

Microclimatic Conditions Regulate Surface Activity in Harvester Ants *Messor barbarus*

Francisco M. Azcárate,^{1,3} Eva Kovacs,² and Begoña Peco¹

Revised February 15, 2007; accepted January 12, 2007

Published online: May 8, 2007

*This paper analyses the effect of microclimatic factors (internal soil temperature, surface temperature and surface relative humidity) on surface activity of *Messor barbarus* harvester ants. We selected 44 colonies in an area of Mediterranean grassland near Madrid (Central Spain), which were monitored for activity between March 1998 and September 1999. Results indicate that microclimatic factors are good predictors of colony activation and intensity of activity. Colonies became active above certain critical values of internal soil temperature and relative humidity. For active colonies, surface temperature was the main regulatory factor for worker departure rate, which peaked at around 25–30°C. Worker speed was positively correlated with surface temperature, although the relationship was weaker for large-sized workers. Microclimatic factors were not enough, however, to predict task allocation outside the nest. The explanation for this aspect of ant behavior probably requires the inclusion of biotic factors in the models.*

KEY WORDS: mediterranean grasslands; ant colonies; temperature; relative humidity; task allocation.

INTRODUCTION

Messor barbarus harvester ants play a key role in Mediterranean grasslands, since they are the main seed predators and participate in a number of

¹Departamento de Ecología, Universidad Autónoma de Madrid, C. U. Canto Blanco, E-28049, Madrid, Spain.

²Kiskunsag National Park, H-6000, Kecskemét, Hungary.

³To whom correspondence should be addressed. E-mail: fm.azcarate@uam.es.

ant-plant interactions (López *et al.*, 1992a, b, 1993a, b; Azcárate and Peco, 2003, 2004; Detrain *et al.*, 2000; Azcárate *et al.*, 2005). It is widely known that seed harvesting by *M. barbarus* varies on a daily and seasonal scale, as a consequence of variability in ant activity outside the nests (hereafter surface activity), amongst other factors. However, the regulation of the surface activity is one of the lesser known aspects of *M. barbarus* foraging behavior, in contrast with other more investigated features such as the foraging spatial patterns (López *et al.*, 1993a, b; Detrain *et al.*, 2000; Azcárate and Peco, 2003) and prey selection criteria (Reyes-López and Fernández-Haeger, 2001, 2002a, b; Azcárate *et al.*, 2005).

The only study known to us that addresses the variability in surface activity of *M. barbarus* found a qualitative association between ambient temperature and ant activity (López *et al.*, 1992a). However, it only included August observations, and did not measure the conditions at the ground level. Research on other species related to *M. barbarus* such as *M. bouvieri*, *M. capitatus* and *M. timidus* has also revealed temperature as a main factor controlling activity patterns (Cerdá and Retana, 1994; Cros *et al.*, 1997; Cerdá *et al.*, 1998a, b; Hensen, 2002; Challet *et al.*, 2005).

More detailed data on other ant species coincide on the value of microclimatic conditions as predictors of activity rhythms on a daily and seasonal scale. Soil surface temperature (Crist and MacMahon, 1991; Crist and Williams, 1999; Morrison *et al.*, 2000; Pol and de Casenave, 2004) mound temperature (Vogt *et al.*, 2003) and relative humidity (Feener and Lighton, 1991; Kaspari, 1993; Lighton *et al.*, 1994; Kaspari and Weiser, 2000) have been found to control ant activity. Other abiotic variables such as sunlight, rainfall and wind intensity are also relevant to the activity of some species (Briese and Macauley, 1980; Cerdá and Retana, 1989; Wirth and Leal, 2001). Activity rhythms determined by physical variables are modulated secondarily by biotic factors such as food availability (Bernstein, 1979; Hobbs, 1985; Crist and MacMahon, 1992; Sanders and Gordon, 2002), internal colony rhythms (Houston *et al.*, 1988; Díaz, 1992), food saturation (Whitford and Ettershank, 1975) and interactions with competing species (Bernstein, 1979; Melhop and Scott, 1983; Cerdá *et al.*, 1998b; Sanders and Gordon, 2000) and/or predators (MacKay, 1982).

Ant surface activity is probably regulated at different steps. First, the shift from inactivity to activity would depend on the achievement of critical values of temperature and relative humidity (Briese and Macauley, 1980; Cros *et al.*, 1997; Cerdá *et al.*, 1998a; Pol and de Casenave, 2004). Biotic factors such as internal colony rhythms and food satiation could also modulate worker activation. Secondly, once the conditions allow workers to leave the nest, the intensity of activity (number and speed of workers) is probably dependent on the quality of these conditions. Soil surface temperature and

relative humidity are involved at this level in some ant species (Nielsen and Baroni-Urbani, 1990; Crist and MacMahon, 1991; Morehead and Feener, 1998; Fernández-Escudero and Tinaut, 1998). And third, the colony can allocate workers to different surface tasks depending on factors such as microclimatic conditions, food availability, or the needs of the colony (Gordon, 1991; Gordon and Mehdiabadi, 1999; Sanders and Gordon, 2002).

The control of ecosystems and organisms by abiotic factors is particularly relevant in the Mediterranean region, where climate is characterized by deep contrasts in moisture and temperature, both daily and seasonally. Microclimate variability is higher in open areas, where it can be regarded as a major structuring force for ant communities, since it permits the coexistence of a larger number of species (Cros *et al.*, 1997; Retana and Cerdá, 2000), and can even modify the competitive prevalence amongst species (Cerdá *et al.*, 1997). However, a strong temporal variability in temperature and/or moisture also restricts the duration of ant activity periods, and hence limits ant-plant interactions.

The main hypothesis of this study is that microclimatic factors are the main determinants of *Messor barbarus* surface activity in Mediterranean grasslands. In particular, we analyze the role of internal soil temperature, soil surface temperature and relative humidity at three levels: (1) colony activation; (2) intensity of activity and (3) task allocation outside the nest.

MATERIALS AND METHODS

Sampling Design and Microclimate Variables

Fieldwork was conducted in a 50-ha grassland area between the Autónoma University campus and the nearest town, Alcobendas (40°32'N, 3°40'W, 15 km north of Madrid, 700 m above sea level). The relief is slightly hilly, on Miocene arkosic substrata, and climate is continentalised Mediterranean (4°C mean in January, 24°C mean in July; 500 mm precipitation, severe summer drought). The grasslands are a species-rich assemblage of therophytes along with the perennial *Poa bulbosa*, and scattered broom thickets (*Retama sphaerocarpa*).

We chose 44 *M. barbarus* nest entrances, each from a different colony, and we monitored a range of variables related to surface activity. All observations were taken between 25 March 1998 and 21 September 1999. Sampling design varied depending on the aspect of activity under analysis, although the same microclimate variables were measured in all cases:

- *Internal soil temperature* (T_i): Measured using a 0.1°C precision soil thermometer, inserted to a depth of 10 cm. Measurement were

always taken within a 50 cm radius of the monitored entrance. Superficial chambers in *M. barbarus* colonies of the study site are normally situated within the upper 10–20 cm soil layers. Therefore, we considered T_i as an indicator of the thermal conditions experienced by workers in the colony's uppermost chambers and galleries.

- *Surface temperature (T_s)*: The same thermometer was used, in this case placed on the ground. The measurement was always conducted on a trail section usually crossed by active workers. During the measurement, the sensor was protected from direct sun radiation using a specifically designed sunshade.
- *Surface relative humidity (RH)*: In this case we used a 0.1% precision thermohygrometer. Measurements were taken at the same point where we recorded surface temperature.

Colony Activation

We considered two possible colony states: *activity* (worker flows through the nest hole), and *inactivity* (no observed ant flows in either the monitored entrance or any others nearby that might be part of the same colony). To ensure the independence of observations, we took one single observation per colony ($n = 44$; 22 active vs. 22 inactive). Every observation was recorded on a different day. For all the inactivity observations, we confirmed the existence of subsequent worker flows, which eliminated the possibility of inactivity due to entrance abandonment.

We then estimated a logistic regression model, in which colony activation was modelled as a function of the three microclimate variables, their squares and all the possible interactions. We estimated the parameters using the *maximum likelihood* method, minimising the loss function and the number of independent variables included. The significance of the model or the inclusion of any new variable was tested using a χ^2 test associated with the difference between the loss function of the model under examination and the previous model.

Activity Intensity

The intensity of surface activity was analysed at both the colony and the individual level. The indicators at the colony level were the *departure* and *return rates* per nest hole, while *worker speed* was used for individual activity.

Departure and *return rates* were defined as the number of workers leaving or entering the nest hole per minute. Each of the variables was estimated by two counts of 2 min, separated by 5 min pauses. Given that worker flows depend on the size of the colony, we analysed three different colonies. We recorded 10 observations per colony, and then estimated a multiple regression model for each one, using a forward stepwise procedure. We included the log-transformed independent variables, the second degree terms and the interactions.

Worker speed was estimated by measuring the time taken by unladen departing workers to cover 20 cm. We recorded speed in 32 colonies. Given that speed is size-dependent (Rissing, 1982), we distinguished three size classes: small (approx. <7 mm length), medium (7–10 mm length) and large (approx. >10 mm length). Each observation in the analysis represented the mean value for three workers in each size class monitored in the field. Data were processed separately for each size class. We estimated polynomial regression models of speed as a function of *Ts* and *RH*, including second degree terms. We also tested the difference in speed between workers of different sizes by applying a repeated measurement ANOVA.

Task Allocation

Parallel to the departure rate counts, we evaluated worker allocation to the following three above-ground tasks:

- *Nest work*, quantified as the percentage of departing individuals devoted to the removal of soil particles from inside the nest.
- *Food processing*, quantified as the percentage of departing individuals laden with various types of waste (fruit, seeds and insect remains, etc.).
- *Foraging*, quantified as the percentage of unladen departing workers. The main mission of these workers was considered to be food supply, although these individuals may occasionally work on other tasks (trail maintenance, surveillance and defence of the foraging area, etc. . .).

The relationship between microclimatic factors and ground tasks was analysed with multiple regression models, using a single active observation per colony ($n = 44$). Dependent variables were angularly transformed (arc sin of the square root; Zar, 1996) prior to the analysis. Together with the independent variables, we included their squared terms and interactions. For the analysis of *nest work*, we also considered the occurrence of moderate rainfall (>3 mm) in the 24 h prior to the observation.

STATISTICA (Statsoft, 1998) package was used for all the analyses.

Table I. Colony Activation

	<i>Estimate</i>	Final loss	$\chi^2(1)$	<i>p</i>
Constant	-8.2544	15.496	30.005	< 0.0001
$RH \times Ti$	0.0088			

Note. Logistic regression model estimated for the probability of surface activity of *M. barbarus* colonies as a function of relative humidity (*RH*) and internal soil temperature (*Ti*). $N = 44$.

RESULTS

Colony Activation

The only variable accepted by the model was the $Ti \times RH$ interaction (Table I). Colony activation responded to a combined increase of internal soil temperature and surface relative humidity (Fig. 1).

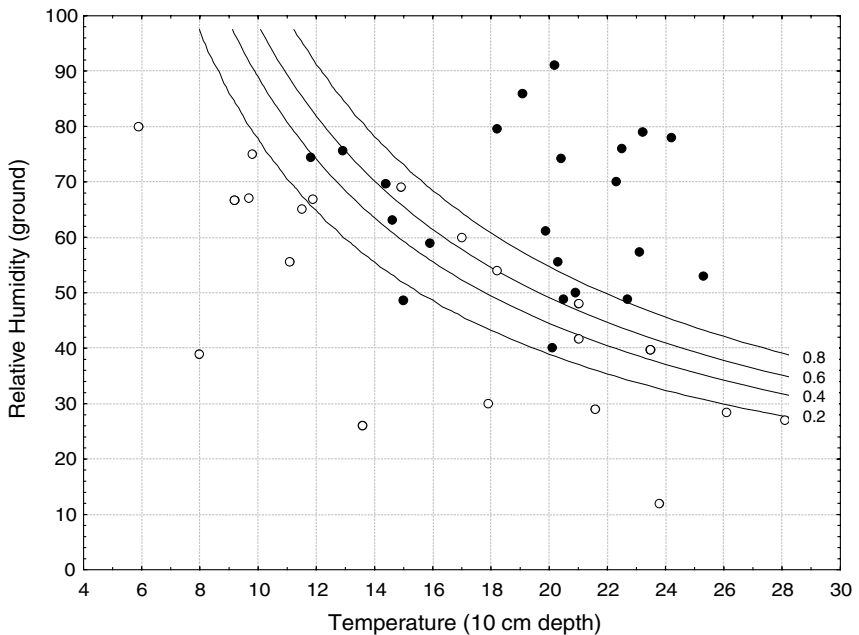


Fig. 1. Colony activation. Logistic regression model estimated for the probability of external activity of *M. barbarus* colonies (isolines) as a function of internal soil temperature (*Ti*) and relative humidity (*RH*). $N = 44$ observations. White: inactive colonies; black: active colonies.

Table II. Intensity of Activity

Model	Variable	Parameters				R^2 and significance			
		Estimate	E.S.	$t(7)$	p	R^2	$d.f.$	F	p
Col. 1	Intercept	-0.5010	0.6532	0.767	0.468	0.82	2;7	16.28	<0.002
	T_s	0.3398	0.0598	5.566	<0.001				
	T_s^2	-0.0064	0.0012	-5.214	0.001				
Col. 2	Intercept	0.2589	0.7410	0.349	0.737	0.82	2;7	15.93	<0.002
	T_s	0.2910	0.0586	4.907	0.002				
	T_s^2	-0.0053	0.0010	-5.314	0.001				
Col. 3	Intercept	-5.2812	2.7799	-1.900	0.099	0.70	2;7	8.28	0.014
	T_s	0.6584	0.1912	3.1906	0.015				
	T_s^2	-0.0116	0.0031	-3.4691	0.010				

Note. Polynomial regression models estimated for \log (departure rate) in three *M. barbarus* colonies. T_s : soil surface temperature; $d.f.$: degrees of freedom.

Intensity of Surface Activity

Soil surface temperature was the only predictive variable of departure rate for the three analysed *M. barbarus* colonies (Table II). The three models show positive coefficients for T_s and negative coefficients for $(T_s)^2$, giving rise to maxima of 26.6, 27.5 and 28.4°C respectively (Fig. 2).

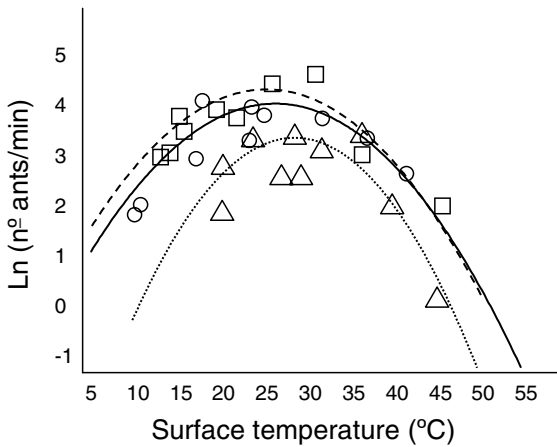


Fig. 2. Intensity of activity. Polynomial regression models predicting worker departure rate (individuals/min) for three *M. barbarus* nest holes as a function of soil surface temperature (T_s). Colony 1: circles, straight line; Colony 2: squares, dashed line; Colony 3: triangles, dotted line.

Table III. Intensity of Activity

Model	Variable	Parameters				R^2 and significance			
		Estimate	E.S.	$t(7)$	p	R^2	$d.f.$	F	p
Col. 1	Intercept	0.5759	1.2681	0.454	0.663	0.53	2;7	4.01	0.069
	T_s	0.2978	0.1161	2.519	0.040				
	T_s^2	-0.0065	0.0024	-2.723	0.030				
Col. 2 (Mod. 1)	Intercept	-1.5142	1.9442	-0.779	0.462	0.59	2;7	5.01	0.044
	RH	0.2328	0.0786	2.792	0.027				
	RH^2	-0.0023	0.0007	-3.000	0.020				
Col. 2 (Mod. 2)	Intercept	-1.7150	1.8155	-0.945	0.376	0.51	2;7	3.72	0.079
	T_s	0.4130	0.1435	2.727	0.029				
	T_s^2	-0.0069	0.0024	-2.676	0.032				

Note. Polynomial regression models estimated for \log (return rate) in two *M. barbarus* colonies. T_s : soil surface temperature; RH : relative air humidity at ground level; $d.f.$: degrees of freedom.

The results for the return rate were considerably more heterogeneous. While the first colony has a slightly significant dependence on T_s , in the second colony two models are possible, with a similar statistical significance. These models are based on RH and T_s respectively (Table III). No satisfactory model was found for the third colony.

Worker speed was positively correlated with surface temperature for all *M. barbarus* size classes, although the relationship was weaker for larger ants (Table IV). There were differences in worker speed in relation to size ($F_{2,62} = 5.867$; $p = 0.005$). The post-hoc Tukey test showed that this result was due to the faster speed of the intermediate individuals (0.95 cm/s S.E. 0.06) in relation to the large sizes (0.82 cm/s S.E. 0.05). The small sizes (0.89 cm/s S.E. 0.06) did not differ significantly from the other size classes.

Task Allocation

Activity concentrated on nest work for the 7 observations taken on the same day or the day after a rain episode equal to or higher than 3 mm (97

Table IV. Intensity of Activity

Worker size	Intercept	Slope	R^2	p
Small	0.017	0.073	0.38	< 0.001
Medium	0.159	0.074	0.32	< 0.001
Large	0.258	0.060	0.23	0.005

Note. Linear regression models estimated for worker speed (cm/s) in *M. barbarus* as a function of surface temperature ($^{\circ}\text{C}$).

Table V. Task Allocation

	Foraging	Food processing
Ti	- 0.01	0.12
Ts	0.19	- 0.04
RH	- 0.18	0.12

Note. Pearson correlation coefficients between the number of workers allocated to *foraging* or *food processing* and the microclimatic variables. No coefficient was significant for $p < 0.05$ ($r_{0.05(2), 35} = \pm 0.325$). Ti: internal soil temperature; Ts: surface temperature; RH: relative humidity. $N = 37$.

to 100% of departing workers). In the remaining 37 observations, the mean percentage was 0.13%, with no records above 1% of the total.

We therefore used the subset of 37 observations unaffected by previous rain in the analysis of the effort spent on *foraging* and *food processing*. As shown in Table V, neither of these two variables correlated significantly with the microclimate factors. It was also impossible to generate significant predictive models based on combinations of these variables.

DISCUSSION

Colony Activation

Internal soil temperature and relative humidity at ground level are good predictors of the activation of *Messor barbarus* colonies. Our results confirm that, at a first step, the shift from inactivity to activity is linked to the achievement of critical values of temperature and relative humidity. However, the interaction between both variables suggests that there are no fixed thresholds: critical temperatures for activity depend on relative humidity, and vice versa.

If internal soil temperature controls ant activity, then the need for heat regulation could determine nest location. In fact, nesting behavior in many ant species is explained in terms of thermal regulation (Hölldobler and Wilson, 1990). In Mediterranean systems, *M. barbarus* usually selects dry and open habitats for nesting (Azcarate and Peco, 2003). This behavior favours soil warming and enables the achievement of critical temperatures. In addition, foraging areas are normally situated in open habitats, which means that their microclimatic conditions (in particular, relative humidity) will be similar to those experienced by the ants when emerging from the nest holes.

Intensity of Surface Activity

Once the workers leave the colony, the intensity of surface activity is fairly predictable from surface temperature. First, worker speed increases with temperature. The same positive relationship has been detected in other ant species (Rissing, 1982; Nielsen and Baroni-Urbani, 1990; Morehead and Feener, 1998; Fernández-Escudero and Tinaut, 1998). In our case, largest ants are less dependent on temperature and, surprisingly, are the slowest, in contrast to findings by Rissing (1982). One possible explanation is that *M. barbarus* might have a division of tasks between size classes, with larger workers possibly spending more effort on controlling activity or inspecting trails, which would slow their pace down.

Second, the departure rate is maximum at 25–30°C, after which it begins to decline. This relationship could simply reflect the species thermal tolerance range. Our activity records varied between 9 and 48°C, an interval comparable to the thermal tolerance range of the close species *M. capitatus* (10° to 46°C, Cerdá *et al.*, 1998a). Another possible explanation is that a body temperature higher than 25–30°C implies an increase in dehydration. However, relative humidity, a better descriptor of water loss, was not admitted by the models.

Other factors such as sun radiation and wind speed may also be involved in the control of ant activity, perhaps influencing the dehydration-thermoregulation balance. Many species have been described as strictly nocturnal or diurnal (Briese and Macauley, 1980; Cros *et al.*, 1997); and wind has been reported as an inhibitor of ant activity (Sheata and Kaschef, 1971; Briese and Macauley, 1980). These factors were not measured systematically in our study, but we did record high day and night departure rates, and we found *Messor* foragers on very windy days, even under the risk of being blown away.

Finally, return rate was the only variable that responded inconsistently to microclimatic variables. Return rate may not be an adequate indicator of ant surface activity for several reasons. First, worker return to the nest is affected by a variety of events (success of the foraging expedition, prey size, need for recruitment, etc.) which probably hinders the effects due to environmental conditions. Second, return flow depends on the number of workers located outside the nest, a function not only of the departure rate, but also of the duration of the activity period. And once the conditions become unfavourable, workers need some time to return to the nest, which could complicate the detection of any relationship between return rate and the factors controlling ant activity.

Task Allocation

According to our results, task allocation outside the nest is not predictable from climate conditions, with the exception of nest work, which is clearly stimulated by rain episodes. After moderate or heavy rain, nest repair becomes the main activity in *Messor barbarus*. In the absence of recent precipitation, the tasks observed outside the nest are essentially reduced to food processing and foraging, and the efforts devoted to each of these activities are not related to microclimate.

In other species, task allocation is highly dependent on biotic factors, which are often intrinsic to the colony (Gordon, 1983, 1986, 1991). For *M. capitatus*, Díaz (1991) suggests that the transition from the ergonomic phase (high worker production) to the reproductive phase implies a summer decline in seed predation. It has also been suggested that the physiological state of workers (Feener and Lighton, 1991) or their physical condition (Nielsen and Baroni-Urbani, 1990) might influence their behavioral characteristics by affecting their efficiency in moving or carrying prey.

Biotic extrinsic factors such as food availability or interactions with neighbouring colonies have also been related to task allocation. Sanders and Gordon (2002) found that *Aphaenogaster cockerelli* adjusts the number of ants engaged in foraging, depending on the food type and distribution. Factors such as the degree of colony saturation (Whitford, 1978) or the rate of food entry (Gordon, 1991) are involved in the control of foraging in other ant species. Finally, in Californian grasslands, Brown and Gordon (2000) found that encounters between neighbouring colonies affected the foraging behavior of *M. andrei*, which suggests that this factor should be considered in the explanation of behavioral flexibility in *Messor* ants.

Implications and Future Research

We have found evidence supporting our main hypothesis for the first and second levels of surface activity: In *M. barbarus*, both the activation and the intensity of the activity are related to microclimatic conditions. Workers need to reach a critical body temperature inside the ant nest before leaving to the surface, where activity is only possible above a critical relative humidity. Once the colony is activated, worker speed and departure rates are quite predictable from ground temperature.

These findings have important implications. First, the microclimate constraints are likely to explain the daily and seasonal rhythms in *M. barbarus* surface activity. Detailed data on this aspect are needed, although preliminary information suggests shifts from diurnal to nocturnal

and from unimodal to bimodal activity patterns depending on the season (F. M. Azcárate and B. Peco, unpubl. data). Seasonal patterns could also change depending on the local climate, as evidence suggests for closely related species. In *M. capitatus*, activity peaks in spring in heavily continentalized grasslands from central Spain (Díaz, 1991), while on the more temperate Mediterranean coast of Catalonia, Cerdá and Retana (1994) found a maximum at the end of summer and the start of autumn. The impact of seed predation in many plant species could be dependent on the coupling between the seed production period and the seasonality of ant activity.

Second, microclimate constraints may help to explain the distribution range and abundance patterns of *M. barbarus* at regional and local scales (Azcárate and Peco, 2004), although the comparison between ant populations located under different climate conditions is necessary to test the universality of our findings. Ant communities in open Mediterranean areas are diverse because microclimate variability permits the coexistence of a larger number of species (Cros *et al.*, 1997; Retana and Cerdá, 2000). However, this microclimate variability can modify the competitive interactions among ant species (Cerdá *et al.*, 1997). We therefore should not discard the possibility of a shift of activity towards less favourable microclimatic conditions when other, perhaps more competitive, species are present in the community together with *M. barbarus*.

Microclimatic conditions are not enough, however, to explain surface task allocation once the colony is active. Further research is needed to disentangle this aspect. Our inconclusive results and data from other species indicate that the control of surface task allocation may be complex, and probably involves factors such as internal colony rhythms or the type, abundance and distribution of food.

ACKNOWLEDGEMENTS

This study was supported by the Spanish Ministry of Science and Technology (projects AMB 990382 and REN 2003-01562) and the Spanish Ministry of Education and Culture (FPI scholarship to F.M. Azcárate).

REFERENCES

- Azcárate, F. M., Arqueros, L., Sánchez, A., and Peco, B. (2005). Seed and fruit selection by harvester ants *Messor barbarus* in Mediterranean grassland and scrubland. *Funct. Ecol.* **19**: 273–284.
- Azcárate, F. M., and Peco, B. (2003). Spatial patterns of seed predation by harvester ants (*Messor* Forel) in Mediterranean grassland and scrubland. *Insectes Sociaux* **50**: 120–126.

- Azcárate, F. M., and Peco, B. (2004). Seed predation by ants (*Messor* spp.) in Iberian Dehesa grassland and scrubland. In Arianoutsou, M., and Papanastasis, V. P. (eds.), *Ecology, Conservation and Management of Mediterranean Climate Ecosystems. Proceedings 10th MEDECOS Conference*. Rhodes, Greece Millpress, Rotterdam, p. 42.
- Bernstein, R. A. (1979). Schedules of foraging activity in species of ants. *J. Anim. Ecol.* **48**: 921–930.
- Briese, D. T., and Macauley, B. J. (1980). Temporal structure of an ant community in semi-arid Australia. *Aust. J. Ecol.* **5**: 121–134.
- Brown, M., and Gordon, D. M. (2000). How resources and encounters affect the distribution and foraging activity of a seed-harvesting ant. *Behav. Ecol. Sociobiol.* **47**: 195–203.
- Cerdá, X., and Retana, J. (1989). Influencia de los factores ambientales sobre la actividad diaria de recolección de la hormiga *Cataglyphis iberica* (Em.) (Hym.: Formicidae). *Anales de Biología* **15**: 75–82.
- Cerdá, X., and Retana, J. (1994). Food exploitation patterns of two sympatric seed-harvesting ants *Messor bouvieri* (Bond.) and *Messor capitatus* (Latr.) (Hym.: Formicidae) from Spain. *J. Appl. Ent.* **117**: 268–277.
- Cerdá, X., Retana, J., and Cros, S. (1997). Thermal disruption of transitive hierarchies in Mediterranean ant communities. *J. Anim. Ecol.* **66**: 363–374.
- Cerdá, X., Retana, J., and Cros, S. (1998a). Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. *Funct. Ecol.* **12**: 45–55.
- Cerdá, X., Retana, J., and Manzaneda, A. (1998b). The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. *Oecologia* **117**: 404–412.
- Challet, M., Jost, C., Grimal, A., Lluc, J., and Theraulaz, G. (2005). How temperature influences displacements and corpse aggregation behaviors in the ant *Messor sancta*. *Insectes Sociaux* **52**: 309–315.
- Crist, T. O., and MacMahon, J. A. (1991). Foraging patterns of *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae) in a shrub-steppe ecosystem: The roles of temperature, trunk trails, and seed resources. *Environ. Entomol.* **20**: 37–46.
- Crist, T. O., and MacMahon, J. A. (1992). Harvester ant foraging and shrubs-steppe seeds: Interactions of seed resources and seed use. *Ecology* **73**: 1678–1779.
- Crist, T. O., and Williams, J. A. (1999). Simulation of topographic and daily variation in colony activity of *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae) using a soil temperature model. *Environ. Entomol.* **28**: 659–668.
- Cros, S., Cerdá, X., and Retana, J. (1997). Spatial and temporal variations in activity patterns of Mediterranean ant communities. *Ecoscience* **4**: 269–278.
- Detrain, C., Tasse, O., Versaen, M., and Pasteels, J. M. (2000). A field assessment of optimal foraging in ants: trail patterns and seed retrieval by the European harvester ant *Messor barbarus*. *Insectes Sociaux* **47**: 56–62.
- Díaz, M. (1991). Spatial patterns of granivorous ant nest abundance and nest site selection in agricultural landscapes of Central Spain. *Insectes Sociaux* **38**: 351–363.
- Díaz, M. (1992). Spatial and temporal patterns of granivorous ant seed predation in patchy cereal crop areas of central Spain. *Oecologia* **91**: 561–568.
- Feener, D. H., and Lighton, J. R. B. (1991). Is foraging in the desert ant, *Messor pergandei* (Hymenoptera: Formicidae), limited by water? *Ecol. Entomol.* **16**: 183–191.
- Fernandez-Escudero, I., and Tinaut, A. (1998). Heat-cold dialectic in the activity of *Proformica longiseta*, a thermophilous ant inhabiting a high mountain (Sierra Nevada, Spain). *Int. J. Biometeorol.* **41**: 175–182.
- Gordon, D. M. (1983). Daily rhythms in social activities of the harvester ant, *Pogonomyrmex badius*. *Psyche* **90**: 413–423.
- Gordon, D. M. (1986). The dynamics of the daily round of the harvester ant colony (*Pogonomyrmex barbatus*). *Anim. Behav.* **34**: 1402–1419.
- Gordon, D. M. (1991). Behavioral flexibility and the foraging ecology of seed-eating ants. *Am. Nat.* **138**: 379–411.

- Gordon, D. M., and Mehdiabadi, N. J. (1999). Encounter rate and task allocation in harvester ants. *Behav. Ecol. Sociobiol.* **45**: 370–377.
- Hensen, I. (2002). Seed predation by ants in south-eastern Spain (Desierto de Tabernas, Almería). *Anales de Biología* **24**: 89–96.
- Hobbs, R. J. (1985). Harvester ant foraging and plant species distribution in annual grassland. *Oecologia* **67**: 519–523.
- Hölldobler, B., and Wilson, E. O. (1990). *The Ants*, Harvard University Press, Cambridge, Massachusetts.
- Houston, A., Schmid-Hempel, P., and Kacelnik, A. (1988). Foraging strategy, worker mortality and the growth of the colony in social insects. *Am. Nat.* **131**: 107–114.
- Kaspari, M. (1993). Body-size and microclimate use in neotropical granivorous ants. *Oecologia* **96**: 500–507.
- Kaspari, M., and Weiser, M. D. (2000). Ant activity along moisture gradients in a neotropical forest. *Biotropica* **32**: 703–711.
- Lighton, J. R. B., Quinlan, M. C., and Feener, D. H. (1994). Is bigger better? – Water-balance in the polymorphic desert harvester ant *Messor pergandei*. *Physiol. Entomol.* **19**: 325–334.
- López, F., Serrano, J. M., and Acosta, F. J. (1992a). Temperature-vegetation structure interaction: The effect on the activity of the ant *Messor barbarus* (L.). *Vegetatio* **99–100**: 119–128.
- López, F., Serrano, J. M., and Acosta, F. J. (1992b). Intense reactions of recruitment facing unusual stimuli in *Messor barbarus* (L.). *Disch. Ent. Z., N. F.* **39**: 135–142.
- López, F., Acosta, F. J., and Serrano, J. M. (1993a). Foraging territories and crop production of a Mediterranean harvester ant in a grassland ecosystem. *Acta Oecologica* **14**: 405–414.
- López, F., Acosta, F. J., and Serrano, J. M. (1993b). Responses of the trunk routes of a harvester ant to plant density. *Oecologia* **93**: 109–113.
- MacKay, W. P. (1982). The effect of predation of western widow spiders (*Araneae: Theridiidae*) on harvester ants (*Hymenoptera: Formicidae*). *Oecologia* **53**: 406–411.
- Melhop, P., and Scott, N. J., Jr. (1983). Temporal patterns of seed use and availability in a guild of desert ants. *Ecol. Entomol.* **8**: 69–85.
- Morehead, S. A., and Feener, D. H. (1998). Foraging behavior and morphology: seed selection in the harvester ant genus, *Pogonomyrmex*. *Oecologia* **114**: 548–555.
- Morrison, L. W., Kawazoe, E. A., Guerra, R., and Gilbert, L. E. (2000). Ecological interactions of *Pseudacteon parasitoids* and *Solenopsis* ant hosts: environmental correlates of activity and effects on competitive hierarchies. *Ecol. Entomol.* **25**: 433–444.
- Nielsen, M. G., and Baroni-Urbani, C. (1990). Energetics and foraging behaviour of the European seed harvesting ant *Messor capitatus*. I. Respiratory metabolism and energy consumption of unloaded and loaded workers during locomotion. *Physiol. Entomol.* **15**: 441–448.
- Pol, P., and de Casenave, J. L. (2004) Activity patterns of harvester ants *Pogonomyrmex pronotalis* and *Pogonomyrmex rastratus* in the Central Monte Desert, Argentina. *J. Ins. Beh.* **17**: 647–661.
- Retana, J., and Cerdá, X. (2000). Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in thermal environment. *Oecologia* **123**: 436–444.
- Reyes-Lopez, J. L., and Fernandez-Haeger, J. (2001). Some factors determining size-matching in the harvester ant *Messor barbarus*: food type, transfer activity, recruitment rate and size-range. *Insectes Sociaux* **48**: 118–124.
- Reyes-Lopez, J. L., and Fernandez-Haeger, J. (2002a). Food storage in the nest and seed selectivity in the harvester ant *Messor barbarus* (*Hymenoptera: Formicidae*). *Sociobiology* **39**: 123–128.
- Reyes-López, J. L., and Fernández-Haeger, J. (2002b). Composition-dependent & density-dependent seed removal rates in the harvester ant *Messor barbarus*. *Sociobiology* **39**: 1–10.
- Rissing, S. W. (1982). Foraging velocity of seed-harvester ants, *Veromessor pergandei*. *Environ. Entomol.* **11**: 905–907.

- Sanders, N. J., and Gordon, D. M. (2000). The effects of interspecific interactions on resource use and behavior in a desert ant. *Oecologia* **125**: 436–443.
- Sanders, N. J., and Gordon, D. M. (2002). Resources and the flexible allocation of work in the desert ant, *Aphaenogaster cockerelli*. *Insectes Sociaux* **49**: 371–379.
- Sheata, M. N., and Kaschef, A. H. (1971). Foraging activities of *Messor aegyptiacus*. *Insect. Soc.* **18**: 215–226.
- Statsoft, Inc. (1998) *STATISTICA for Windows (Computer program manual)*, StatSoft, Inc., Tulsa, Oklahoma
- Vogt, J. T., Smith, W. A., Grantham, R. A., and Wright, R. E. (2003). Effects of temperature and season on foraging activity of red imported fire ants (*Hymenoptera: Formicidae*) in Oklahoma. *Environ. Entomol.* **323**: 447–451.
- Whitford, W. G. (1978). Foraging in seed harvester ants *Pogonomyrmex* spp. *Ecology* **59**: 185–189.
- Whitford, W. G., and Ettershank, G. (1975). Factors affecting foraging activity in Chihuahuan desert harvester ants. *Environ. Entomol.* **4**: 689–696.
- Wirth, R., and Leal, I. R. (2001). Does rainfall affect temporal variability of ant protection in *Passiflora coccinea*? *Ecoscience* **8**: 450–453.
- Zar, J. H. (1996). *Biostatistical Analysis, 3rd edition*, Prentice-Hall, New Jersey, p. 662.