

The structure of foraging activity in colonies of the harvester ant, *Pogonomyrmex occidentalis*

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The timing of activity by desert dwelling poikilotherms can be critical to survival. In the western harvester ant, colonies that have higher levels of genetic diversity forage for longer time periods in the morning than colonies with less diversity. We determined whether the advantage of early foraging colonies was consistent by examining foraging behavior at other times of day and year. We used a combination of activity monitoring and temperature measurement at the nest entrance to quantify foraging activity during the morning and evening summer foraging periods in both June and August. The duration of morning and evening foraging was significantly positively correlated both within and across seasons—some colonies have a consistent advantage in foraging. The temperature range over which colonies foraged was also consistent across time, suggesting that intercolony differences are a consequence of variation in the thermal ranges/preferences of the colony's workers. The duration of foraging during this study was correlated with the duration of foraging measured 6 years earlier, suggesting that it is an aspect of colony phenotype. *Key words:* activity pattern, compensation, foraging, genetic diversity, harvester ants, *Pogonomyrmex*. [*Behav Ecol* 21:337–342 (2010)]

The timing of activity in desert animals is a critical adaptation. As temperatures rise to lethal levels during the middle of the day, desert animals, particularly small poikilotherms, are forced to cease activity. Desert ants often cannot forage during the hottest portions of summer days, returning to their underground nests. Although some species are extraordinarily thermophilic (e.g., *Cataglyphis* spp., Wehner et al. 1992), most species of ants display clear thermal preferences for foraging that are a function of soil surface temperature (e.g., Morehead and Feener 1998; Vogt et al. 2003; Pol and Lopez de Casenave 2004; Bucy and Breed 2006; Azacarate et al. 2007). In temperate deserts, a single foraging period occurs during midday early in the season, when maximum temperatures are not lethal. As maximum daily temperatures increase, the time for foraging expands but eventually reaches a point when midday temperatures become too hot, resulting in a bimodal pattern of foraging activity (e.g., Pol and Lopez de Casenave 2004; Bucy and Breed 2006). If daytime temperature becomes too great, some species shift from diurnal to nocturnal activity (Brown et al. 1979; Mehlhop and Scott 1983).

Ant species differ in the temperature ranges over which they are active (Hölldobler and Wilson 1990, Table 10-1). Although there is typically strong diurnal thermal partitioning, seasonal effects of temperature are not usually observed (e.g., Albrecht and Gotelli 2001). Differences in thermal tolerance frequently are related to behavioral dominance among competing species. A broad thermal range for foraging is implicated in the success of 2 invasive ant species—the red imported fire ant (Wuellner and Saunders 2003) and Argentine ants (Abril et al. 2007; Carpintero et al. 2007). A number of studies have shown that, within ant communities, there is a trade-off between temperature and competitive dominance. Dominant species often forage at the most temperate times, with subordinate species relegated to thermal extremes (e.g., Cerdá

et al. 1997, 1998; Bestelmeyer 2000; Retana and Cerdá 2000; Albrecht and Gotelli 2001; Cerdá 2001; Thomas and Holway 2005). However, a recent study of a Mediterranean ant community found that thermal range and competitive dominance were strongly positively correlated (Santini et al. 2007), suggesting that the trade-off may not always occur.

Although several studies have addressed the importance of variation in thermal range of activity among species (e.g., Ruano et al. 2000), relatively little work has addressed the consequences of variation in thermal tolerances or preferences within a species. Among-colony differences in the timing of activity were noted by early naturalists (McCook 1879; Eddy 1970). Some of this variation in the timing of activity can be attributed to differences in the exposure of ant colonies to solar radiation (Cole 1994; Crist and Williams 1999; Pol and Lopez de Casenave 2004). Colonies that are more exposed to direct sunlight, because the nest has less vegetative cover or because they are on more southerly slopes (in the northern hemisphere), receive more sunlight and are active earlier in the morning and in the season.

In the western harvester ant, *Pogonomyrmex occidentalis* (Creson), colonies differ in the temporal pattern of activity, and these differences are correlated with genetic diversity of workers within colonies (Wiernasz et al. 2008). After accounting for differences in colony size and the exposure of the nest, those colonies with higher genetic diversity begin foraging earlier in the morning and forage for a longer duration. The earliest foragers belong to a nonrandom subset of patrines within the colony, suggesting that worker patrines may differ in their thermal tolerances or preferences. The extent of the differences in the onset of colony activity are substantial and consistent: 20–25 min is the standard deviation of onset times from 3 separate studies (Cole et al. 2008; Wiernasz et al. 2008; Lubertazzi D, Wiernasz DC, Cole BJ, unpublished data). Variation in the onset of foraging significantly affects foraging success. Colonies that begin foraging earlier collect significantly more food (Cole et al. 2008) and are more likely to discover a food source before their neighbors and subsequently monopolize it (Lubertazzi D, Wiernasz DC, Cole BJ,

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unpublished data). A colony that begins foraging one standard deviation earlier than the population mean acquires 17% more food during the morning foraging period, a difference that may account for the higher growth rates observed in colonies with high levels of genetic diversity (Cole and Wiernasz 1999; Wiernasz et al. 2004).

The relationship between genetic diversity and foraging effectiveness in *P. occidentalis* was derived from observations of the morning activity period in the early summer. The inference that genetic diversity enhances colony performance with respect to food retrieval would be undermined if late onset colonies were able to compensate by foraging more during some other time period (i.e., in the evening). It is also possible that colonies that were at an apparent disadvantage in June, when the previous studies were conducted, might forage more at some other time during the year. In this paper, we address 2 issues: 1) one is the temporal pattern of morning foraging consistent at different times of day and year? and 2) to what extent does soil surface temperature account for the differences in foraging activity among colonies? We compared the pattern of morning and evening foraging activity and foraging behavior in early summer (June) versus late summer (August) to address these issues.

If some colonies have a consistent advantage with respect to foraging duration, then we expect a positive correlation between the duration of morning and evening foraging as well as the duration of foraging at different times of year. Foraging duration might then be determined largely by the thermal preferences/tolerances of the colony's workers. Soil surface temperature changes in a regular way with time (Figure 1; see Materials and methods for how these data are generated), delimiting the period during the day when the colony can be active. The consistent advantage hypothesis predicts that 1) the temperature range for morning and evening foraging will be positively correlated; 2) the temperature at which activity begins in the morning will be positively correlated to the temperature at which activity ceases in the evening; and 3) the temperature at which a colony ceases foraging in the morning is predicted to be positively correlated with the temperature at which foraging begins in the evening.

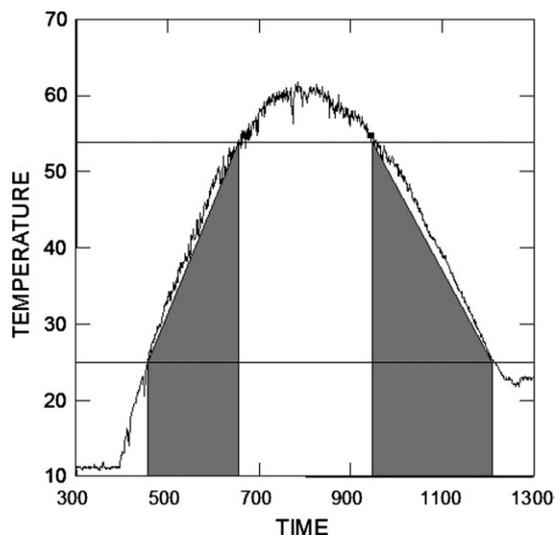


Figure 1
Soil surface temperature (degree Celsius) over the course of a day (minutes from midnight) for a single colony. When there are minimum and maximum temperatures for activity, there are 2 activity periods. Note that starting and cessation temperatures will be correlated across activity periods.

However, it is also possible that the colonies that had the longest foraging durations in the morning could have shorter foraging durations at other times of day or in other seasons. This pattern could be produced by 2 general mechanisms, competitive displacement and compensation, which will both generate a negative correlation between the duration of foraging at different times.

The competitive displacement hypothesis predicts a negative correlation (trade-off) between the duration of morning and evening foraging or between foraging durations at different times of year. As with the consistent advantage hypothesis, the putative mechanism involves differences between colonies in the thermal range of the colony's workers, but the critical difference is that how early a colony begins foraging determines how long it will forage. Late onset colonies may forage for relatively brief durations in the morning because they are competitively displaced by early onset colonies. Conversely, the onset of foraging in these colonies will occur at higher temperatures and, thus earlier, in the evening. By starting earlier, they are able to discover and monopolize food resources and forage longer during the evening. In addition to a negative correlation between morning and evening foraging duration, this hypothesis predicts that the onset temperature for both morning and evening foraging should be negatively correlated with the time that foraging ceases.

Alternatively, colonies may adjust their foraging effort within a broadly constrained thermal range (similar for all colonies) in order to regulate food collection over longer timescales. Consequently, the duration of the foraging interval may vary both diurnally and seasonally. If colonies forage to maintain food levels, briefer durations of foraging in one period may be compensated by a longer duration in the next foraging period. This dynamic compensation would result in a negative correlation between foraging durations in successive foraging intervals. Because this hypothesis suggests that food collection determines foraging activity, it makes no predictions about the temperatures at which colonies become active.

We measured the duration of both morning and evening foraging in early and late summer in order to differentiate among these hypotheses. We associated both onset and cessation of foraging with precise measurements of temperature at the nest entrance to assess the relative importance of a colony's thermal range as a determinant of colony foraging success.

MATERIALS AND METHODS

The data were collected from colonies within or near our permanent harvester ant study site (for a detailed description of the habitat, see Wiernasz and Cole 1995; Cole and Wiernasz 2002). Most of the colonies chosen for this study are part of a long-term project to monitor reproductive outputs of colonies (Wiernasz DC and Cole BJ, unpublished data), and some colonies were used previously in a study of the relationship between colony activity patterns and genetic variation (Wiernasz et al. 2008).

Activity monitoring

Activity was monitored for each colony from a distance of approximately 5 m, observing activity with binoculars. Especially when the colony is not very active, workers are very wary, and observers who come too close can delay the onset of a colony's activity. Colony activity is scored on a scale from 0 to 3 as follows: 0 = colony inactive, no workers present; 1 = a single worker has emerged from the nest (or 2 if they are near the nest entrance); 2 = more than one ant has emerged from the nest; however, they are all remaining on or very near the nest cone, moving in convoluted paths; 3 = foraging.

Workers are moving purposefully away from the nest, past the cleared area around the nest, and frequently in a fairly straight line. These activity levels correspond very broadly to Gordon's (1986, 1991b) patrollers and nest maintenance workers (activity levels 1 and 2) and foragers (level 3). All the data in this paper concern the transition to foraging—level 3. The onset of foraging activity is the time when activity level in the colony first rises to level 3 for an extended period—typically at least 2 consecutive measurements (~15 min); onset time was then recorded as the first time level 3 was achieved. Under some circumstances, the presence of spiders or horned lizards can cause the ants to remain inactive. In these cases, activity was not scored for that colony on that day. Foraging was determined to have stopped when ants were no longer leaving the nest—that is, when activity fell below level 3 for at least 2 successive intervals. We did not consider ants returning from foraging trips in our measurement of foraging. Activity was checked in all colonies until every colony was at activity level 0 for at least 2 successive circuits.

Two observers made activity measurements, walking a circuit of approximately 15 colonies at 15-min intervals. Approximately 30 colonies can be observed in a single time period; these equal one block of colonies. We found no observer effects in preliminary analyses and analyzed all data without considering observer. Activity monitoring was begun before any ants became active in the morning and continued until all colonies had become active. During the morning foraging period, activity typically begins at about 0730 h Mountain Daylight Time (MDT) and stops by noon. We refer to the second foraging period as the evening foraging period, which begins at about 1630 h and stops by 2030 h MDT. We give times in minutes from midnight.

Temperature monitoring

Soil surface temperature measurements were collected from a sensor within 2 cm of the nest entrance using a Sable Systems Versatile Field Network of 30 thermocouple boxes. We recorded temperature once per minute throughout the day. On rare occasions, the temperature data collectors failed. The temperature measurements that we use in this paper are those recorded at the time foraging activity was first observed and when it ceased.

We monitored activity from colonies in 2 blocks—a total of 58 colonies. The thermocouple boxes were transferred between blocks 1 and 2 after the morning activity had completely ceased and before the evening activity started. If we designate the blocks by 1 and 2 and the morning and evening activity periods with M and E, respectively, a data collection sequence consisted of 3 evenings and mornings in the first block followed by 3 evenings and mornings in the second block: E1, M1, E1, M1, E1, M1, E2, M2, E2, M2, E2, and M2. This sequence was repeated once, generating a total of 6 morning and evening foraging periods. We measured activity in June (18 June to 3 July 2005) and then repeated the entire data collection procedure described above in August (27 July to 8 August 2005). We obtained temperature and activity data for a total of 18 evening and 23 mornings (Figure 2). Rainfall in the afternoon or evening, particularly during the August, interrupted data collection reducing the total number of samples.

Data analysis

The hypothesis that colonies have a consistent advantage or that colonies compensate make alternative predictions about the relationship between morning and evening activity. We used all the available data for a colony after first removing statistically the effect of season, block, and colony \times season

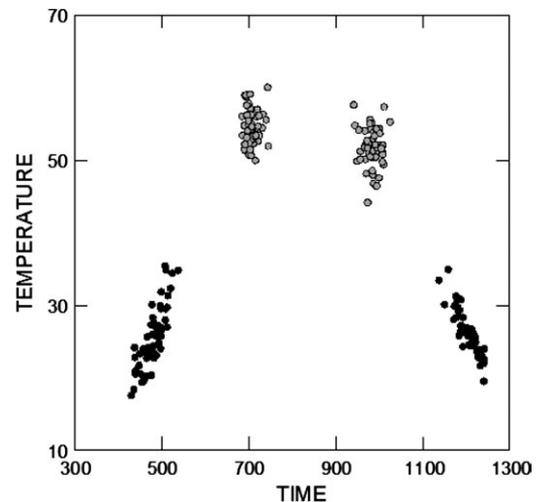


Figure 2

The times and temperatures at which foraging begins and ceases for the colonies in this study. Each point represents the colony effect calculated for the data across both seasons.

interactions (details of the analysis are given in Table S1) to obtain the estimates of colony activity parameters. When we test for a possible trade-off between the 2 seasonal samples, we did not remove the seasonal effects. To test for differences between these data collected in 2005 and an earlier study in 1999, we used only the data from the June morning samples of 2005 because the data were collected during a similar period during 1999 (Wiernasz et al. 2008). The temperature range of foraging is the number of degrees over which foraging occurred. The duration of foraging is the difference in minutes between the cessation of activity and the onset of activity. Analyses based on a specific a priori predictions from a single hypothesis employed one-tailed tests, whereas those that compared predictions from alternative hypotheses used 2-tailed tests.

RESULTS

The 3 hypotheses make distinguishing predictions about the correlation between the duration of morning and evening foraging. Morning and evening foraging duration were significantly positively correlated ($r = 0.53$, $N = 56$, $P = 0.00003$, 2 tailed, Figure 3a). This result strongly supports the consistent advantage hypothesis while negating the other hypotheses, which predicted either a negative or no correlation.

We found no support for a trade-off in the duration of morning and evening foraging. The trade-off hypothesis predicts that the early onset of foraging leads to a longer foraging duration through resource monopolization, leading to a negative correlation between the onset and cessation of foraging in both the morning and evening. For both the morning ($r = 0.33$, $N = 56$, $P = 0.013$) and the evening ($r = 0.31$, $N = 56$, $P = 0.02$), the correlation was actually positive—colonies that began foraging earlier also tended to cease foraging earlier.

If compensation occurs over shorter time intervals, the duration of foraging in successive time intervals (e.g., and evening foraging period and that of the following morning) is predicted to be negatively correlated. We examined 25 independent pairs of consecutive durations; 9 compared morning and evening foraging on the same day, whereas 16 compared evening foraging on 1 day with morning foraging on the next day (because of the data collection protocol, fewer days with morning and evening samples are expected). The average

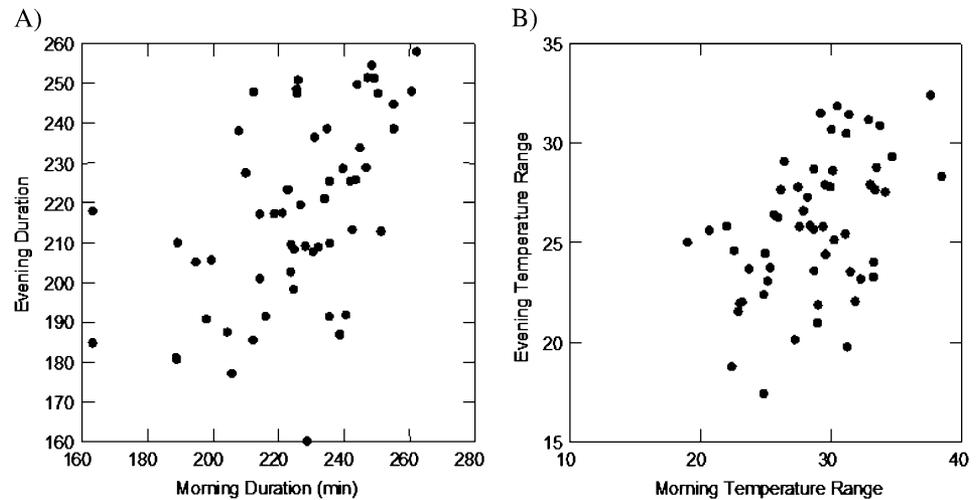


Figure 3

The relation between morning and evening activity periods. Panel (A) shows the positive correlation between the duration of foraging in the morning and evening. Panel (B) shows the same for the temperature range of foraging in the morning and evening.

correlation over all pairs was 0.30 (0.27 for within day periods and 0.32 for overnight comparisons). Twenty of the correlations were positive (significant in a 2-tailed binomial test, $P = 0.003$). Five of the individual correlations were significant—all of them positive. None of the 5 negative correlations were significant ($P > 0.3$ in all cases). The preponderance of positive correlations strongly suggests that short-term compensation does not influence the overall pattern of foraging activity.

Because the duration data support the consistent advantage hypothesis, we tested the predictions that this hypothesis makes about the temperature of activity. Overall, the morning and evening temperature ranges were positively correlated as predicted ($r = 0.47$, $N = 56$, $P = 0.0003$; one tailed, Figure 3b). The June and August samples were individually significant as well (June: $r = 0.54$, $N = 58$, $P < 0.00001$; August: $r = 0.24$, $N = 56$, $P < 0.035$ one-tailed test, for both comparisons). If temperature is an important determinant of foraging range, the thermal end points of a colony's foraging are also predicted to be consistent. As predicted, the temperature that foraging begins in the morning was positively correlated with the temperature that foraging ceases in the evening ($r = 0.40$, $N = 56$, $P = 0.012$) and the temperature that foraging ceases in the morning was positively correlated with the temperature that foraging begins in the evening ($r = 0.23$, $N = 56$, $P = 0.045$, both one-tailed tests).

The temperature range over which foraging occurred in June was less than in August, both for the morning (difference of 8.1° , $t = 10.1$, $P \ll 0.0001$, degrees of freedom [df] = 57) and evening (2.9° , $t = 3.55$, $P < 0.001$, df = 55) activity periods (Figure 4). These seasonal differences were primarily due to changes at the cooler temperatures (morning onset, evening cessation). In August, colonies became active in the morning at significantly cooler temperatures (average difference = 6.5° , $t = 8.6$, df = 57, $P < 0.001$, Figure 4) and also foraged until temperatures were significantly cooler in the evening (average difference = 2.5° , $t = 4.0$, df = 57, $P < 0.0001$). Whereas the temperature at which activity started in the evening did not differ from June to August (average difference = 0.4° , $t = 0.9$, df = 57, $P > 0.3$), the temperature that activity stopped in the morning was on average 1.5° greater in August than in June ($t = 4.1$, df = 57, $P < 0.001$). Those colonies that were the latest to begin foraging in June (or the earliest to cease foraging) showed the largest change in the temperature of foraging. This resulted in a significant colony by season interaction effect in those measures that changed significantly for colonies (see Table S1).

This study included 38 colonies in which morning foraging activity was also quantified in June 1999 (Wiernasz et al. 2008). The duration of foraging in this and the earlier study was highly positively correlated ($r = 0.46$, $P < 0.002$, one-tailed test, $N = 38$). The correlation is due entirely to the correlation of onset times ($r = 0.50$, $P < 0.001$, one-tailed tests) because the cessation of foraging was not correlated ($r = 0.06$, $P = 0.37$).

DISCUSSION

Colonies are distinct in their foraging activity. On a given day, foraging activity may be influenced by weather, by the presence or absence of predators, and by the actions of patrollers (e.g., Brown and Gordon 2000; Gordon 2002; Greene and Gordon 2007). Over the course of a season and the lifetime of the colony, the presence of predators and the effects of weather even out, leaving intrinsic differences among colonies. These differences support the hypothesis that some colonies have a consistent advantage in foraging. In accord with our earlier

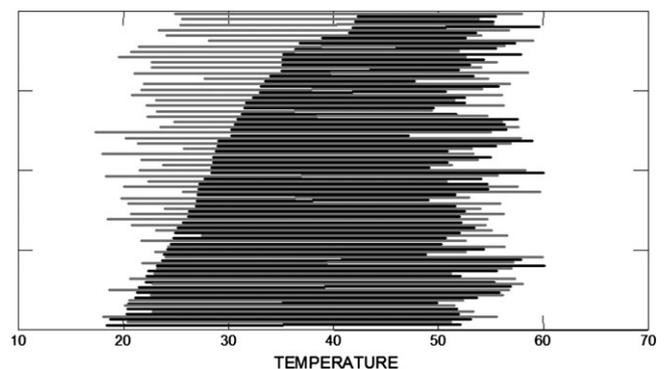


Figure 4

The temperature range for activity of colonies during the morning activity period. The lower temperature is the onset temperature, whereas the upper temperature is the cessation temperature for foraging. The data from June are given by the solid black bar. The data from the August data set are shown in gray. Colonies are ranked by the onset temperature in June. The August data from a colony are stacked directly above the June data from the same colony. Note the expansion of activity by colonies during the cooler portions of the morning, particularly among colonies that began foraging at higher temperature in June. This results in a highly significant colony \times season interaction term for morning onset temperature.

study of the temporal pattern of foraging in this species (Wiernasz et al. 2008), we found no evidence that colonies compensate for shorter foraging in one time by foraging for longer durations at other times. Although the colonies with the shortest duration of morning and evening foraging in June tended to show the greatest expansion in foraging duration in August, evidence consistent with the hypothesis that colonies compensate across seasons, this colony by season interaction effect did not modify the overall pattern. Colonies did not adjust their foraging effort based on previous effort, rather those that foraged more in the morning also foraged more in the evening, in both June and August and across at least a 6-year time interval.

Colonies differed significantly and consistently in their pattern of foraging. We also observed seasonal differences—the temperature range in August was generally greater than in June. The sensors used in this study measure soil surface temperature, but temperatures below the surface are likely to be different (Cole 1994), with relatively warmer subsurface temperatures in August compared with June. As a consequence, colonies begin foraging at cooler surface temperatures in August and cease foraging at cooler temperatures in the evening. June evenings also were cooler than August evenings, and foraging activity in June ceased before sunset, whereas in August typically continued up to and slightly after dark. The cessation time for evening foraging was probably measured less accurately in August due to the difficulty of seeing foragers in the fading light. It is also possible that the cessation of evening foraging was modulated by nightfall more than by falling temperatures. The extension of morning foraging to higher temperatures in August may also be a consequence of physiological acclimation by foragers to warmer temperatures, leading to later morning cessation times in August compared with June.

The consistent advantage hypothesis predicts that differences in the activity of colonies are due to differences in the temperature over which they can be active. The temperature range over which colonies foraged was strongly correlated across time periods, suggesting that intercolony differences are a consequence of variation in the thermal ranges/preferences of the colony's workers. The minimum temperature required for activity was highly correlated (morning starting temperature and evening cessation temperature); however, the maximum temperatures at which the colonies foraged were much less correlated. The weaker relationship between foraging activity and high temperature may be a consequence of physiological limits to activity in workers (Lightner and Turner 2004).

Although the starting time and duration of foraging activity was correlated between 1999 and 2005, cessation time was not. In part, this reflects the general finding of this paper that the timing of activity at the hottest parts of the day was not as consistent as the response to time or temperature during the cooler parts. However, in the earlier study (Wiernasz et al. 2008), the criteria for determining the cessation of foraging differed from this study, whereas those that determined the onset were the same. Cessation of foraging was defined as the time that the last forager returned rather than the time that it left. This methodological difference may account for some of the differences between correlations for the onset and cessation of activity.

Our failure to find any evidence of compensation or a trade-off is somewhat surprising, given the many circumstances under which animals display compensation with respect to foraging. One of the most common examples is the interplay between feeding and predation risk (Sih 1980; Lima 1988; Nonacs and Dill 1990; Brown 1999; Kotler et al. 2004; Verdolin 2006). Maintenance of dietary balance is another example of when foraging is frequently compensatory (e.g., Fewell and

Winston 1992; Camazine 1993; Berner et al. 2005). Work by Gordon (1991a, 1992), among others, provides evidence that colonies of ants regulate food intake. Colonies that were experimentally prevented from foraging foraged at higher intensities when released from these constraints. Compensation in this example is largely numerical—it is not known whether there is an expansion of foraging time. However, in *P. occidentalis*, we have shown that colonies send workers out at a rate that is relatively independent of the total duration of foraging (Cole et al. 2008). What we know of foraging in *P. occidentalis* suggests that an increase in the number of foragers would require an increase in the duration of foraging.

The lack of compensation at the colony level is likely to be a consequence of the colony consisting of multiple behavioral phenotypes. If individual workers have a limited range of temperatures over which they forage, the range of the colony is greatly expanded by having a large number of behavioral types (patrilines). Previous work with *P. occidentalis* suggests that the onset of foraging differs among patrilines (Wiernasz et al. 2008). By mating with a variety of males, the queen obtains genotypes that supply a wider variety of thresholds, particularly lower thresholds for activity at a particular temperature, enhancing the colony's performance (Beshers and Fewell 2001; Oldroyd and Fewell 2007). Similarly, temperature variation in honeybee hives is lower when colonies contain a large number of patrilines compared with a single patriline (Jones et al. 2004). Increased genetic variability in a patriline's tendency to fan during thermoregulation allows genetically diverse honeybee colonies to maintain greater homeostatic control of temperature. In harvester ants, the consistency across foraging periods within a day and across time periods suggests that the pattern of foraging activity is an inherent characteristic of colonies. However, the magnitude of the correlation between the temperature range of morning and evening foraging ($r = 0.47$) guarantees that additional factors contribute to the differences among colonies in temporal pattern.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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