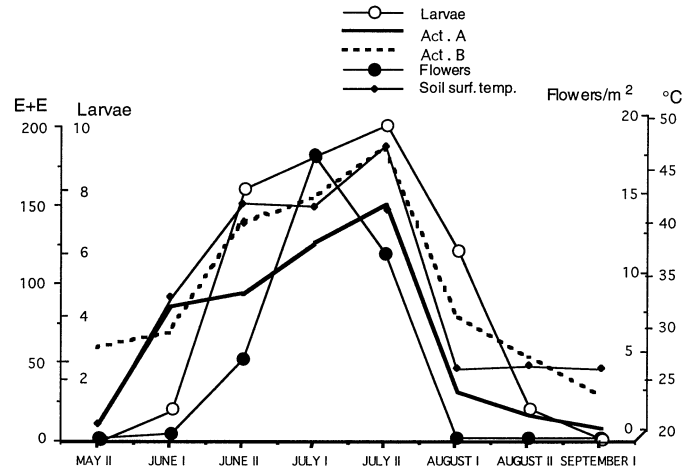


**Fig. 4** Evolution during the vegetative period of ant activity in nests A and B, entries+exits ($E + E$), of the presence of larvae (10 = maximum presence, 0 = larval absence), of the presence of *flowers* (flowers per m$^2$) and of the average temperature of the soil surface (*Soil surf. temp*); *I* first 2 weeks of the month, *II* second 2 weeks

**Table 4** Pearson $r^2$ values between activity of the nests A and B, soil-surface temperature (*surface temp.*) larvae and abundance of flowers

| | Surface temp. | Flowers | Larvae | Activity A | Activity B |
|---|---|---|---|---|---|
| Surface temp. | 1 | 0.6415* | 0.7305* | 0.9192* | 0.8510* |
| Flowers | – | 1 | 0.8004* | 0.8271* | 0.8540* |
| Larvae | – | – | 1 | 0.8241* | 0.9431* |
| Activity A | – | – | – | 1 | 0.9256* |
| Activity B | – | – | – | – | 1 |

* $P<0.05$

The two nests were similar in dynamics (Fig. 1), although this similarity falters when we examine the intensity of the activity, especially at the beginning and at the end (May and September) of the active period. At these times nest A had far fewer entries and exits than did nest B. During these periods, nest A began to be active 1 h later than did nest B (Fig. 2). The structure of both nests was differentiated mainly by the size of the stones covering the nests. Nest A was beneath a stone 182 cm$^2$ in area and 3.5 cm thick, whereas nest B was initially beneath one 143 cm$^2$ in area and 3 cm thick and afterwards below one 21 cm$^2$ in area and 1 cm thick. The smaller size allowed the second stone to heat up earlier than did the stone of nest A and thus heat the chambers below. As a result, nest B became active earlier. The differences in the intensity of activity were not explained by differences in population between the nests, since 186 workers and a queen for nest A versus 190 workers and three queens for nest B, constitute similar nest sizes.

The study of 41 foraging excursions indicated that, regardless of soil-surface temperatures, *P. longiseta* spent a large amount of time foraging in vegetation, accounting for 44.9 (SEM 3.3)% of the time measured, which is a high percentage, given that vegetal cover was only
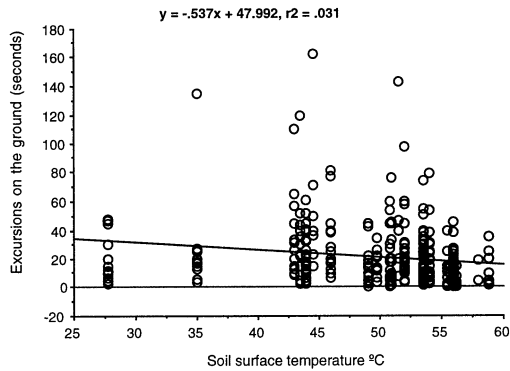
**Fig. 5** Relationship between the duration of foraging excursions over the soil surface and soil-surface temperature. Each *point* represents an excursion
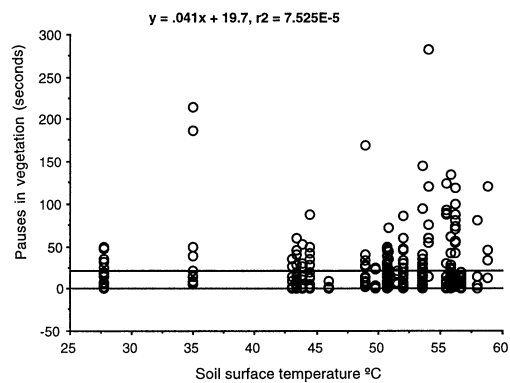


**Fig. 6** Relationship between the duration of pauses in the vegetation and soil-surface temperature. Each *point* represents a pause

15.7%. The visits to vegetation can be attributed to searchers for food, in which the ant minutely searched every branch of the plant, although on occasions we observed an ant climb rapidly to the upper part of the plant and stay for a few seconds. The ants rarely remained immobile.

The relationship between the duration of foraging activity on the soil surface and soil temperature was low ($r = 0.176$; $P = 0.0015$). However, when the temperature increased there was a more direct relationship, as can be deduced from the fact that the foraging excursions lasted no more than 42 s when temperatures exceeded 55°C (Fig. 5) and that, when the soil-surface temperature exceeded 50°C (Fig. 6), there were many stops of less than 20 s in vegetation. Such visits owe more to the evasion of high temperatures than to the search for food, as can be seen by their duration and worker behaviour.

The study of foraging excursions also showed that *P. longiseta* can forage for more than 1 min when the soil temperature is greater than its CTM of 51.1°C (Fig. 5). This is probably due to the speed of movement which, although not measured quantitatively, was greater when the soil temperature was high, and the fewer stops made by the ant on the soil surface.

The differences between the two environments, vegetation and soil surface, were clear, given that the vegeta-
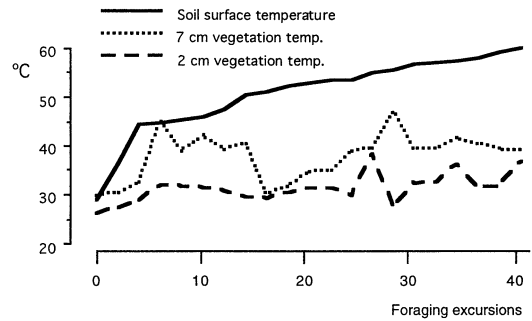


**Fig. 7** Soil-surface temperature, temperature in the vegetation at 2 cm and at 7 cm high, reached during the *P. longiseta* foraging excursions

tion temperature measured at 7 cm never exceeded 32°C, while the surface temperatures reached 58.8°C, showing that the vegetation acted as a refuge from the heat (Fig. 7).

### Critical thermal maximum

The CTM for this species, 51.1 (SEM 0.8)°C (range 52.3–48.8°C; $n = 39$), is a high value, showing resistance to high temperatures. The CTM of *P. ferreri* was 50.4 (SEM 0.9)°C (range 52.3–49.0°C, $n = 27$), a value very close to that of *P. longiseta*.

### Discussion

Temperature proved to be the most influential variable in the daily activity of *P. longiseta*. This is not surprising, given that the activity analysed takes place outside. The most influential factors on behaviour are therefore likely to be those most representative of the environment where the activity occurs. This is especially true for ants, given their small size and their lack of wings which results in body temperature becoming the same as surrounding temperatures (Casey 1981). Coupled with the fact that *P. longiseta* raises itself by 2 mm when walking during high temperature, the soil-surface temperature has the strongest effect on activity, especially considering that the soil surface undergoes the most extreme conditions during the period when the ant is most active.

The strong relationship between the highest temperature and maximum activity underscored the thermophilous nature of this species. Such behaviour has also been observed in other species such as *Cataglyphis iberica* (Cerdá and Retana 1989), *Cataglyphis bombycina* (Wehner et al. 1992) and the genus *Ocymyrmex* (Marsh 1985a), which enables these species to collect prey that has died from high temperatures and that other species cannot reach. For *P. longiseta*, the carrying of solid food increases during the hour of maximum heat ($r = 0.87$, $P = 0.0001$), but this increase is also related to the increase in activity ($r = 0.83$, $P = 0.0004$) (Fernández-Escudero and Tinaut, in press a). We cannot therefore

**Table 5** Critical thermal maximum (*CTM*), maximum surface temperature (*surface temp.*) tolerated by the ant, and the percentage (%) that surface temperature exceeds the CTM of the ant

| Species | Surface temp. (°C) | CTM (°C) | Difference (%) |
|---|---|---|---|
| *Cataglyphis bombycina*[a] Roger | 62 | 54.4 | 12.3 |
| *Pogonomyrmex rugosus*[b] Emery | 55 | 53.8 | 2.2 |
| *Ocymyrmex barbiber*[c] Emery | 67 | 51.4 | 30.4 |
| *Camponotus detriticus*[d] Emery | 63 | 53.8 | 17.2 |
| *Myrmecocystus mimicus*[e] Wheeler | 60 | 48.4 | 24.0 |
| *Myrmecocystus depilis*[e] Forel | 60 | 47.4 | 26.6 |
| *Myrmecocystus romanei*[e] Snelling | 60 | 46.1 | 30.2 |
| *Myrmecocystus mexicanus*[e] Wesmael | 30 | 44.2 | –32.1 |
| *Proformica longiseta* | 60 | 51.1 | 13.1 |
| *Proformica ferreri* | – | 50.4 | – |

[a] Wehner 1989
[b] Whitford and Ettershank 1975
[c] Marsh 1985b
[d] Curtis 1984b
[e] Kay and Whitford 1978

consider one cause alone (heat) to be responsible for the increased number of prey. On the other hand, we cannot discount this as a way of avoiding clashes with other ants, given that this species, in the study zone, shares its territory only with species of small size (*Leptothorax* and *Tetramorium*) which have an activity rhythm which is biased towards the beginning and end of the day, but no interaction was noted with respect to *P. longiseta*. Only in narrow contact zones with *F. lemani* did we observe conflict in the flowers (Fernández-Escudero 1994).

In addition, we have found that the activity of *P. longiseta* over the course of the year strongly correlates with temperature, as with the availability of and demand for food in the nest (Fig. 4, Table 4). We attribute the coincidence that *P. longiseta* is more active on the hottest days, when the most food is outside the nest and when the need for food is greatest, to the brevity of the vegetative period in high mountains and to the fact that this species must spend the winter without larvae or eggs.

With respect to the heat resistance of *P. longiseta*, we have found that it has one of the highest CTM values, close to that of *Ocymyrmex barbiger*, followed by those of *Pogonomyrmex rugosus* and *C. bombycina*, species that live in arid environments, but different from a nocturnal species such as *Myrmecocystus mexicanus* (Table 5).

Some species, including *P. longiseta*, can stay active in temperatures exceeding their CTM by even more than 30% (Table 5). Survival is achieved by the ant (1) walking on its tiptoes and thereby lifting itself off the ground an additional few millimetres; (2) increasing its speed to raise the amount of heat exchange with the air so its body loses heat more quickly (Marsh 1985b); and, mainly, by (3) continually using thermal refuges (Whitford and Ettershank 1975; Kay and Whitford, 1978; Wehner 1989; Wehner et al. 1992) on shady or elevated sites,

where the temperature is lower and where its body temperature can drop, as shown by Marsh (1985b). These techniques are advantageous in hot environments, given the small size of the workers, allowing them to lose heat rapidly (Willmer and Unwin 1981; Heatwole and Harrington 1989). As a specific case, *P. longiseta* is peculiar in its capacity to remain active at temperatures of nearly 60°C, in view of the fact that it can raise itself only 2 mm off the ground, as opposed to 4 mm in species such as *C. bombycina* (Wehner 1989) or *O. barbiger*, this height allowing temperature reductions of up to 5°C (Marsh 1985b). Another significant aspect is that the use of thermal refuges by *P. longiseta* is camouflaged, as almost half of its foraging time is spent in vegetation, where the temperatures can be more than 25°C lower on the soil surface. In the vegetation, this ant searches for liquid or solid food, regardless of soil-surface temperatures. Seeking refuge is evident only under extreme conditions, when temperatures exceed 55°C, whereupon the number of excursions over the soil decreases and the frequency of stops increases (Figs. 5, 6).

Aside from the thermal refuges, increased speed of movement accompanies high temperatures (as noted above), which, when coupled with the frequent presence of wind and the normally low air temperatures in high mountains, could be sufficient for *P. longiseta* not to reach its CTM for long enough to cause death.

In summary, the study zone proves to be a peculiar habitat where insects must endure cold summer air, typical of high mountains (Table 1) and soil temperatures approaching 60°C, under predominantly arid conditions. All this obliges species such as *P. longiseta* to be adapted to high temperatures, like species from the desert and, at the same time, to be adapted to a short active period alternating with a long inactive period in which it must survive the harsh winter.

## References

Ayre GL (1958) Some meteorological factors affecting the foraging of *Formica subnitens* Creighton (Hymenoptera: Formicidae). Insectes Soc 5:147–157

Baroni-Urbani C, Aktac N (1981) The competition for food and circadian succession in the ant fauna of a representative Anatolian semi-steppic environment. Bull Soc Entomol Suisse 54:33–56

Bernstein RA (1979) Schedules of foraging activity in species of ants. J Anim Ecol 48:921–930

Bosch J, Alsina A, Cerda X, Retana J (1987) Incidence du cycle biologique et de la disponibilite des ressources alimentaires sur le regime trophique d'une fourmi. Vie Milieu Ser C Biol Terr 37:237–242

Casey TM (1981) Behavioural mechanisms of thermoregulation. In: Heinrich B (ed) Insect thermoregulation. Wiley, New York, pp 80–114

Cerda X, Retana J (1988) Descripción de la comunidad de hormigas de un prado sabanoide en Canet de Mar. Ecologia 2:333–341

Cerda X, Retana J (1989) Influencia de los factores ambientales sobre la actividad diaria de recolección de la hormiga *Cataglyphis iberica* (Em) (Hym.: Formicidae). Anal Biol 15:75–82

Cloudsley-Thompson JL (1989) Temperature and the activity of ants and other insects in Central Australia. J Arid Environ 16:185–192

Cros S (1986) Contribucio al coneixement de l'etologia i l'ecologia de *Proformica nasuta* (Nylander 1856) (Hymenoptera: Formicidae). MSc thesis, University of Bellatera, Barcelona

Cros S, Cerda X, De Haro A (1992) Ritmos de actividad de dos hormigas, *Proformica nasuta* y *Cataglyphis iberica* en Bellaterra (Vallés Occidental). El Medi Natural del Vallés 2:106–112

Curtis BA (1984a) Activity of the Namib Desert dune ant, *Camponotus detriticus*. S Afr J Zool 20:41–48

Curtis BA (1984b) Temperature tolerance in the Namib Desert dune ant, *Camponotus detriticus*. J Insect Physiol 31:463–466

Delye G (1968) Recherches sur l'écologie, la physiologie et l'éthologie des fourmis du Sahara. PhD thesis, Université d'Aix-Marseille, France, pp 25–47

Fellers JH (1989) Daily and seasonal activity in woodland ants. Oecologia 78:69–76

Fernandez-Escudero I (1994) Estudio de la biología de Proformica longiseta Collingwood, 1978 (Hymenoptera, Formicidae). PhD thesis University of Granada, Spain, pp 111–151

Fernández-Escudero I, Tinaut A (in press, a) Foraging strategies and dietary preferences of a high mountain ant (Hymenoptera: Formicidae). Ekol Pol

Fernández-Escudero I, Tinaut A (in press, b) Ovarian maturation under cold winter conditions in a high-mountain ant (Hymenoptera: Formicidae). Environ Entomol

Fernandez-Escudero I, Tinaut A, Ruano F (1993) Rock selection for nesting in *Proformica longiseta* Collingwood, 1978 (Hymenoptera: Formicidae) in a Mediterranean high mountain. Int J Biometeorol 37:83–88

Fernandez-Escudero I, Ballesta M, Tinaut A (1994) Worker polymorphism in *Proformica longiseta* Collingwood, 1978 (Hymenoptera: Formicidae). Sociobiology 24:39–46

Font Tullot I (1983) Climatología de España y Portugal. Publ Inst Nac Metereol, Madrid, pp 227–228

Gano KA, Rogers LE (1983) Colony density and activity times of the ant *Camponotus semiestaticus* (Hym.: Form.) in a shrub steepe community. Ann Entomol Soc Am 76:958–963

Gomez JM, Zamora R (1992) Pollination by ants: consequences of the quantitative effects on a mutualistic system. Oecologia 91:410–418

Harkness RD (1977) Quantitative observations on the foraging of nests of an ant (*Cataglyphis bicolor*) in Greece. Acta Entomol Jugosl 13:21–33

Heatwole H (1991) The ant assemblage of a sand-dune desert in the United Arab Emirates. J Arid Environ 21:71–79

Heatwole H, Harrington S (1989) Heat tolerances of some ants and beetles from the pre-Saharan steppe of Tunisia. J Arid Environ 16:69–77

Heatwole H, Muir R (1979) Thermal microclimates in the pre-Saharan steppe of Tunisia. J Arid Environ 2:119–136

Heatwole H, Muir R (1989) Seasonal and daily activity of ants in the pre-Saharan steppe of Tunisia. J Arid Environ 16:49–67

Heinze J, Hölldobler B (1994) Ants in the cold. Memorabilia Zool 48:99–108

Hölldobler B, Taylor RW (1983) A behavioral study of the primitive ant *Nothomyrmecia macrops* Clark. Insectes Soc 30:384–401

Jimenez Olivencia Y (1991) Los paisajes de Sierra Nevada. Cartografía de los sistemas naturales de una montaña mediterránea. Universidad de Granada, Granada, pp 168–178

Kay CAR, Whitford WG (1978) Critical thermal limits of desert honey ants: possible ecological implications. Physiol Zool 51:206–213

Mani MS (1968) Ecology and biogeography of high altitude insects. Junk, The Hague, pp 275–310

Mani MS (1990) Fundamentals of high altitude biology. Oxford and IBH, New Delhi, pp 9–18

Marsh AC (1985a) Microclimatic factors influencing foraging patterns and success of the thermophilic desert ant *Ocymyrmex barbiger*. Insectes Soc 32:286–296

Marsh AC (1985b) Thermal responses and temperature tolerance in a diurnal desert ant *Ocymyrmex barbiger*. Physiol Zool 58:629–636

Mehlop P, Scott NJ Jr (1983) Temporal patterns of seed use and availability in a guild of desert ants. Ecol Entomol 8:69–85

Morafka DJ, Adest GA, Aguirre G, Recht M (1981) The ecology of the Bolson Tortoise *Gopherus flavomarginatus*. In: Barbault R, Halffter G (eds) Ecology of the Chihuahuan desert. Ed Instituto de Ecología, México, pp 35–78

North RD (1993) Entrainment of the circadian rhythm of locomotion activity in wood ants by temperature. Anim Behav 45:393–397

Orlovsky NS (1994) Climate of Turkmenistan. In: Fet V, Atamuradov KI (eds) Biogeography and ecology of Turmenistan. Kluwer, Dordrecht, pp 23–48

Pisarski B (1978) Comparison of various biomes. In: Brian MV (ed) Production ecology of ants and termites. Cambridge University Press, London, pp 326–331

Prieto P (1983) Flora de la tundra de Sierra Nevada. Secr Publ University of Granada, Granada, pp 81–95

Retana J, Cerda X, Alsina A, Bosch J (1988) Field observations of the ant *Camponotus sylvaticus* (Hym: Formicidae) diet and activity patterns. Acta Oecol, Oecol Gen 9:101–109

Rosengren R, Fortelius FW (1986) Light: dark induced activity rhythms in *Formica* ants. Entomol Gen 11:221–228

Sokal RS, Rohlf FJ (1995) Biometry. Freeman, New York, pp 409–423

Sømme L, Block W (1991) Adaptations to alpine and polar environments in insects and other terrestrial arthropods. In: Lee R, Denlinger D (eds) Insects at low temperature. Chapman and Hall, New York, pp 318–359

Tinaut A (1979) Estudio de la mirmecofauna de los Borreguiles del S. Juan (Sierra Nevada) (Hym: Formicidae). Bol Asoc Esp Entomol 3:173–183

Tinaut A (1981) Estudio de los Formícidos de Sierra Nevada. MSc thesis, University of Granada, Spain, pp 29–49

Tinaut A, Fernandez-Escudero I (1993) El medio abiótico de *Proformica longiseta* Collingwood, 1978, una hormiga de la alta montaña mediterránea (Hymenoptera: Formicidae). Zool Baetica 4:57–74

Wehner R (1989) Strategien gegen den Hitzetod. Thermophilie und Thermoregulation bei Wüsternameisen (*Cataglyphis bombycina*). Jubiläumsband. Akad Wiss Lit Mainz:101–112

Wehner R, Marsh AC, Wehner S (1992) Desert ants on a thermal tightrope. Nature 357:586–587

West NE (1983) Ecosystems of the world 5. Temperature deserts and semi-deserts. Elsevier, Amsterdam, pp 1–522

Whitford WG, Ettershank G (1975) Factors affecting foraging activity in Chihuahuan desert harvester ants. Environ Entomol 4:689–695

Willmer PG, Unwin DM (1981) Field analyses of insect heat budget: reflectance, size and heating rates. Oecologia 50:250–255