



RESEARCH PAPER

Solar Elevation Triggers Foraging Activity in a Thermophilic Ant

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Abstract

Nycthemeral rhythm is an important biological trait that allows animals to escape predation and competition and, conversely, to coincide with mutualists. Although laboratory studies have shown that the rhythm depends on both endogenous factors and cyclic environmental cues, the latter is often poorly understood, particularly in the wild. Because insects are mostly ectothermal organisms, their activity rhythm is often thought to depend directly on ground temperature. In Mediterranean habitats, *Cataglyphis* ants are well known for their unusual thermoresistance, allowing them to forage in summer at the central hours of the day when the ground reaches temperatures that are lethal to their competitors. However, we show that the rhythm of *Cataglyphis floricola* in south-western Spain is governed by light cues rather than by temperature. First, variations in ant traffic at the nest entrance were better explained by solar elevation angle than by ground temperature on both seasonal and daily scales. Second, if ants waited for the ground to reach a threshold temperature to start their activity, we would expect similar temperatures regardless of the opening hour. However, we found a significant increase in ground temperature as opening hour got later in the day. Third, by using a simple experimental set-up that increased the apparent solar elevation over the nest entrance, we provoked a delay of nest closure time. We discuss the relevance of these results with respect to the life history of *Cataglyphis* species and their possible consequences in relation to global warming.

Introduction

Most animals alternate foraging with other activities at a specific rhythm, on both a daily and annual scale. From an ecological and evolutionary perspective, such partitioning of time is important because it potentially reduces negative interactions among sympatric species (Kronfeld-Schor & Dayan 2003). Foraging at different hours of the day or during different seasons of the year may, for example, reduce interference competition (Alanärä et al. 2001), predation (Fenn & MacDonald 1995) and parasitism (Feener 1988; Orr 1992). Species rhythm may also condition interactions among mutualists (Boulay et al. 2007; Ranganathan et al. 2010). Determining

the cues that drive a species' rhythm of activity is therefore a key question to understand species coexistence.

Ant communities are often structured by trade-offs between dominance and thermoresistance, whereby co-occurring species have different foraging schedules in relation to their position along a hierarchy (Albrecht & Gotelli 2001). This is particularly evident in Mediterranean and subtropical habitats where ground temperature shows considerable daily and monthly fluctuations (Cerdá et al. 1997, 1998; Bestelmeyer 2000; Albrecht & Gotelli 2001; Holway et al. 2002; Thomas & Holway 2005). Small-sized species with limited thermoresistance often occupy a dominant rank in the hierarchy, while subordinates

forage at more extreme temperatures. For example, the genus *Cataglyphis* regroups about a hundred species distributed exclusively in Old World arid, desertic and semidesertic habitats. They are often considered submissive species that hardly defend a food source against competitors (Cerdá et al. 1998). However, they have evolved numerous adaptations, including the continuous production of heat shock proteins (Gehring & Wehner 1995), long legs that separate the body from the ground surface (Cerdá et al. 1997; Clémencet et al. 2009) and the use of thermal refuges (Cerdá & Retana 2000) that allow them to forage at temperatures (>50°C) that are not tolerated by dominant species (Lenoir et al. 2009).

The fact that an ant species presents several adaptations to temperature does not necessarily imply that this factor is the pacemaker of its foraging activity. Nevertheless, most studies suggest that ant activity rhythm is directly triggered by ground temperature. For example, in seed-harvesting ants, the daily pattern of activity changes between the cold and hot seasons (Whitford et al. 1981; Azcárate et al. 2007; Cole et al. 2010). In winter, colonies have a unimodal peak of activity around noon. As diurnal ground temperature increases during spring and summer, colonies start foraging earlier and stop later but make a long break at midday. A correlation between ant activity and temperature has been reported in a number of other non-granivorous species as well (Nuss et al. 2005; Yamamoto & Del-Claro 2008; Chong & Lee 2009). Although such correlative data provide important pieces of information, they might also be confounding because, at a local geographical scale, temperature may roughly correlate with other environmental cues like light intensity and solar elevation. In a recent study, correlative data were combined with an experimental approach to show that nest inbound and outbound movements of *Myrmecia pyriformis* foragers are driven exclusively by light intensity and not by temperature (Narendra et al. 2010).

The aim of the present study was to test the role of ground temperature and solar elevation in triggering the foraging activity of the thermophilic ant *Cataglyphis floricola* Tinaut 1993. Although this species has a rudimentary recruitment system (Amor et al. 2010), workers mainly use path integration and landmark learning to find their way outside the nest. Therefore, we hypothesized that foraging could be conditioned by solar cues rather than solely by temperature. First, we used general linear models and general additive models to test the correlation between the amount of traffic at the nest entrance with ground temperature and average solar eleva-

tion, both at seasonal and at daily temporal scales. Second, we tested the correlation between the opening and closing nest hour and ground temperature. In *C. floricola*, workers use small stones and sand to close the nest entrance at the end of the daily activity period (Video S1, Supporting Information). This behaviour may have evolved as a mean to protect the colony against predators and parasites (Hölldobler & Wilson 1990). If workers wait for the ground surface to reach a specific temperature to start/stop foraging, we expected the slope of the regression of opening/closing hours against temperature to be non-significantly different from 0. Finally, we experimentally increased the apparent solar elevation over the nest entrance and decreased ground temperature and tested whether this manipulation delayed nest closure.

Material and Methods

Model Species and Study Site

Cataglyphis floricola lives in semi-arid sandy areas around the lower basin of the Guadalquivir River, south-western Spain (F. Amor & P. Ortega, unpubl. data). The species has two distinct colour morphs that might be classified as two distinct species in the future. However, we conducted our study on the bicolour morph, exclusively. We used colonies from three populations, approximately 35 km apart. The Doñana National Park (DNP; 37°01'21"N 6°27'07"W) is a sclerophyllous scrubland. Villamanrique de la Condesa (VMC; 37°13'21" 6°18'46"W) and Aznalcazar (AZN; 37°16'16"N 6°13'05"W) are two open forests dominated by scarce pine trees (*Pinus pinea*). The climate in the region of study is mostly Mediterranean with Atlantic influence. Rainfalls, concentrated between Sept. and Apr., average 580 mm per year. Summers are generally very hot (air temperature exceeding 40°C), while winters are relatively mild.

Colonies of *C. floricola* contain up to 600 monomorphic workers (Amor et al., unpubl. data). They are strictly monogynous and monodomous, with one single entrance per nest. They mostly feed on dead insects, aphid honeydew and the petals of *Halimium halimifolium* (Cistacea). Colonies hibernate during the winter, from Oct. to late Mar.

Monitoring Foraging Activity

Foraging activity was measured on a total 62 randomly chosen nests at DNP, VMC and AZN.

Measurements were taken between Mar. and Sept. from 2005 to 2009. Each nest was observed during 1 d only, starting at least 1 h before the beginning of the activity and ending about 1 h after the activity ceased. For 36 nests, the number of nest inbounds and outbounds was counted during periods of 10 min every hour and extrapolated to 1 h. For the remaining 26 nests, the whole activity was monitored by videotape recording. Workers engaged in nest maintenance activities that did not move more than a few centimetres away from the nest entrance were not accounted for in this measure.

During each session of observation, ground temperature at the nest entrance was recorded to the nearest 0.1°C every 10 min using HOBO® data loggers. Temperatures were then averaged per hour.

Seasonal Variation in Ant Activity with Ground Temperature and Solar Elevation

To test the correlation between colony foraging activity and either temperature or solar elevation, we calculated the total ant traffic (the sum of outbounds and inbounds) from 08:00 to 20:00 h solar time for 40 colonies from DNP. This time interval encloses the beginning and end of activity throughout the year. Differences in ant traffic were compared between months using a linear model (lm) in R (R Development Core Team) in which the nest was the statistical unit and the month of observation was the predictor variable. Significant differences were assessed using backward contrast analysis in which non-significantly different levels (months) were progressively regrouped until reaching the minimum adequate model (Crawley 2007). Then, the average daily traffic in each month from Mar. to Sept. was regressed against either the average solar elevation or the average ground surface temperature from 08:00 to 20:00 h during the respective month. Because ant traffic was likely to vary with colony size which may also vary throughout the year, we included the average colony size (number of workers) during each month as an additional predictor. Average colony size per month was obtained from the excavation of 36 nests in 2008 and 2009 at DNP.

The average ground surface temperature was obtained by temperature recordings every hour from 08:00 to 20:00 h from Mar. to Sept. 2007 independently of ant activity monitoring. Temperature data were collected at two spots of DNP surrounded by *C. floridicola* nests using HOBO® data loggers. The average solar elevation per month was obtained by averaging the solar elevation angle calculated every

hour from 08:00 to 20:00 h on days 5, 15 and 25 of each month between Apr. and Sept. 2007. Solar elevation angle was obtained from <http://www.susdesign.com/sunangle/index.php>. Although both temperature and solar elevation data were obtained from only 1 yr, the average values per month vary little from year to year, and we assume data for 2007 to be good estimates for the period 2005–2009.

Daily Variations in ant Activity with Ground Temperature and Solar Elevation

The daily pattern of *C. floridicola* foraging activity was analysed using ant traffic at the nest entrance of the 40 previously mentioned colonies monitored at DNP plus similar data collected between Mar. 2005 and Sept. 2009 from 17 and five colonies of AZN and VMC, respectively. Data were standardized by dividing colonies' traffic at each hour by the maximum hourly traffic during that day. This allowed us to remove between-season and between-nest variations in total activity. Yet, the daily pattern of ant activity still varies greatly throughout the year and is difficult to model using polynomial regression. We therefore fitted a generalized additive mixed model (GAMM) using the mgcv package for R. The model was fitted using the quasi-binomial error distribution with the standardized ant traffic as the response variable and ground temperature, solar elevation and their interaction as fixed predictors. The colony was included as a random factor.

Nest Opening and Closure

In Aug. 2007, the opening hour and respective ground temperature of 17 nests located at VMC were monitored for 7 consecutive days. These data were then analysed by fitting a general linear mixed model using nlme package for R. Opening hour and ground temperature were the response variable and fixed factor, respectively. The colony was included as a random factor. If ground temperature triggered ant nest opening, we expected the slope to be non-significantly different from 0.

Nest closure hour was also monitored at the same locality between 30th Aug. and 7th Sept. 2007. Every second day during 8 d, the hour of closure and ground temperature of 10 colonies were recorded. At intermediate days, sun elevation on the nest entrance was manipulated 1.5 h before the expected closure hour using two mirrors (Fig. 1). One mirror (M1; 25 × 30 cm) was placed directly on the ground at approximately 0.5 m from the nest

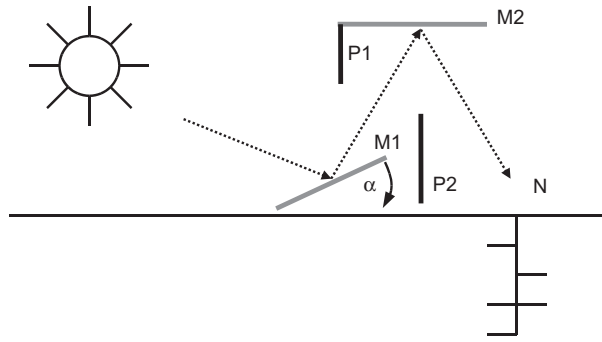


Fig. 1: Experimental set-up to modify the apparent solar elevation angle on the nest entrance (N). Sun rays were reflected by mirrors M1 and M2 but were precluded from reaching the nest directly by two cardboard panels (P1 and P2). The angle α was modified throughout the experiment to maintain an apparent solar elevation angle twice higher than without mirror.

entrance with the reflecting side up and inclined from the horizontal line by an angle α . The second mirror (M2; 25 × 30 cm) was placed in between M1 and the nest entrance (N), at approximately 40 cm from the ground, with the reflecting side down. Two cardboard panels (P1 and P2) precluded sun rays reaching N directly. The angle α was progressively modified throughout the experiment to maintain an apparent solar elevation angle on N about twice higher than without mirrors. For the ants, the modification of solar elevation was only partial as they could still use information from non-deviated polarized light reaching the nest entrance. Temperature at the nest entrance was also cooled down by 2°C. General linear mixed models were then fitted to compare the hour of and temperature at nest closure between manipulated and non-manipulated nests. If solar elevation determined the nest closing hour, we expected manipulated nests to close significantly later than non-manipulated nests. By contrast, if temperature triggered nest closure, we expected manipulated nests to close significantly earlier than the non-manipulated nests. Moreover, as for nest opening, we expected the slope between the hour of closure and ground temperature not to differ significantly from 0.

Results

Seasonal Variations in *Cataglyphis floricola* Activity

The season of activity of *C. floricola* could be divided into three periods (Fig. 2; lm: $F = 16.09$, $df = 2$, $p < 0.0001$). At the beginning of the season (Mar.–Apr.), ant traffic at the nest entrance ranged

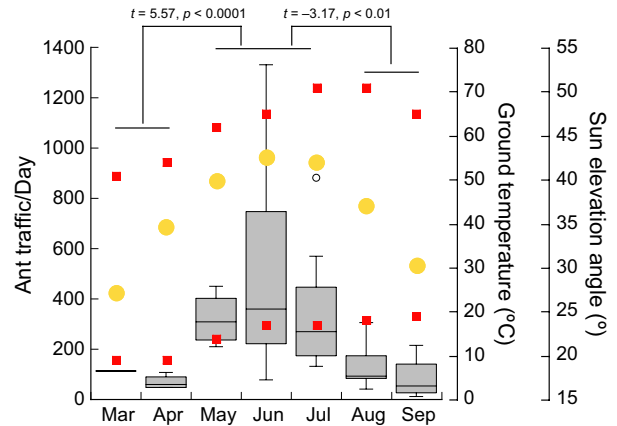


Fig. 2: Variation in daily ant traffic (sum of inbounds and outbounds) at the nest entrance between 8:00 and 20:00 solar time throughout the year, in relation to the average daily range of ground temperature (minimum and maximum; red squares) and average solar elevation angle (yellow circles).

between 30 and 270 inbound and outbound foraging movements per day. Then, ant traffic increased significantly to up to 1300 movements per day between May and July ($t = 5.57$, $p < 0.0001$). Aug. and Sept. marked the end of the season of activity with a significant decrease in ant traffic ($t = -3.17$, $p < 0.01$). Ground surface temperature during the day also increased slowly during the spring but reached its maximum in July and Aug., about a month after the peak of activity of *C. floricola*. As a result, ant traffic throughout the year was not significantly correlated with ground temperature (lm: $F_{1,5} = 0.46$, $p = 0.5259$, $R^2 = 0.08$) even when variations in colony size were accounted for (lm: $F_{1,3} = 2.52$, $p = 0.2104$, $R^2 = 0.56$). By contrast, ant traffic was correlated with the average solar elevation angle between 8:00 and 20:00 h, both when colony size was and was not accounted for (lm: $F_{1,3} = 9.09$, $p = 0.0181$, $R^2 = 0.92$ and $F_{1,5} = 8.33$, $p = 0.0343$, $R^2 = 0.63$, respectively).

Daily Variations in *Cataglyphis floricola* Activity

Ant traffic at the nest entrance also varied greatly throughout the day. The GAMM conducted on unstandardized activity explained a relatively small amount of variance ($R^2 = 0.34$). The results indicated that ground temperature alone did not significantly affect ant traffic at the nest entrance (Fig. 3; $df = 1.0$, $F = 0.75$, $p = 0.39$). However, both solar elevation and the interaction between solar elevation and temperature had a significant effect on ant traffic (Fig. 3; $df = 1.0$, $F = 5.34$, $p = 0.02$ and

df = 7.4, $F = 6.01$, $p \leq 0.001$). Hence, when sun elevation was low (below 20°), ant traffic was low irrespectively of ground temperature. When sun elevation increased, so did ant traffic. It was higher when sun elevation reached 70° and ground temperature was 48°C. At warmer ground temperature, the ant traffic started to decrease, even when sun elevation was high, probably because of a physiological limitation of ants to support very high temperatures. This difference in the daily pattern of activity is well exemplified on Fig. 4, showing ant traffic at two different nest entrances on 25th May 2005 and on 5th July 2007. In May, when ground temperature was still relatively mild throughout the day, ant traffic followed a bell-shaped pattern centred on the hour of highest solar elevation. By contrast, in July, when ground temperature reached more than 60°C, ant traffic slowed down at midday.

Nest Opening and Closure

Ninety-two per cent of the observed variance in nest opening temperature was owing to differences between nests, while the variance explained by within-nest differences was only 8% (Fig. 5a). If ants waited for the ground to reach a threshold temperature to start their activity, variations in temperature at nest opening would have been independent of the opening hour. However, we found a significant increase in ground temperature as opening hour got

later in the day, (lme: $t_{87} = 7.69$, $p < 0.0001$) suggesting that the ants did not wait until ground temperature reached a threshold temperature to start the activity.

Nest closure time occurred 8 min 51 s \pm 1 min 38 s later in mirror-manipulated than in non-manipulated conditions (Fig. 5b; lme: $t_{69} = 2.85$, $p = 0.0063$). Temperature at nest closure also varied more between than within nests (75% vs. 25%, respectively) and was on average $2.0 \pm 0.4^\circ\text{C}$ lower in manipulated colonies. Moreover, the slope of the regression between nest closure hour and ground temperature was highly significant (lme: $t_{69} = -7.84$, $p < 0.0001$), suggesting that nests did not close at a fixed temperature.

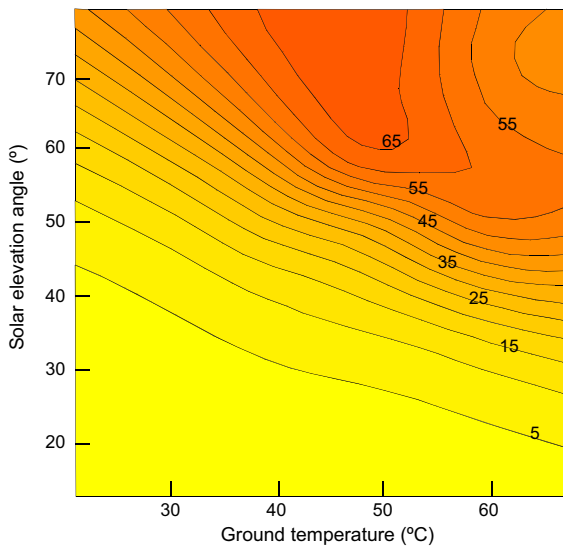


Fig. 3: Relation between ground temperature, solar elevation angle and the daily pattern of *Cataglyphis floricola* activity. Numbers on the constant lines and red intensity denote standardized foraging activity (%).

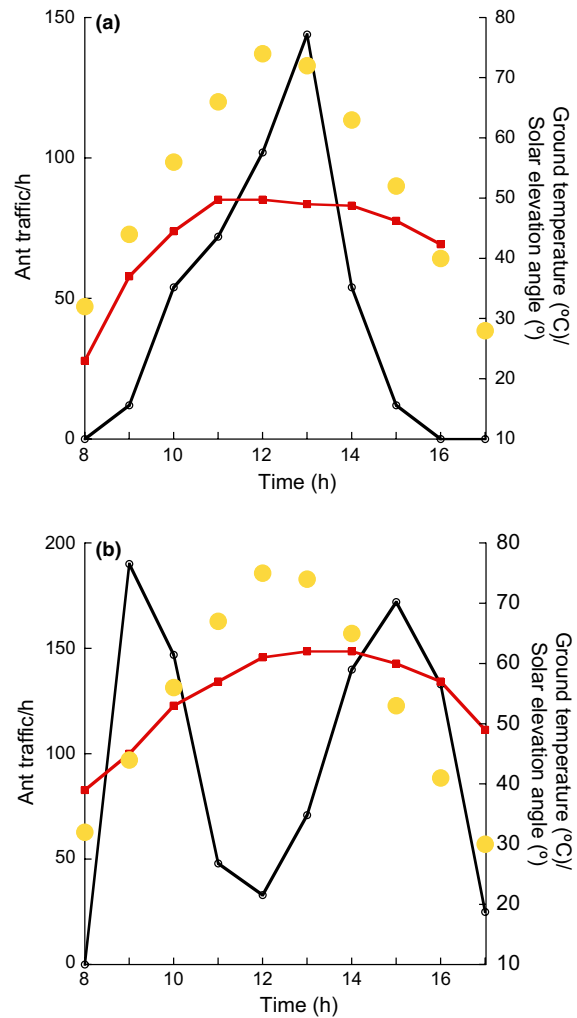


Fig. 4: Two examples of daily variation in ant traffic (black lines) at the entrance of two nests recorded on 25th May 2005 (a) and 5th July 2007 (b). Red squares and yellow circle represent the mean ground temperature and solar elevation, respectively.

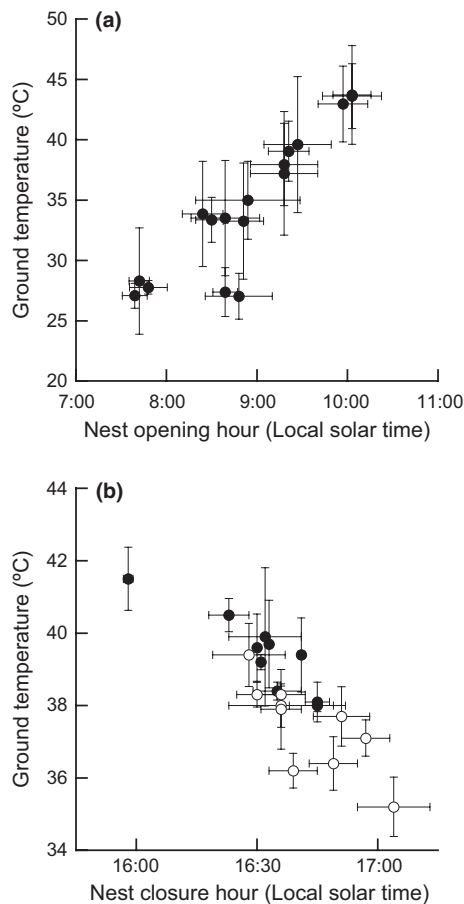


Fig. 5: Relation between nest opening (a) and closure (b) temperature and hour. Each circle represents the mean value (\pm SE) for different nests monitored during 4–7 d consecutively. For nest closure, open and filled symbols represent manipulated (with mirrors) and control conditions, respectively.

Discussion

The present study clearly demonstrates that the beginning and end of foraging activity of the thermophilic ant *C. floricola* is triggered by solar cues rather than directly by temperature. First, the pattern of foraging activity is better explained by variations in average solar elevation than by differences in ground temperature both at the seasonal and at daily scales. Second, in contrast to what would be expected if temperature triggered ant activity, the nest opening and closing hours correlated with ground temperature. Third, experimentally increasing solar elevation and decreasing temperature at the nest entrance delayed nest closure.

The role of light and solar cues on ant activity has seldom been investigated. To the best of our knowledge, only one recent study has experimentally

addressed this question. Like in the case of *C. floricola*, it was shown that the foraging activity of the Australian bull ant, *M. pyriformis*, is triggered by light cues though in the opposite way (Narendra et al. 2010). Hence, in this nocturnal species, foragers wait for a significant reduction in light intensity to leave their nest. On the contrary, most studies directly point out temperature as the major determinant of ant activity (Hölldobler & Wilson 1990; Cole et al. 2010). On a seasonal and daily scale, both factors are roughly correlated. Temperature is generally higher in summer and during the light phase than in winter and during the dark phase. However, earth thermal inertia delays ground cooling after the reduction of solar radiation. This allowed us to distinguish, by means of linear and additive models, between both effects. This showed that ant traffic at *C. floricola* nest entrance was better explained by solar elevation than by ground temperature. Hence, ant traffic in late summer and in the evening was already low while ground temperature remained high.

The use of nest material to close the nest at the end of the activity period is a peculiar behaviour found in a few ant genera, including *Cataglyphis*, *Messor*, *Harpegnathos* and *Pogonomyrmex* (Hölldobler & Wilson 1990 and references therein). Its main function is probably to protect the colony against predators and parasites during the night. In *C. floricola*, one single guard ant closes the nest with small stones and sand approximately 15–30 min after the end of foraging (ESM; FA pers. obs.). The apparent synchrony between the end of foraging and nest closure suggests that foragers and guards might rely on light cues to stop foraging and close the nest, respectively. By contrast, ground temperature may not provide reliable cues to close the nest. Hence, ground temperature when *C. floricola* colonies opened/closed the nest correlated with the hour of opening/closure. Such highly significant correlations were not expected if the colony waited for a specific temperature to start/stop activity. Ground temperature at the time of opening/closure varied more between colonies than between consecutive days. These variations could be due to differences in microenvironmental conditions, some nests being more in the shade than others. The demographic condition of a colony (e.g. number of workers) and an idiosyncratic component of worker behaviour could also explain these variations.

By using a relatively simple experimental set-up, we could modify the light reaching the nest entrance, and consequently the hour of closure. This

clearly demonstrated that light cues rather than temperature determine nest closure. Although the delay of closure was significant, it was relatively small (8 min 51 s). This suggests that nest closure is probably influenced by a number of other variables that correlate with solar elevation in natural conditions but that were not affected by our experiment. This is the case, for example, of light intensity and endogenous factors that govern workers' internal clock.

All species in the *Cataglyphis* genus are thermophilic. Several morphological (long legs), behavioural (fast moving and the use of thermal refuges) and physiological (heat shock protein synthesis) adaptations confer them an extraordinary elevated thermotolerance (Gehring & Wehner 1995; Cerdá & Retana 1997, 2000; Clémencet et al. 2009). In the case of *C. floricola*, workers' critical thermal maximum (CTM) measured in the laboratory is 50°C (Cerdá 2001), which is 5–10 degrees higher than other sympatric ant species. This gives *C. floricola* a clear advantage against competitors that are forced to forage during the cooler season of the year, or at dawn and dusk. For example, *Tapinoma nigerrimum*, one of the most dominant species in Western Mediterranean, can hardly support temperatures exceeding 40°C. It is active during the day in early spring and very early in the morning in summer (Cerdá et al. 1989). By contrast, in the National Park of Doñana, *C. floricola* is the only ant species that forages at midday in June–July. However, foraging at the warmest hours of the day entails important limitations. Contrarily to many ant species that deposit chemical marks on the substrate to communicate the location of a valuable food source to their nestmates, *Cataglyphis* species generally forage individually. Pheromone temperature sensibility was suggested to constitute a major constrain on the recruitment capacities of *Cataglyphis* species (Ruano et al. 2000). Instead, *Cataglyphis* species rely on important individual cognitive capacities to find their way back home on the basis of path integration and visual landmark learning (Wehner & Lanfranconi 1981; Knaden & Wehner 2005; Ronacher 2008; Wehner 2009). This probably explains why *C. floricola* foragers need solar elevation angle upon 20° to correctly recognize shapes distributed on the horizon and be able to return to their nest.

Although our results emphasize the role of solar elevation angle in determining *C. floricola* activity, they do not exclude the possibility that extreme temperatures limit this species' foraging activity. On the one hand, the effect of solar elevation on ant

traffic daily pattern depended on the temperature. At relatively mild temperature, solar elevation triggered ant activity, but when temperature exceeded 48°C, ant activity decreased, irrespective of solar elevation. On the other hand, although total ant traffic correlated with the average day length between Mar. and Sept., *C. floricola* is completely inactive from late Oct. to early Mar. most probably because of cool temperature rather than solely because of short day length.

Finally, our results may predict a tragic scenario for the future of *Cataglyphis* species in a global changing world. As ground temperature will increase as a consequence of global warming, *Cataglyphis* species, like all ant species, may be forced to reduce their foraging activity during the central hours of the day. Most species might adapt to these new conditions and compensate the reduction in diurnal activity by starting to forage earlier in the morning. However, *Cataglyphis* species that need a minimum solar elevation angle to forage may show less plasticity to advance and retard their foraging onset and offsets, respectively. Global warming may therefore limit greatly their foraging behaviour and inflict a net competitive disadvantage against other species. Further monitoring of colony activity in the long term will be necessary to give more credence to this scenario.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Video S1: *Cataglyphis floricola* worker closes her nest at the end of daily activity.

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