

RESEARCH ARTICLE

Different effects of temperature on foraging activity schedules in sympatric *Myrmecia* ants

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SUMMARY

Animals avoid temperatures that constrain foraging by restricting activity to specific times of the day or year. However, because temperature alters the availability of food resources, it is difficult to separate temperature-dependent effects on foraging and the occupation of temporal niches. By studying two congeneric, sympatric *Myrmecia* ants we isolated the effect of temperature and investigated whether temperature affects foraging schedules and causes the two ants to be active at distinct times of the day or year. We monitored foraging activity and identified the ants' temperature tolerance in the laboratory by determining (1) critical thermal minima and maxima (CT_{min} and CT_{max}) and (2) the relationship between walking speed and temperature. Ants of *Myrmecia croslandi* were diurnal throughout the year, but ceased above-ground activity during winter. Surface temperature at the onset of foraging was 9.8–30.1°C, while their laboratory CT_{min} and CT_{max} were 10.4 and 48.5°C, respectively. Time of foraging onset was significantly influenced by surface temperature at time of sunrise and of onset. Ants of *Myrmecia pyriformis* were nocturnal throughout the year. Surface temperature at the onset of foraging was 5.4–26.2°C, while their laboratory CT_{min} and CT_{max} were 8.2 and 41.6°C, respectively. Time of foraging onset was not influenced by surface temperature, but solely by sunset time. We conclude that temperature determines the timing of foraging as well as the daily and seasonal foraging activity in *M. croslandi*, but has less obvious effects on *M. pyriformis*. In both species, CT_{max} was greater than temperatures at the natural foraging times.

Key words: ants, diurnal, nocturnal, temperature tolerance, walking speed.

INTRODUCTION

Animals, including mammals, birds and insects occupy distinct temporal niches by being active during specific periods of the year and/or at specific times of the day (Lynch et al., 1980; Kotler et al., 2002; Kronfeld-Schor and Dayan, 2003). The maintenance of such discrete seasonal and daily activity patterns allows animals to avoid predators, to reduce conflict with competitors and to optimally exploit food resources (Schoener, 1974; Kronfeld-Schor and Dayan, 2003). To determine suitable times of activity, animals may monitor environmental variables such as light (Kotler et al., 1991; Elangovan and Marimuthu, 2001; Narendra et al., 2010) and temperature (Grubb, 1978; Fraser et al., 1993) as well as anticipate daily events such as sunrise and sunset with the aid of their internal circadian clocks (de Groot, 1983; Welbergen, 2008).

Similar to other animals, ants also partition their niches by being active during specific periods of the year and at specific times of the day. While light intensity affects seasonal and daily activity patterns of ants (Creighton, 1953; Narendra et al., 2010), it is the role of temperature in governing activity that has been extensively investigated (e.g. Fellers, 1989; Heatwole and Harrington, 1989; Cerda et al., 1998; Ruano et al., 2000). Most ant species forage at surface temperatures between 10 and 45°C (Hölldobler and Wilson, 1990). For instance, workers of *Rhytidoponera convexa* and *Solenopsis invicta* forage at temperatures of 13–31 and 15–43°C, respectively (Briese and Macauley, 1980; Porter and Tschinkel, 1987).

Variations in foraging patterns may depend, partly, on the thermal biology of ant species (Pol and de Casenave, 2004). Behavioural responses of ants to temperature changes include switching from diurnal to nocturnal activity (Briese and Macauley, 1980; Fellers, 1989; Heatwole and Muir, 1989), switching from continuous to bimodal activity (Sheata and Kaschef, 1971; Greenaway, 1981; Marsh, 1985a; Heatwole and Harrington, 1989; Heatwole and Muir, 1991) or even aestivating or hibernating during particular seasons (Talbot, 1943; Briese and Macauley, 1980).

Critical and lethal thermal tolerance limits are used to determine physiological responses of ants to temperature changes and to establish thermal limits on ant foraging. The upper and lower thermal tolerance limits constrain an animal's performance (reviewed by Angilletta et al., 2010) and limit its distribution, abundance and survival (Gray et al., 1997). Hence, tolerance limits encompass the full range of temperatures at which animals can be active. However, animals rarely forage at critical tolerance limits (McConnachie et al., 2007). They may nevertheless be forced to forage close to these limits as a result of predation pressure or competition. For instance, Saharan desert ants risk exposure to harmful temperatures by foraging at their critical thermal limit of 53.6°C to avoid their predator lizards that cannot tolerate such high temperatures (Wehner et al., 1992). In the Mediterranean region, subordinate species of ants that are heat tolerant are forced to forage close to their critical limits to gain a competitive advantage over more dominant ant species that are heat intolerant (Cerda, 2001).

Although ants experience daily and seasonal temperature fluctuations while foraging, only a few studies have addressed thermal tolerance of ants in the context of their foraging activity (e.g. Heatwole and Harrington, 1989). In addition, as temperature alters the availability of food resources and the distribution of vegetation, pinpointing the sole effect of temperature on foraging has been difficult (Ruano et al., 2000). Species that utilise the same resources in the same ecological niche but at distinct times of the day, and therefore at different temperatures, have been suggested to be essential models for identifying the significance of temperature on foraging (Begon et al., 1987). Such models would also help determine whether temperature drives animals to be active at different times. Such an ideal model system of congeneric and sympatric species has been identified in the Australian ant genus *Myrmecia* (Greiner et al., 2007; Narendra et al., 2011). Two sympatric *Myrmecia* ants (Fig. 1) occupy discrete temporal niches in summer: the diurnal *Myrmecia croslandi*, Taylor, and the nocturnal *Myrmecia pyriformis*, Smith (Narendra et al., 2010). The discrete temporal niches they occupy are characterised by fluctuations in ambient light and surface temperature. Light intensity at sunset has already been shown to determine the onset of foraging of the nocturnal species (Narendra et al., 2010). By identifying tolerated temperatures both in the field and in the laboratory, we investigated (1) whether temperature determines or modifies the onset of foraging of both species and (2) whether temperature restricts each species to their distinct temporal niche. If temperature has an effect on the foraging schedules of the two species, we would expect (1) their daily and seasonal foraging activity to be dependent on temperature, (2) workers to tune their activity to match preferred temperature ranges and (3) the range of temperatures they tolerate to correspond to the foraging limits in the field.

MATERIALS AND METHODS

Study site and study species

The study was conducted in 2009 and 2010 at the Australian National University's campus field station in Canberra, Australia (35°16'50"S, 149°07'50"E).

Myrmecia croslandi workers (also known as 'jack jumpers') are monomorphic and measure 11 mm in body length. *Myrmecia pyriformis* workers exhibit size polymorphism and their body length ranges between 14 and 25 mm. Both species forage individually on nearby trees such as *Eucalyptus macrorhyncha* and *Eucalyptus viminalis* or on the ground. They return to the nest with prey such as flies, earwigs, spiders, beetles and moths during summer. In addition, *M. croslandi* workers have also been observed feeding on exudates of sap-sucking homopteran insects (A.N., unpublished observations).

Environmental data

Surface temperature was recorded to a precision of $\pm 0.1^\circ\text{C}$ using type T thermocouples connected to a Datataker[®] data logger (model 500 with memory card, Datataker Industrial Data Logger Systems, Scoresby, VIC, Australia), with a platinum resistance thermometer as a reference. The thermocouple recorded the top 2 mm of soil temperature at 15 s intervals within 50 m of each nest. Data were downloaded once a week.

Monitoring activity patterns

We studied two nests for each species. At each nest, we monitored the outbound forager traffic for at least 60 min before and 40 min after the onset of foraging. We counted the number of workers that crossed a reference circle of 30 cm around the nest entrance in 10 min bins. The two species were observed on the same day to minimise



Fig. 1. The two sympatric *Myrmecia* ants: (A) the diurnal *M. croslandi* and (B) the nocturnal *M. pyriformis* (photographs by Ajay Narendra).

variations in weather conditions between days. Foraging activity was recorded on days when a 5 min change in sunrise time occurred between Austral summer (January) and spring (September) (Bureau of Meteorology: <http://bom.gov.au>). In total, we observed *M. croslandi* on 22 days and *M. pyriformis* on 42 days. The difference in the number of sampling days is due to *M. croslandi* not being active on the surface in winter.

Other astronomical data, such as sunset time and astronomical twilight time period for each day of recording, were obtained from the Bureau of Meteorology. Sunrise is defined as the instant at which the upper edge of the sun appears above an ideal horizon. Sunset is defined as the instant the upper edge of the sun's disc coincides with an ideal horizon (Bureau of Meteorology). The morning astronomical twilight is the period from when the centre of the sun's disc is 18 deg below the horizon until sunrise. The evening astronomical twilight is the period from sunset until the time when the centre of the sun's disc is 18 deg below the horizon.

Temperature tolerance

We used two measures to determine the temperature tolerance of individuals of both species: (1) the critical thermal maximum (CT_{\max}) and critical thermal minimum (CT_{\min}) and (2) the temperature-dependent mean walking speed of individuals. CT_{\max} and CT_{\min} as used here are not lethal temperatures, but are defined as the temperatures at which locomotion of individuals became impaired and individuals lost the ability to escape conditions that could result in death in the field (Schumacher and Whitford, 1974; Kay, 1978). In the laboratory, recovery is possible after short exposures to CT_{\max} and CT_{\min} . The use of CT_{\max} and CT_{\min} is justified because ants equilibrate quickly with their direct environment because of their small bodies. Furthermore, the determination of CT_{\max} and CT_{\min} in this procedure did not harm

the animals. While CT_{\max} and CT_{\min} values indicate the temperature tolerance of individuals, they may not always be ecologically relevant. We have attempted to provide an ecologically sensitive measure of temperature tolerance by determining the relationship between the walking speed of ants and temperature.

These experiments were carried out within the activity time window of each species, during the day for *M. croslandi* (December–February 2009–2010, Austral summer) and during the night for *M. pyriformis* (in April 2009, Austral autumn). Individual ants were placed inside a cylindrical plastic tube chamber, 10 cm long and 4 cm wide, which was then placed in an incubator in a constant-temperature cold room ($5 \pm 1^\circ\text{C}$). Both ends of the plastic tube were covered with a mesh to allow free circulation of air and through which a copper–constantan thermocouple probe was connected to a Physitemp[®] BAT-12 thermometer (Physitemp, Clifton, NJ, USA). For both CT_{\max} and CT_{\min} experiments, the ants were kept at 25°C for 30 min prior to testing by setting the temperature of the incubator. We chose this temperature (25°C) as ant colonies are thought to maintain their nest temperatures at about 25°C (Banschbach et al., 1997) and certain ants (*Linepithema humile*) exhibit maximum temperature tolerance when acclimated to 25°C (Jumbam et al., 2008). For CT_{\max} and CT_{\min} experiments we increased and decreased temperature, respectively, from 25°C at a rate of $0.6\text{--}0.8^\circ\text{C min}^{-1}$ (see Fig. 2A). Similar rates close to $1.0^\circ\text{C min}^{-1}$ have previously been used in studies with ectotherms (Christian and Morton, 1992; Mitchell et al., 1993; Lutterschmidt and Hutchison, 1997a; Lutterschmidt and Hutchison, 1997b; Hu and Appel, 2004; Chown et al., 2009). Both the heating and cooling rate were controlled by turning the incubator on or by switching the incubator off. The placement of the thermocouple probe inside the plastic tube chamber ensured that we continuously measured the temperature the ants experienced. We also placed moist cotton wool inside the tube to prevent desiccation of the ants.

To check whether ant temperature tracked chamber temperature closely without significant lag, we inserted a type T thermocouple probe (0.2 mm individual wire diameter) into the thorax of three dead *M. croslandi* ants and three dead *M. pyriformis* ants. The ants were then placed into the chamber along with a thermocouple that monitored chamber temperature. The three ants for each species were measured individually along with the chamber temperature using separate thermocouples connected to a multichannel datalogger (Datataker 500, BIOLAB Pty Ltd, Mulgrave, VIC, Australia) with thermocouples referenced against a platinum resistance thermometer. The datalogger was connected to a computer and controlled by DeLogger data acquisition software using a 1 s

sampling rate (v. 4, Sven Holwell, BIOLAB Pty Ltd). The dead ants were kept at 25°C for 30 min and the protocol used to determine CT_{\max} and CT_{\min} of live ants was replicated. We found that ant temperatures track chamber temperature very closely at ramp speeds between $0.63^\circ\text{C min}^{-1}$ (Fig. 2B) and $0.75^\circ\text{C min}^{-1}$ (Fig. 2C). These temperatures serve as a measure of the equilibrium temperature of an ant without evaporative cooling and metabolic heat production (Bakken, 1976; Christian and Morton, 1992). As ants are small insects with low body mass, this temperature is approximately equal to their body temperature (Casey, 1981; Marsh, 1985b; Terblanche et al., 2007).

The experiments in 2009/2010 yielded unusually high CT_{\max} values for both species. We therefore determined CT_{\max} for an additional six ants of each species using more sensitive type T thermocouple probes (see above) and found CT_{\max} , but not CT_{\min} , to be lower by about 10%, indicating that the initial probe had provided incorrect readings. We scaled the results from our initial experiments accordingly. In addition, to check the linearity of ramp speeds in our incubator and the possible effects of varying ramp speeds, we repeated CT_{\max} experiments on two different days in March 2011 with *M. croslandi* at ramp speeds of 0.48 and $0.67^\circ\text{C min}^{-1}$ using type T thermocouples (0.2 mm wire) placed inside five chambers that allowed us to record chamber temperatures for five ants simultaneously using the same data logging system as described above. All thermocouples used in this study were calibrated against a mercury thermometer ($\pm 0.1^\circ\text{C}$) with temperature varied by an ice bath (0.5°C) or by using a thermostatically controlled water bath (Thermomix, B. Braun Melsungen, Melsungen, Germany).

For both CT_{\max} and CT_{\min} experiments, ants were video recorded for the total duration of the experiment, using a Sony DSR-PD 170p or a Sony HDR-CX550 video camcorder at 25 frames s^{-1} . We viewed the long axis of the plastic tube and the display on the Physitemp BAT-12. The temperature at which individuals lost coordination and the ability to right themselves (the instant at which an individual fell on its back and was unable to stand on all its legs) as observed on a monitor outside the cold room was noted as CT_{\max} . The temperature at which individuals became stationary followed by a lack of response to gentle prodding by a probe was noted as CT_{\min} . We analysed video footage to calculate the walking speed of ants (see below).

Analysis

Activity patterns

We used a generalised linear regression analysis to examine the effect of sunrise/sunset time, surface temperature at sunrise/sunset

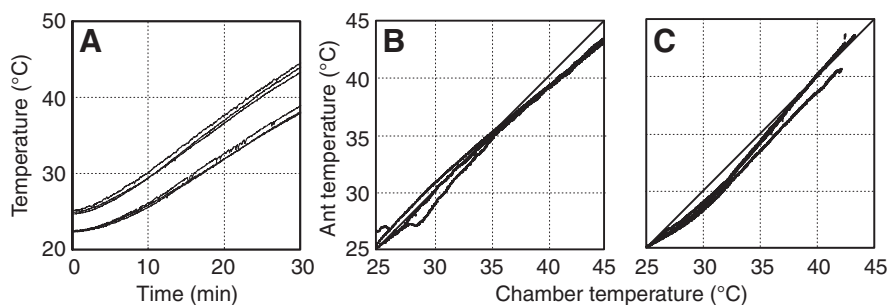


Fig. 2. The degree to which the temperature of ants tracks the temperature measured in experimental chambers. (A) Temperature ramp measured in six tube chambers simultaneously using type T thermocouples. Note that absolute temperature in chambers depends on their position in the incubator, but that the temperature ramps are linear with a mean of $0.67^\circ\text{C min}^{-1}$ (range $0.61\text{--}0.72^\circ\text{C min}^{-1}$). (B and C) Ant temperature against chamber temperature as measured with thermocouples inserted into the thorax of three dead ants each of *M. croslandi* (B) and *M. pyriformis* (C). Ramp speed was 0.63 and $0.75^\circ\text{C min}^{-1}$, respectively. Slopes for the six examples lie between 0.86 and $1.1^\circ\text{C ant temperature/chamber temperature}$ with $r^2 > 0.99$ in all cases.

and surface temperature at onset of foraging on the time of onset of foraging. Any parameters that were not significant were dropped from the final model, as described in detail elsewhere (Narendra et al., 2010). As we measured the above variables according to changes in time of onset, time of foraging onset was considered the independent variable.

Temperature tolerance

We report the mean CT_{max} and CT_{min} values of individual ants from different nests. To determine whether the CT_{max} and CT_{min} of the diurnal and nocturnal species were different, a Mann–Whitney U -test was used, in order to account for the non-parametric nature of the data obtained from both experiments. To determine the walking speed, we used a custom-made MATLAB-based video analysis program (J. Hemmi and R. Parker, The Australian National University) to obtain x - and y -coordinates of the head position of the ant every second. From the change in coordinates of the head, we calculated the speed of the ant in $cm\ s^{-1}$ and determined the speed every minute, averaged over 1 min. For each ant we averaged values in $5^\circ C$ bins and determined the means and standard errors across all animals. We analysed the walking speed of ants in different temperature ranges using a Kruskal–Wallis and a Dunn's *post hoc* test.

RESULTS

Daily and seasonal foraging activity

Myrmecia croslandi workers were exclusively diurnal, but the time at which they exited the nest changed depending on surface temperature (Fig. 3A–E). On one day when the temperature at midday was above $38.0^\circ C$, *M. croslandi* workers did not leave their nest at all. On this day, the mean (\pm s.d.) temperature at the time ants would typically start foraging (between 08:00 and 10:00 h) was $26.7\pm 2.9^\circ C$, much higher than normal ($N=13$; Fig. 3A). On seven summer days between January and February, worker activity shifted from being continuous throughout the day (unimodal) to being bimodal (e.g. Fig. 3B,C). This switch in activity occurred when temperature near midday exceeded $35.0\pm 1.3^\circ C$ ($N=7$). Workers left the nest in two bouts during the cooler periods of the day, i.e. in the morning and evening. Mean (\pm s.d.) temperature at the time of foraging onset in the morning and evening was $23.6\pm 2.6^\circ C$ ($N=7$) and $29.3\pm 4.6^\circ C$ ($N=7$), respectively (e.g. Fig. 3C). Foraging activity was identified to be bimodal if peak activity had not been reached within 7 h after sunrise (Fig. 4; compare black with red lines). The only exception to this rule was one hot day when onset of foraging occurred late in the afternoon at 16:20 h when the temperature had dropped to $30.1^\circ C$ (Fig. 5A and Fig. 6B). On a cooler day in summer, when the temperature near midday was $25.0^\circ C$, onset of foraging occurred in the morning at 09:30 h when the temperature was $23.2^\circ C$ (Fig. 3B).

These ants completely ceased above-ground activity during the Austral winter (Fig. 5A). Workers ceased activity following a day when the temperature at sunrise was only $3.5^\circ C$. The large circular nest entrance, distinct in summer, gradually reduced in size and was completely covered during winter. We noted the first signs of foraging again in early October (Austral spring).

We never saw bimodal activity in *M. pyriformis* in response to surface temperature fluctuations (Fig. 3F–J). The onset of daily foraging activity occurred exclusively during the twilight period throughout the year (Fig. 4; grey lines). *Myrmecia pyriformis* workers were active throughout the study period with the exception of two cold winter days when the surface temperature at sunset dropped below $5^\circ C$ (Fig. 3H and Fig. 5B).

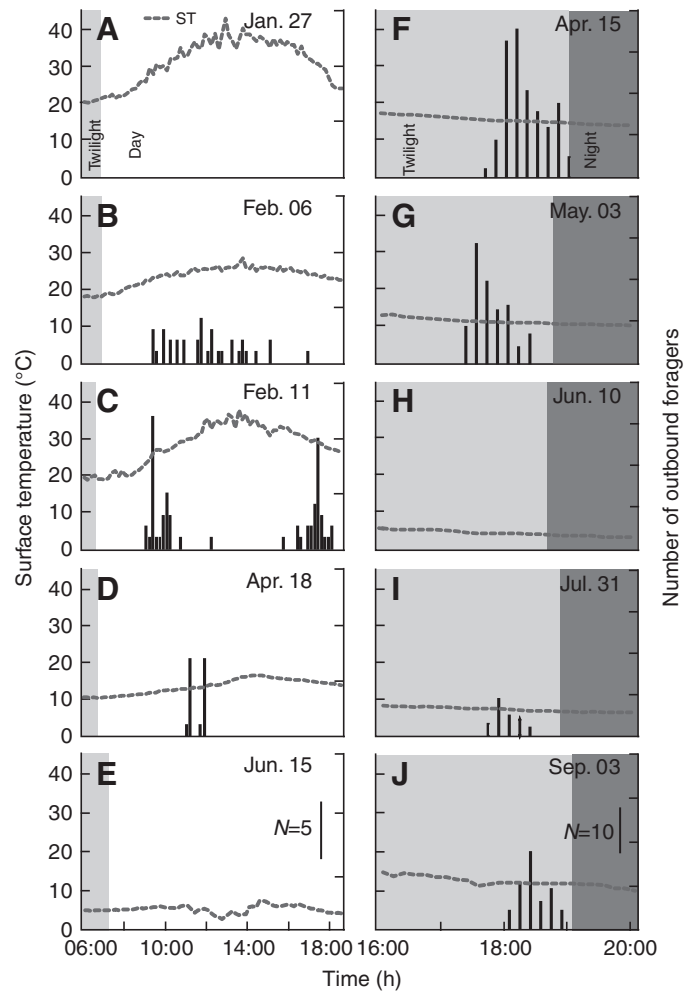


Fig. 3. Examples of daily patterns of outbound foraging activity in *M. croslandi* (A–E) and *M. pyriformis* (F–J). Dashed line is surface temperature and solid bars indicate the number of outbound workers. Panels A–E and F–J have been arranged according to decreasing sunrise times. *Myrmecia croslandi* is not active when surface temperature is high in summer (A) and when surface temperature drops below $3.5^\circ C$ in autumn (E). *Myrmecia pyriformis* is only inactive at surface temperatures below $5^\circ C$ (H).

The daily onset of foraging

The onset of foraging for *M. croslandi* occurred exclusively during the day at both nests from January to May (Fig. 5A). As foraging started at similar surface temperatures at the two nests we combined the data for our analysis (Fig. 6A,B). Temperature at the onset of foraging ranged between $9.8^\circ C$ in autumn and $30.1^\circ C$ in summer (nest A: mean \pm s.d. $19.9\pm 4.8^\circ C$, $N=7$; nest B: $19.8\pm 5.5^\circ C$, $N=7$) and temperature at sunrise ranged between $5.8^\circ C$ in autumn and $20.4^\circ C$ in summer (nest A: mean \pm s.d. $14.3\pm 4.8^\circ C$, $N=7$; nest B: $12.7\pm 7.0^\circ C$, $N=7$).

In *M. croslandi*, time of foraging onset was not significantly affected by sunrise time (Fig. 6A; $F_{1,13}=0.75$, $P=0.405$), but was influenced by surface temperature at sunrise ($F_{1,13}=19.75$, $P<0.001$) and temperature at time of foraging onset (Fig. 6B; $F_{1,13}=19.67$, $P<0.001$).

On 20 days of observation from January to May, outbound *M. croslandi* foragers encountered a wide range of surface temperatures from 10 to $40^\circ C$ (Fig. 7A). The majority of foragers, however, chose to leave the nest when temperatures were between 25 and $30^\circ C$.

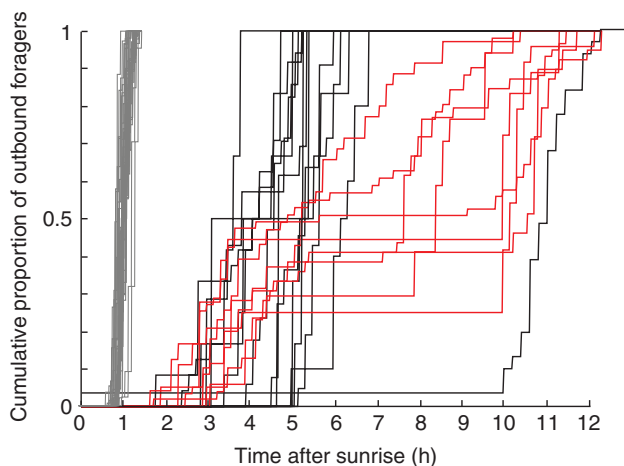


Fig. 4. Cumulative proportion of daily outbound *M. croslandi* workers (black lines: unimodal; red lines: bimodal) and *M. pyriformis* workers (grey lines). For *M. croslandi*, foraging activity was identified to be bimodal if peak activity was not reached by 7 h after sunrise (red lines).

The onset of foraging of *M. pyriformis* occurred exclusively during twilight at both nests from January to September (Fig. 5B) (see also Narendra et al., 2010). As foraging started at similar surface temperatures at the two nests we combined the data for our analysis (Fig. 6C,D). Temperature at onset of foraging ranged between 5.4°C in winter and 26.2°C in summer (nest A: mean±s.d. 9.8±2.6°C, $N=19$; nest B: 12.9±6.3°C, $N=23$). Temperature at sunset during onset of foraging ranged between 5.5°C in winter and 26.7°C in summer (nest A: mean±s.d. 9.8±2.6°C, $N=19$; nest B: 13.4±6.1°C, $N=23$).

In *M. pyriformis*, time of foraging onset was significantly influenced by sunset time (Fig. 6C; $F_{1,38}=499.40$, $P<0.001$) as shown previously (Narendra et al., 2010) but was not dependent upon surface temperature at sunset ($F_{1,38}=0.13$, $P=0.7$) or temperature at onset of foraging (Fig. 6D; $F_{1,38}=0.64$, $P=0.4$).

On 20 days of observation, from January to May, outbound *M. pyriformis* foragers encountered a wide range of surface temperatures between 5 and 30°C (Fig. 7B). The majority of foragers, however, chose to leave the nest when surface temperatures were between 10 and 15°C.

Temperature tolerance

CT_{max} was significantly different between the diurnal and nocturnal species (Mann–Whitney U -test, $P<0.001$, $U=0.0$), being higher in *M. croslandi* (mean±s.d. 48.5±1.1°C) than in *M. pyriformis* (41.6±1.7°C). CT_{min} was also significantly different between the diurnal and nocturnal species (Mann–Whitney U -test, $P<0.001$, $U=4.7$), being higher in *M. croslandi* (10.4±0.7°C) than in *M. pyriformis* (8.2±1.1°C).

While CT_{max} and CT_{min} indicate the extreme temperatures that these ants can tolerate in a laboratory environment, walking speeds provide us with a more ecologically relevant measure of tolerance limits for both species. This is especially true of the CT_{max} experiment, given the high values for both species.

Walking speeds of *M. croslandi* workers remained low and relatively unchanged at temperatures between 10 and 20°C (Fig. 8A). Walking speeds rapidly increased between 20 and 30°C and then remained constant until the CT_{max} was reached. However, as the sample record in Fig. 8B shows, ants continued to move intermittently, even at higher temperatures. In *M. croslandi*, the

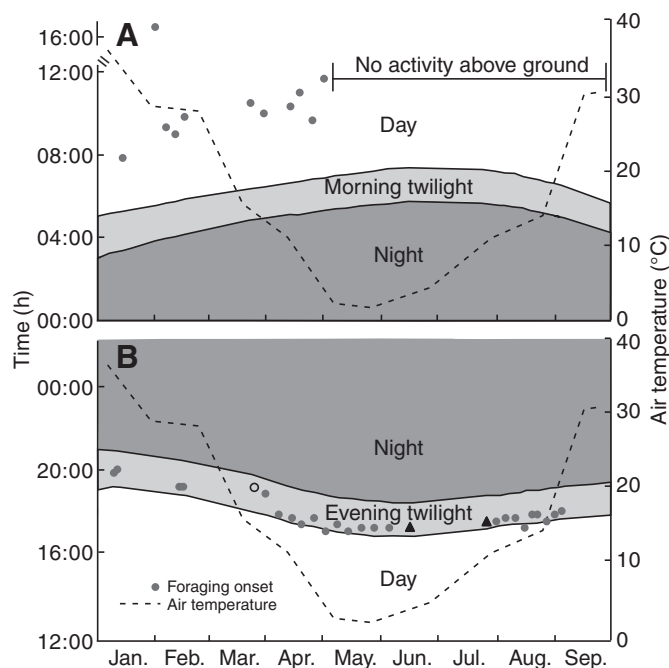


Fig. 5. Seasonal variation in onset of foraging for (A) *M. croslandi* and (B) *M. pyriformis* from January to September. Filled circles indicate onset of foraging, which is defined as the instance when the first forager left the nest followed by outbound forager activity in two consecutive 10 min bins. In B, filled triangles indicate inactivity above ground and open circles indicate an interrupted day of recording due to bad weather. Approximate monthly averages of the maximum air temperature (dashed line), obtained from the Gungahlin weather station, Canberra (<http://www.gungahlinweather.com>), are shown on the secondary y-axis. The morning twilight period ends with sunrise and sunset begins the evening twilight period.

maximum increase in walking speed (2.4 cm s⁻¹) occurred at a temperature range between 20 and 30°C (Fig. 8A; Dunn's *post hoc* test, $P<0.01$). Walking speeds of *M. pyriformis* workers remained low between 5 and 30°C, but increased significantly at temperatures above 30°C until the CT_{max} was reached. In *M. pyriformis*, the maximum increase in walking speed (0.73 cm s⁻¹) occurred at a temperature range between 30 and 40°C (Fig. 8A; Dunn's *post hoc* test, $P<0.001$). In both cases a significant increase in walking speed occurred at temperatures close to those at the upper end of the typical activity range in the field (indicated by horizontal bars in Fig. 8A). The increase in temperature affected walking speed in both *M. croslandi* (Kruskal–Wallis test, $P<0.0001$, $K=83.72$) and *M. pyriformis* (Kruskal–Wallis test, $P<0.0001$, $K=127$).

In a separate experiment with *M. croslandi* (Fig. 8C), we found that mean ant walking speed was not affected by different ramp speeds of 0.48 and 0.67°C min⁻¹ at 20–25°C ($P=0.87$, d.f.=8, $t=0.1588$, t -test), at 25–30°C ($P=0.67$, d.f.=10, $t=0.4272$, t -test) and at 30–35°C ($P=0.80$, d.f.=10, $t=0.2525$, t -test). However, compared with Austral summer 2009–2010, speeds were much slower when we tested these animals in Austral autumn 2011, when above-ground activity was already drastically reduced because of prolonged cool weather that had produced temperatures close to those at which *M. croslandi* normally ceases above-ground activity for the winter months.

DISCUSSION

Two sympatric ant species, *M. croslandi* and *M. pyriformis*, were found to be active at different times of the day and year. We investigated

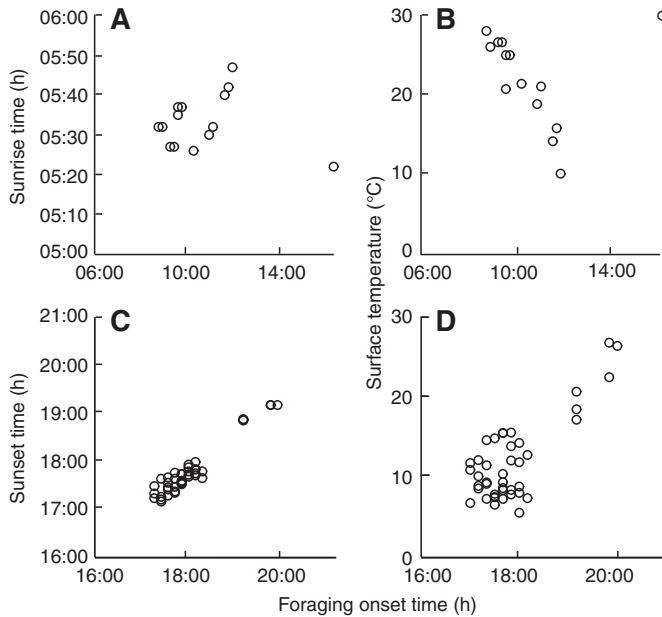


Fig. 6. Relationship between time of foraging onset and (A) sunrise time for *M. croslandi*, (B) surface temperature at onset for *M. croslandi*, (C) sunset time for *M. pyriformis* and (D) surface temperature at onset for *M. pyriformis*. Sampling was carried out at every 5 min change in sunrise time. Data shown are from two nests for each species.

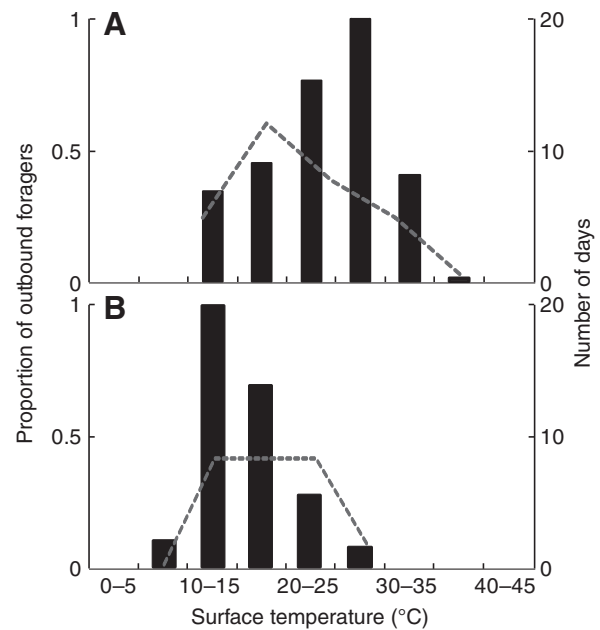


Fig. 7. Relation between proportion of outbound foragers and surface temperature in (A) *M. croslandi* and (B) *M. pyriformis*. Maximum number of workers for *M. croslandi* is 174 and for *M. pyriformis* is 708. The number of sampling days (dashed line) at different temperature bins is shown on the secondary y-axis. Temperatures shown are for periods between January and May when both ants are active. Bins contain values less than or equal to the upper bin boundary in this and following figures.

whether their different foraging schedules could be explained by the ants' thermal biology. We determined the relationship between surface temperature and onset of foraging of diurnal and nocturnal ants under natural conditions and identified their ecologically relevant thermal tolerance limits. Surface temperature at sunrise and at onset determined the time at which onset of foraging occurred in the diurnal *M. croslandi*, whereas only sunset time determined the time of foraging onset in the nocturnal *M. pyriformis*. The CT_{max} of both ants was high and beyond the maximum temperature at which both ants left the nest. However, the maximum increase in walking speed occurred at temperatures closer to those at which both species ceased foraging under natural conditions. Monitoring walking speed may thus prove to be useful in determining ecologically relevant tolerance limits of ants and possibly other walking insects, especially as CT_{max} does not always correspond to animals' natural activity limits.

Relationship between outbound foraging activity and surface temperature in the diurnal ant

Myrmecia croslandi workers began foraging at a wide range of surface temperatures (9.8–30.1°C) and completely ceased above-ground activity during the Austral winter (Fig. 5A). The onset of foraging for *M. croslandi* was dependent on the temperature at sunrise and not sunrise time (Fig. 6A). In addition, *M. croslandi* tuned its daily activity to avoid temperatures over 35°C (Fig. 3A,C). From January to May, most workers chose a narrow range of temperatures between 25 and 30°C to leave the nest (Fig. 7A), even though they could tolerate much higher temperatures as shown in our laboratory experiments (Fig. 8).

Temperature tolerance in the diurnal ant

Myrmecia croslandi workers had a CT_{max} of 48.5°C. This CT_{max} is comparable with that of desert ants such as *Cataglyphis cursor*

(CT_{max} 50°C) (Wehner et al., 1992; Clémencet et al., 2009). The CT_{max} of *M. croslandi* was inconsistent with their upper outbound foraging limit (30.1°C). Workers had a CT_{min} of 10.4°C which is comparable with that of other Australian diurnal ants such as *Iridomyrmex purpureus* (CT_{min} 14°C) (Greenaway, 1981) and North American desert honey ants *Myrmecocystus* spp. (CT_{min} 11.2–12.0°C) (Kay and Whitford, 1978). The CT_{min} of *M. croslandi* was consistent with their lower outbound foraging limit (9.8°C).

Temperature tolerance and activity times in the diurnal ant

In the field, *M. croslandi* workers avoided both high and low surface temperatures. Workers usually avoided exiting the nest at temperatures over 35°C by switching to bimodal activity, delaying the time of forager exit and ceasing outbound activity when the temperature reached 38°C (Fig. 3A,C, Fig. 5A and Fig. 6B). On days when bimodal activity was observed, workers usually left the nest at warmer temperatures in the evening compared with temperatures at the time of foraging onset in the morning. These results indicate that workers recognise temperatures associated with particular times of the day through either internal (e.g. using their circadian clocks) (Majercak et al., 1999) or external mechanisms (e.g. using patterns of solar radiation) (Quiring and McNeil, 1987). This would then allow *M. croslandi* workers to temporally organise their foraging activity to avoid high temperatures. When foraging ants were exposed to temperatures above 30°C in the field, their walking speeds increased and they resorted to jumping for locomotion (P.J., unpublished observations). By jumping, workers raised their bodies above the hot ground boundary layer to where it is probably cooler (Christian and Morton, 1992) and reduced the time spent on the ground. Workers also engaged in thermal respite behaviour (i.e. seeking shelter under shrubs and climbing vegetation; P.J. and A.N., unpublished observations) similar to workers of *Cataglyphis bombycina* (Heatwole

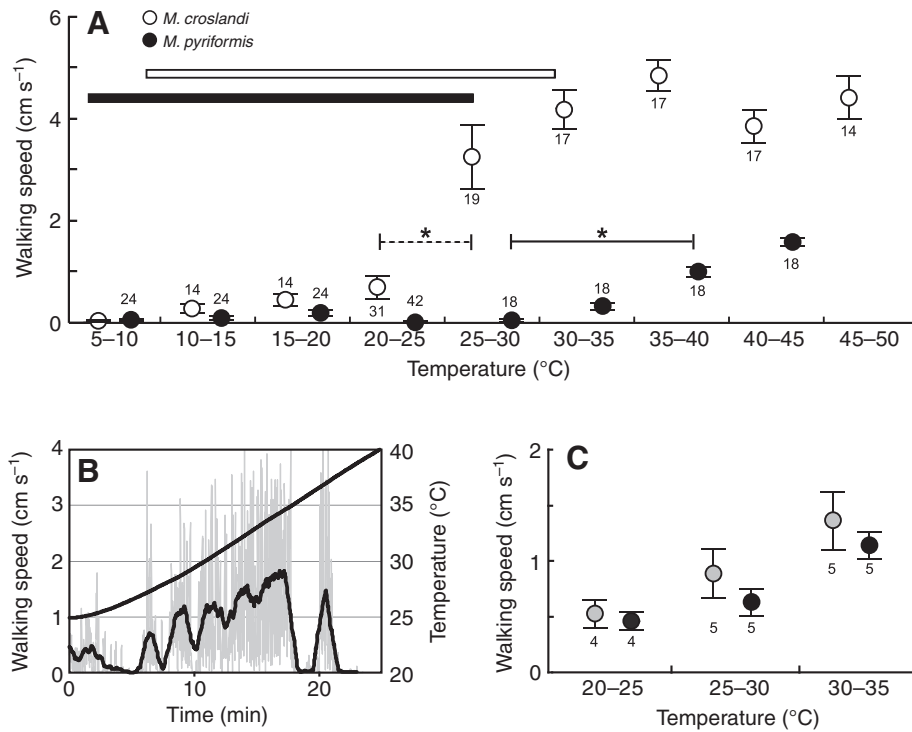


Fig. 8. Relationship between mean walking speed and temperature. (A) Data are means (circles) and standard errors. Open circles: *M. croslandi*; black circles: *M. pyriformis*. The natural foraging temperature range is indicated by horizontal bars for *M. croslandi* and *M. pyriformis*. The largest significant changes in walking speed are shown by a broken line bracket for *M. croslandi* and a continuous line bracket for *M. pyriformis*. Walking speed for $>25^{\circ}\text{C}$ is from critical thermal maximum (CT_{max}) experiments and for $<25^{\circ}\text{C}$ from critical thermal minimum (CT_{min}) experiments. Numbers close to data points are sample sizes. (B) Example of a walking speed recording over time for *M. croslandi*. Walking speed sampled at 1 s intervals is shown in grey, and as a 1 min running average as a thick black line. The smooth black line shows temperature as measured with a type T thermocouple at 1 s^{-1} sampling rate (right y-axis scale). (C) Comparing walking speeds at different ramp speeds ($0.48^{\circ}\text{C min}^{-1}$, grey circles; $0.67^{\circ}\text{C min}^{-1}$, black circles) for five individuals of *M. croslandi*. Otherwise conventions as in A. One ant in each experiment did not experience temperatures in the $20\text{--}25^{\circ}\text{C}$ range. Note that overall speeds are lower than in A, possibly because ants were tested in Austral autumn, close to the end of their seasonal above-ground activity period.

and Harrington, 1989) that cool off by spending three-quarters of their foraging time in thermal refuges where the temperature is lower and where excess body heat can be lost (Wehner et al., 1992).

In the laboratory, ant walking speed rapidly increased at temperatures between 20 and 30°C . These temperatures may indicate a point of thermal discomfort at which rapid movement is initiated (Hanna and Cobb, 2007). At temperatures above 30°C , walking speed remained relatively constant around maximum walking speed until the CT_{max} was reached (Fig. 8A). Such a trend of increasing speed followed by constant high speed at high temperatures has been reported in other diurnal ectotherms such as lizards and geckos (Huey and Bennett, 1987; Bergmann and Irschick, 2006). An increase in stride frequency and acceleration in such situations results in a large power output which may aid jumping (Wilson et al., 2000; Bergmann and Irschick, 2006). In the laboratory, biomechanical or biochemical limitations were probably preventing the ants from changing their gait from running to jumping as they would normally do in the event of an increase in temperature in the field. In order to perhaps compensate for the lack of jumping and the inability to escape, ants probably continued to move at very high speeds until they were no longer able to do so. It may be beneficial for *M. croslandi* workers to change their walking speed in such a manner in order to tolerate short-term exposure to high temperature encountered while foraging during the day.

While ant walking speed has rarely been used as a measure of thermal tolerance, the relationship between walking speed and temperature has been investigated in a few ant species such as *Messor pergandei*, *Pogonomyrmex occidentalis* and *Ocymyrmex barbiger*. These ants also walk or run faster as temperatures increase (Creighton, 1953; Taylor, 1977; Marsh, 1985a) (reviewed by Heatwole, 1996). Interestingly, when we tested *M. croslandi* in Austral autumn, close to the time when these ants stop above-ground activity for the season, we found them to walk much more slowly when confronted with a temperature ramp from 20 to 35°C

(Fig. 8C), compared with their response during the summer months (Fig. 8A). Seasonal differences in the thermal biology of these ants and their underlying mechanism are thus worthy of further investigation.

In the field, workers presumably avoided temperatures below 10°C by ceasing above ground activity. In the laboratory, workers were unable to tolerate temperatures below 10°C and became motion impaired at temperatures around 12°C .

As both field and laboratory experiments (walking speeds) show that workers attempt to avoid temperatures above 30°C and below 10°C , it appears that *M. croslandi* workers utilise the complete thermal range available to them during their activity window (Fig. 7A, Figs 8 and 9).

Relationship between outbound foraging activity and surface temperature in the nocturnal ant

Myrmecia pyriformis workers foraged at a wide range of surface temperatures ($5.4\text{--}26.2^{\circ}\text{C}$) and were active throughout most of the year (Fig. 5B). Outbound activity stopped only when the temperature at sunset dropped below 5°C (Fig. 3H and Fig. 5B). We have confirmed that the onset of foraging of *M. pyriformis* is dependent on sunset time (Fig. 6C), but not temperature at sunset. However, light intensity at sunset explains the remaining variation in activity times (Narendra et al., 2010). Most workers left the nest at temperatures between 10 and 15°C (Fig. 7B) even though they could tolerate much higher temperatures, as shown in our laboratory experiments (Fig. 8A).

Temperature tolerance in the nocturnal ant

Myrmecia pyriformis workers had a CT_{max} of 41.6°C , comparable with that of diurnal species such as *I. purpureus* (CT_{max} 43.5°C) (Greenaway, 1981). Workers had a CT_{min} of 8.2°C which is comparable with that of the nocturnal desert ants *Myrmecocystus mexicanus* and *M. navajo* in North America (CT_{min} range for both species -0.4 to 9.0°C) (Kay and Whitford, 1978).

Temperature tolerance and activity times in the nocturnal ant

As *M. pyriformis* workers rarely if ever encountered surface temperatures above 30°C during foraging, we observed no behavioural responses to high temperature in the field. Therefore, the effect of high temperature on foraging within their normal activity range was less obvious (Fig. 7B and Fig. 9). However, in the laboratory, when exposed to temperatures outside their activity window, workers displayed signs of discomfort above 30°C (Fig. 8A) which indicates an obvious effect of high temperature on activity. Foragers avoided low temperature extremes in the field by ceasing outbound activity when temperature dropped below 5°C, and became immobilised at temperatures below 10°C in the laboratory (Fig. 7B, Fig. 8A and Fig. 9). Thus, outbound foraging activity in this species appears to be restricted by low temperature extremes as indicated by both field and laboratory experiments (walking speed).

Discrepancies between critical temperature and natural foraging limits

In both ants, there was a large discrepancy between CT_{max} and surface temperatures experienced during natural foraging. This discrepancy may arise as a result of differences in natural and laboratory conditions. For instance, ants exposed to temperatures above 40°C under natural conditions face the risk of desiccation, whereas in laboratory experiments we kept desiccation in check by providing ants with water. Thus, the upper tolerance limit in the field may be much lower as individuals must avoid rapidly heating conditions as well as dehydration.

Discrepancies between CT_{max} and natural foraging temperatures have also been reported in *M. mexicanus* where workers stop activity 10°C below their CT_{max} (Kay, 1978). This discrepancy further validates the use of walking speed in our study. In the laboratory, CT_{max} in both *Myrmecia* ants did not reflect the upper outbound foraging limit of workers in the field. However, temperatures at which thermal discomfort was displayed by increasing walking speed were more closely related to the upper temperature limits of outbound foraging in the field.

The CT_{min} of *M. pyriformis* was higher than the minimum temperature at which workers left the nest (5.4°C). Under natural conditions, workers may be able to forage at these low temperatures through seasonal acclimatisation during winter resulting from exposure to slowly changing low temperatures (Scott and Pettus, 1979;

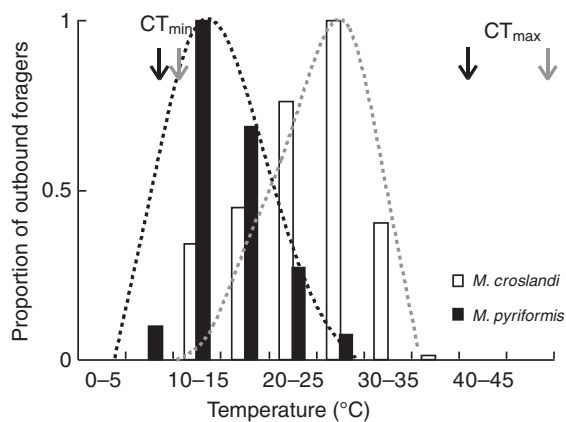


Fig. 9. Summary of outbound foraging activity and tolerated temperatures for diurnal *M. croslandi* and nocturnal *M. pyriformis* (see also Fig. 6). CT_{max} and CT_{min} are indicated for *M. croslandi* (grey arrows) and *M. pyriformis* (black arrows). Spline fits centred on the temperature at which the highest proportion of workers left the nest for *M. croslandi* (dotted grey line) and *M. pyriformis* (dotted black line) are shown.

Angilletta, 2009). The ability to acclimate for future cold or warm weather may be a beneficial, adaptive response in temperate species that encounter seasonal temperature fluctuations (Levins, 1969; Kristensen et al., 2008). This may explain why *M. pyriformis* workers can operate at low temperatures in the field as winter progresses but workers tested in autumn are unable to tolerate such low temperatures in the laboratory. Furthermore, foraging ants may also rely on behavioural adaptations to avoid low temperatures, unlike in the laboratory where they have to rely solely on physiological responses. One possibility is that *M. pyriformis* workers thermoregulate in the field by spending the coldest parts of the night on trees where temperatures may be warmer (Stevenson, 1985). However, slow walking speeds at temperatures below 10°C indicate that foraging at these temperatures may not be very efficient.

Factors restricting ants to discrete temporal niches

The thermal biology of the congeneric and sympatric, diurnal and nocturnal ants now enables us to address whether temperature restricts these ants to their respective temporal niches. Through our combined field and laboratory experiments, we have shown that the diurnal *M. croslandi* workers exploit the complete thermal range available to them for above-ground activity. Hence, it appears that these ants are restricted to their current temporal niche by thermal constraints on activity. If this were the case for the nocturnal ant, one would expect *M. pyriformis* to also utilise the complete thermal range available to them by becoming diurnal in winter, especially as the diurnal *M. croslandi* ceased above-ground activity from May onwards. Temperatures during the day in winter are well within the tolerated summer temperature range of the nocturnal *M. pyriformis* but workers do not change their activity rhythm to become diurnal. However, temperature-dependent shifts in foraging activity are common in ants (e.g. Greenaway, 1981; Heatwole and Muir, 1989). For instance, the seed harvester ant *Pheidole militica* is diurnal in winter to avoid low temperatures during the night and nocturnal in summer to avoid high temperatures during the day (Hölldobler and Möglich, 1980). Therefore, the thermal biology of *M. pyriformis* does not explain why these ants are nocturnal. Competition between *M. pyriformis* and *M. croslandi* is also unlikely to restrict these nocturnal ants to their current temporal niche. Some ants shift from a nocturnal to a diurnal lifestyle when the competing species is removed: workers of *Myrmica* species, for instance, shift from nocturnal to diurnal activity at food baits when competitive *Formica* species are excluded (Vepsäläinen and Savolainen, 1990). However, in winter, *M. pyriformis* continues to be nocturnal in the absence of *M. croslandi* with onset of foraging triggered by light intensity at sunset (Narendra et al., 2010). Hence, neither temperature nor competition between the two species currently restricts *M. pyriformis* to a strictly nocturnal lifestyle. However, factors such as other ants, predation pressure or sensory limitations (Greiner et al., 2007; Narendra et al., 2011) may play a role in this particular case of temporal niche partitioning.

In summary, temperature determines both the daily and seasonal outbound foraging activity in *M. croslandi* but has less obvious effects on foraging in *M. pyriformis*, as the seasonal pattern of activity in this nocturnal species is more influenced by the timing of sunset. Furthermore, temperature determines the discrete timing of foraging in the diurnal *M. croslandi* but not in the nocturnal *M. pyriformis*, although foraging rate may change with season. *Myrmecia croslandi* workers tune their activity to avoid both high and low temperatures through daily and seasonal changes in foraging patterns, while *M. pyriformis* workers avoid low temperature extremes. As both species seem to monitor their environment to avoid unfavourable temperatures, it will be of interest to investigate processes that allow them to do so.

In both species, the CT_{max} did not correspond to the natural foraging limits. However, the relationship between walking speed and temperature appears to be a more ecologically sensitive measure of temperature tolerance. Future experiments could investigate the underlying mechanisms that allow such high temperature tolerance in these two species and determine whether this ability is conserved among other species across the *Myrmecia* genus.

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