

Temperature-mediated coexistence in temperate forest ant communities

J.-P. Lessard · R. R. Dunn · N. J. Sanders

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Abstract Patterns of ant species diversity are well documented and yet the mechanisms promoting species coexistence among communities are often elusive. Two emerging hypotheses that account for coexistence in ant communities are the discovery-dominance tradeoff and the dominance-thermal tolerance tradeoff. Here we used behavioural assays and community-level sampling from ant assemblages in the southern Appalachians, USA to test for the discovery-dominance and dominance-thermal tolerance tradeoffs. Species that were behaviourally dominant during interspecific interactions tended to forage in a narrow window of generally warmer temperatures, whereas subordinate species tended to forage in a wide range of temperatures, including colder temperatures. Species that foraged at lower temperature tended to be behaviourally subordinate, suggesting that a dominance-thermal tolerance tradeoff promotes coexistence in this system. Species richness was positively related to site average annual temperature and within-site variation in ground temperature, suggesting that temperature also shapes the structure of ant communities and regulates diversity. There was no relationship between the ability of a species to discover food resources and its behavioural dominance, contrary to the predictions of the discovery-dominance tradeoff

hypothesis. In sum, our results show that temperature plays numerous roles in promoting regional coexistence in this system.

Keywords Coexistence · Dominance · Temperature · Tradeoff · Formicidae · Coweeta LTER

Introduction

Ants are ubiquitous in most terrestrial ecosystems and, as a result, the factors regulating the structure of ant communities have been well studied (Davidson, 1977; Savolainen and Vepsäläinen, 1988; Yanoviak and Kaspari, 2000; Albrecht and Gotelli, 2001; Sanders and Gordon, 2003; Parr et al., 2005). Hölldobler and Wilson (1990) noted that competition is ‘the hallmark of ant ecology’, and numerous studies have indicated that competition can shape ant communities (Bernstein and Gobbel, 1979; Fellers, 1987; Savolainen and Vepsäläinen, 1988; Herbers, 1989; Andersen, 1992; Sanders and Gordon, 2003; Parr et al., 2005). Evidence for the role of competition includes behavioural dominance hierarchies (Vepsäläinen and Pisarski, 1982; Fellers, 1987; Savolainen and Vepsäläinen, 1988; Perfecto, 1994; Sanders and Gordon, 2003), hump-shaped dominance-diversity relationships (Andersen, 1992; Parr et al., 2005), and the alteration of native ant communities in the presence of dominant introduced species (Holway, 1999; Porter and Savignano, 1990; Sanders et al., 2003). In sum, results from these studies suggest that competitively dominant species often shape the structure of ant communities.

If competition is a strong determinant of the structure of ant communities, a key question becomes what allows multiple ant species to coexist in a given habitat (Andersen, 2008). One possibility is that species coexist because of

J.-P. Lessard (✉) · N. J. Sanders
Department of Ecology and Evolutionary Biology,
University of Tennessee, 569 Dabney Hall, Knoxville,
TN 37996, USA
e-mail: jlessard@utk.edu

R. R. Dunn
Department of Biology, North Carolina State University,
120 David Clark Labs, Box 7617, Raleigh,
NC 27695-7617, USA

tradeoffs between dominance over resources and foraging efficiency (see Davidson, 1998 for a review). Behaviourally dominant ant species can displace behaviourally subordinate ant species at transient food resources. They do so by use of overt aggression, which leads to submissive behaviour, and usually escape by the subordinate species. Early in the study of ant interactions, Wilson (1971) noted a divergence in the competitive strategies of ant species at transient food sources. Such divergences may allow subordinate ant species to coexist with dominant species. One hypothesis is that behaviourally subordinate species are better at discovering than at defending food resources (Fellers, 1987), such that the ability of a species to discover food resources is inversely related to its ability to defend those resources. This hypothesis has been coined “the discovery-dominance tradeoff” by Fellers (1987) who studied behavioural interactions in a guild on woodland ants in Maryland.

A second mechanism that might allow coexistence in ant communities is the partitioning of possible foraging temperatures. In addition to being structured by competition, resource access in ants is shaped by the abiotic environment, and in particular, temperature (e.g., Bestelmeyer, 2000; Cerdá et al., 1997; 1998a). Species vary in their abilities to forage at different climatic conditions such that the abiotic environment can influence competitive outcomes. For example, Cerdá et al. (1997; 1998) found that behaviourally dominant ant species were less successful than subordinate species at exploiting food resources under extremely warm temperatures. Thus, to understand the relative importance of factors structuring ant communities, field studies should consider both the role of species interactions and how such interactions vary with the environmental conditions. Though a dominance-thermal tolerance tradeoff in ant communities has been documented in several systems (Bestelmeyer, 2000; Cerdá et al., 1997; 1998), few studies have simultaneously assessed the effects of both local interspecific interactions and the abiotic environment on ant community structure (but see Bestelmeyer, 1997; Cerdá et al., 1997; 1998).

Behavioural tradeoffs are a current focus of research in ant community ecology, and it has been proposed that tradeoffs may promote species coexistence and the maintenance of ant diversity both locally and regionally (Feener et al., 2008). We take advantage of systematic variation in the abiotic environment along an elevational gradient to explore how behavioural tradeoffs and temperature interact to shape ground-dwelling ant communities within and among sites. Specifically, we examine the possibility of a dominance-thermal tolerance tradeoff whereby differences in foraging temperature regimes allow behaviorally dominant and subordinate ant species to coexist. We also consider the alternative hypothesis that the ability of

subordinate species to discover and exploit food resources allows them to coexist with dominant species (Fellers, 1987; LeBrun and Feener, 2007).

Methods

Study site

We conducted this study at six sites along an elevational gradient (591–1,001 m) at the Coweeta Hydrologic Laboratory Long-Term Ecological Research (hereafter Coweeta LTER) site in the southern Appalachians, USA (35.0° N, 83.5° W). An average of 1,800 mm of rain falls each year, and the mean annual temperature is approximately 13°C (January minimum = 3°C; July maximum = 19°C) (Swank and Crossley, 1988). Temperature at Coweeta LTER generally decreases with increasing elevation while precipitation increases with elevation (Knoepp and Swank, 1998; Swift et al., 1988).

Sites were located in mixed oak forests. Each site was 800 m² (40 m × 20 m). Dominant tree species in the vicinity of our study sites include *Carya spp.*, *Quercus prinus*, *Q. rubra*, *Liriodendron tulipifera*, *Betula alleghaniensis* and *B. lenta*. Dense patches of *Rhododendron maximum* are also common and reduce the amount of sunlight that reaches the forest floor at many sites.

Sampling ant assemblages

We recorded the number of ant species and workers present at bait stations at each of the six sites. Baits are appropriate to test for behavioural tradeoff because they represent the kind of patchy and ephemeral food source for which ground-foraging ants often compete. We performed baiting trials during the first 3 weeks of September 2005. Bait stations were white laminated cards (9 cm × 14 cm) arranged 10 m apart in a 3 × 5 grid. A 15-ml portion of cat food (Laura Lynn; 11% protein, 4% fat, 78% moisture) was deposited on each of the laminated white cards at the beginning of each session. During a baiting session, we visited each station 20, 40, 60, and 80 min after the baits were placed. Each baiting session was repeated four times at each site with at least two days separating each visit to a site. For each site, we performed two baiting sessions before 1:00 pm, and two sessions between 1:00 and 6:00 pm to capture potential diurnal shifts in foraging activity. Thus, at each site we made 240 observations (15 baits × 4 obs. day⁻¹ × 4 sessions). We also conducted one baiting session over a consecutive 24-h period to examine nocturnal foraging activity, but only two species of ants [*Aphaenogaster rudis* Enzmann, *Prenolepis imparis* Emery (1893)] were observed foraging at night.

We used pitfall traps, hand collecting, and Winkler samplers to estimate the number of ant species present at each site. We positioned pitfall traps (55 mm diameter, 75 mm deep) within 1 m of bait stations. At each site, we operated pitfall traps within 2 days following the end of the last baiting session. Each pitfall trap was partially filled with propylene glycol (low toxicity antifreeze), buried flush with the ground, and left in place for 48 h. Even though pitfall traps sample both diurnal and nocturnal ant assemblages, they accurately represent the relative activity of ground-dwelling ants foraging during the day. In this system, daily temporal species turnover at bait stations is minimal, such that a large majority of the ants foraging at night also forage during the day (Lessard, unpubl. data). In July 2005, during the peak in ant activity, we performed hand collecting and Winkler extraction at each site to sample those species that might not be captured by pitfall traps. We visually searched the litter at each site for 10 min, hand collecting any ants found. At each site we also collected five randomly placed leaf-litter samples (0.5 m × 0.5 m) separated by at least 5 m. The leaf-litter samples were transferred to Winkler sacks and suspended for 48 h. Because estimating dominance and discovery ability requires knowledge about both the relative abundance of species and behavioural interactions, only those taxa ($n = 7$) that were recorded both in pitfall traps and at baits were included in the test of discovery-dominance tradeoff and dominance-thermal tolerance tradeoff. Because only *A. rudis* was the only abundant species on bait cards at the highest elevation site, no interspecific interactions were observed at that site. Thus we did not include species data from this high elevation site in our tests of behavioural tradeoffs. Voucher specimens are in RRD's collection at North Carolina State University.

Quantifying behavioural interactions

For each observation at a bait station, we recorded any behavioural interactions between workers of different species within the first 20 s of the beginning of the observation. Behavioural interactions at baits were classified into one of the three following categories: (1) neutral, (2) aggressive, (3) submissive. The simultaneous presence of at least two non-conspecific workers that did not interact with one another, or observations of antennation between two non-conspecific workers, was scored as a neutral interaction. Aggressive interactions included biting, stinging, spraying or bumping into the worker of another species causing it to immediately leave the bait station. Submissive interactions included any physical contact between two different species that resulted in one species backing up or leaving the bait station. An interaction could be scored in

multiple categories. For example, if a species sprayed another with formic acid leading to the escape of the ant being sprayed, the attacker would get scored as aggressive and the victim would be scored as submissive. For each observation at a bait station, only the first interaction observed between species during the first 20 s was scored.

We estimated behavioural dominance using both Fellers's dominance index (1987) and a variation of Fellers's dominance index. Thus we performed all analyses of dominance twice, once with each dominance index. Fellers's dominance index is calculated by dividing the number of aggressive interactions by the sum of non-neutral interactions (aggressive/aggressive + submissive). Here, because three of the species studied had a dominance index of 1, we modified Fellers's index so as to create more variation in dominance scores among species. We estimated the modified dominance index by dividing the number of aggressive interactions by the sum of all interactions [aggressive/(aggressive + submissive + neutral)]. Both behavioural dominance indices range between 0 and 1, where a species with a "0" score was always submissive or neutral in its encounters with other species, and a species with a "1" score was always aggressive. Both dominance indices were estimated by pooling species interactions from all five sites. To prevent underestimating or overestimating behavioural dominance, we included in our analyses only taxa that engaged in at least five non-neutral interactions (aggressive or submissive) and/or engaged in at least 25 total interactions (aggressive or submissive or neutral).

Estimating discovery ability

We estimated the discovery ability of each species by pooling the total number of baits discovered across all sites. The total number of baits discovered was then compared to a null expectation to factor out the effect of local abundance. For a given species x , the null model consisted of the sum of all the baits discovered by each species (\sum of discovered baits sp. 1 + discovered baits sp. 2 + ...) divided by the sum of all the pitfall traps from which each species was recorded (\sum no. pitfall trap records sp. 1 + no. pitfall trap records sp. 2 + ...) and multiplied by the number of pitfall traps in which species x was recorded (see LeBrun and Feener, 2007 for details).

Discovery ability was estimated by obtaining the residuals of a 1:1 regression line (slope = 1, intercept = 0) between the null model and the number of baits discovered by each species. Thus for each species, we obtained a residual that reflected how its discovery ability departed from a null expectation based on the local abundance of the species. These residuals were used as a dependent variable

in the test of discovery-dominance tradeoff. To test for the discovery-dominance tradeoff, we assessed whether discovery ability was negatively related to dominance. A negative relationship indicates that behaviourally dominant ants discovered proportionally fewer baits than did behaviourally subordinate ants.

We further estimated discovery ability by determining the mean time to bait discovery. For each baiting session, we determined the time at which each species had at least one worker on the bait (i.e., 20, 40, 60 or 80 min). We then estimated, for each species, the mean time to discovery by averaging the time at which a species discovered bait in all of the baiting sessions at which the species was recorded. We then tested whether mean time to discovery was related to dominance using linear regression.

Abiotic variables

We used a handheld infrared thermometer to record the temperature at which ants were foraging at each bait station. We recorded ground temperature each time a species was observed at a bait station. Previous studies have shown that ground temperature accurately represents the microclimate to which ants are exposed while foraging and an excellent predictor of ant activity (O'Neill and Kemp, 1990). Previous similar studies have also used ground temperature to estimate thermal limits of ant foraging activity (Cerdá et al., 1998).

We also obtained annual air and soil temperature averages from the Coweeta LTER climatic data (data from 2000 to 2005). Minimum and maximum air temperatures were recorded by a datalogger and compared to a maximum/minimum thermometer installed below the sensor. Soil temperatures were recorded (at a 5 cm depth) using thermocouples wired to a datalogger and compared to readings taken using a REOTEMP soil thermometer (for more details, see <http://coweeta.ecology.uga.edu>). Because abiotic data were available only for the five highest elevation sites, all analyses including annual temperature averages were limited to these sites.

Dominance-thermal tolerance tradeoff

To determine if a dominance-thermal tolerance tradeoff existed we related the dominance index of each species to the temperature envelope within which it foraged. We examined the relationship between temperature and dominance by estimating the minimum, maximum and mean temperature at which each species was recorded at bait stations. We then assessed whether any of these estimates of foraging temperature regime were related to behavioural dominance using simple linear regression. If the relationship is positive, then there is a tradeoff

between the ability of a species to dominate food resources, and its ability to forage in cold (stressful) climatic conditions. However if there is no statistical relationship, then there is no evidence for a dominance-thermal tolerance tradeoff.

To assess whether species tended to forage under different temperature regimes, we compared for each species the mean temperatures at bait stations across all sites, using an ANOVA. To ensure the independence of the data, if more than one species was detected at a bait, we included in our analyses a temperature record only for the species for which we had the lowest total number of temperature records (i.e., usually *A. rudis* was eliminated). We also estimated for each species the range and standard deviation of temperatures at which they foraged to test whether the size of the foraging temperature range was related to dominance. For this analysis, we again used simple linear regressions. If the relationship is negative, then species that are behaviourally dominant have small foraging temperature ranges, and subordinate species have large foraging temperature ranges. Thus a negative relationship between foraging temperature range and dominance suggests a mechanism by which these species coexist.

Results

In total, we detected 17 species along the elevational gradient at Coweeta LTER. Based on pitfall trap catches, the most abundant species were *A. rudis* (83%), *P. imparis* (16%) and *Myrmica punctiventris* Roger (15%). Ant species richness generally decreased with increasing elevation ($r^2 = 0.82$, $P = 0.03$). The total number of species recorded at a site varied from two species at the highest elevation site to nine species at a mid-elevation site. Also, the total number of ant species recorded at a site was positively, though not significantly, related to the coefficient of variation in maximum ground temperature recorded for that same site ($r^2 = 0.55$, $P = 0.08$). Average annual air and soil temperatures were negatively related to elevation (air: $r = 0.94$, $P < 0.05$; soil: $r = 0.92$, $P < 0.01$).

Estimating discovery ability and dominance requires both bait and pitfall trap records. We recorded a total of 15 species in pitfall traps, but only 9 of them were also recorded at baits (Table 1). Out of these nine species, seven engaged in at least five non-neutral encounters and/or a total of at least 25 interactions. Therefore, we used these seven species to test for the discovery-dominance tradeoff and the dominance-thermal tolerance tradeoff. A total of seven species were included in our analyses, which is a number comparable to previous similar studies (LeBrun and Feener, 2007; Feener et al., 2008).

Table 1 List of species recorded at baits (B) and in pitfall traps (P) at five sites along the elevational gradient at Coweeta LTER

	Elevation (m)				
	591	782	795	865	1,001
<i>Aphaenogaster fulva</i> Roger			BP		
<i>Aphaenogaster rudis</i> Enzmann	BP	BP	BP	BP	BP
<i>Brachymyrmex depilis</i> Emery			P		
<i>Camponotus chromaioides</i> Bolton		BP	B		
<i>Formica rubicunda</i> Emery		B		B	
<i>Formica subsericea</i> Say	B	BP	BP	B	
<i>Lasius alienus</i> (Foerster, 1850)			B	BP	B
<i>Myrmecina americana</i> Emery	P	P	P	P	B
<i>Myrmica punctiventris</i> Roger	P	BP	P		
<i>Paratrechina faisonensis</i> (Forel)		BP			
<i>Prenolepis imparis</i> Emery (1893)	BP	P	BP	BP	
<i>Stenamma</i> sp. a	P	P	P	P	P
<i>Stenamma</i> sp. b	P	P	P		P
<i>Temnothorax curvispinosus</i> Mayr 1866		B	BP		
<i>Temnothorax longispinosus</i> Roger	B	B		B	

Discovery-dominance tradeoff

We made a total of 360 observations at baits, and inter-specific encounters occurred in 77% of those observations. These numbers are similar to those of other similar studies (e.g., Feener et al., 2008). Dominance was not related to discovery ability whether we used Fellers's dominance index as an estimator of behavioural dominance ($r^2 = 0.002$, $df = 6$, $P = 0.91$) or a modified version of Fellers's index ($r^2 = 0.02$, $df = 6$, $P = 0.74$; Fig. 1).

We also used a temporal approach to estimate discovery ability and found that mean time to discovery was not related to dominance. Dominant species were not slower to discover baits than were subordinate species. Mean time to discovery was not significantly related to either the

Fellers's dominance index ($r^2 = 0.22$, $df = 6$, $P = 0.29$) or a modified version of the Fellers's index ($r^2 = 0.17$, $df = 6$, $P = 0.35$).

Dominance-thermal tolerance tradeoff

Using Fellers's dominance index, behavioural dominance was not related to minimum ($r^2 = 0.41$, $df = 6$, $P = 0.12$), maximum ($r^2 = 0.17$, $df = 6$, $P = 0.37$) or mean ($r^2 = 0.15$, $df = 6$, $P = 0.39$) foraging temperatures. However, using the modified version of the Fellers's index, dominance was positively related to the minimum temperature at which a species was recorded at baits ($r^2 = 0.83$, $df = 6$, $P < 0.01$; Fig. 1), though dominance was not significantly related to mean ($r^2 = 0.00$, $df = 6$, $P = 0.88$) or maximum ($r^2 = 0.30$, $df = 6$, $P = 0.20$) foraging temperature. That is, species that forage at lower temperature tended to be behaviourally subordinate.

Estimates of foraging temperature ranges were also related to dominance. Subordinate species tended to have larger foraging temperature ranges than did dominant species (maximum-minimum temperature: $r^2 = 0.56$, $df = 6$, $P = 0.04$; standard deviation: $r^2 = 0.58$, $df = 6$, $P = 0.05$; Fig. 2). Overall there was a significant difference in the average temperature at which species foraged (ANOVA, $F_{6, 1164} = 2.72$, $P < 0.01$; Fig. 3).

Discussion

Overall, we found that temperature shapes the structure of ground-dwelling ant communities among several sites in the southern temperate forest system. Though both dominant and subordinate species foraged during warmer temperatures, behaviourally subordinate species tended to forage at temperatures below those at which dominant species foraged. However, subordinate ant species were not better at discovering resources than were behaviourally

Fig. 1 Dominance-temperature tolerance versus discovery-dominance tradeoff. The figures show **a** minimum foraging temperature recorded for each species as it relates to its behavioural dominance and **b** discovery ability as it relates to behavioural dominance. Here dominance is a modified version of Fellers's dominance index wherein for each species, dominance is the ratio of aggressive interactions to all interactions

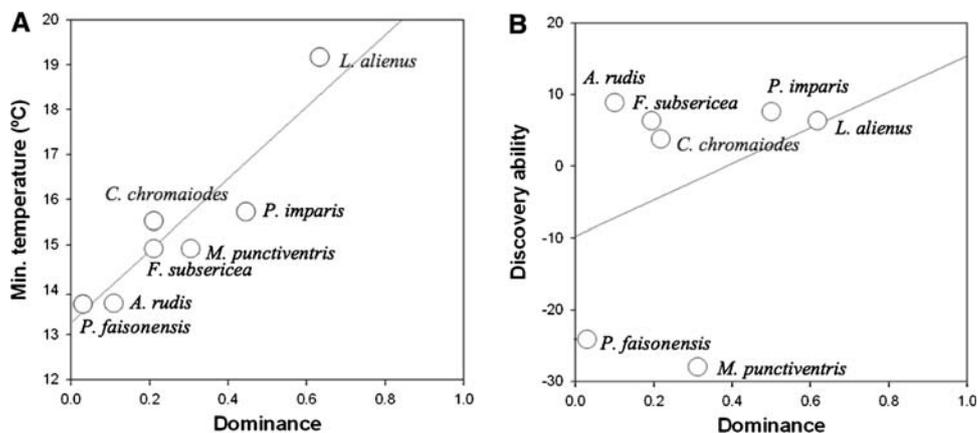


Fig. 2 Foraging temperature range as a function of behavioural dominance. We estimated temperature range using two different metrics: **a** maximum-minimum temperature record and **b** standard deviation of temperature records

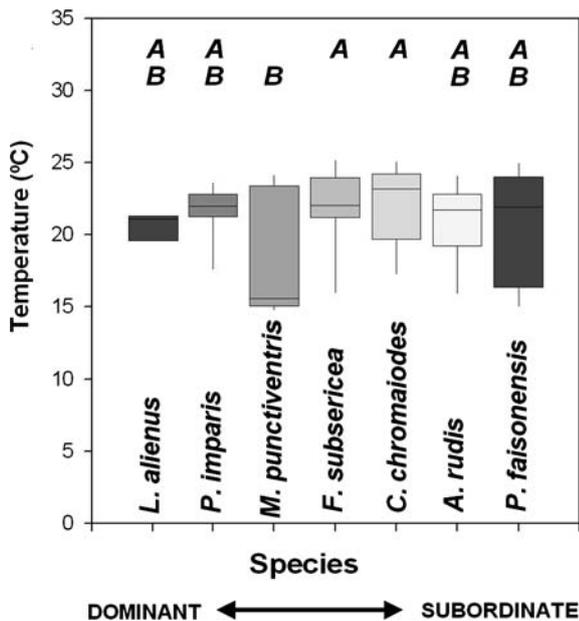
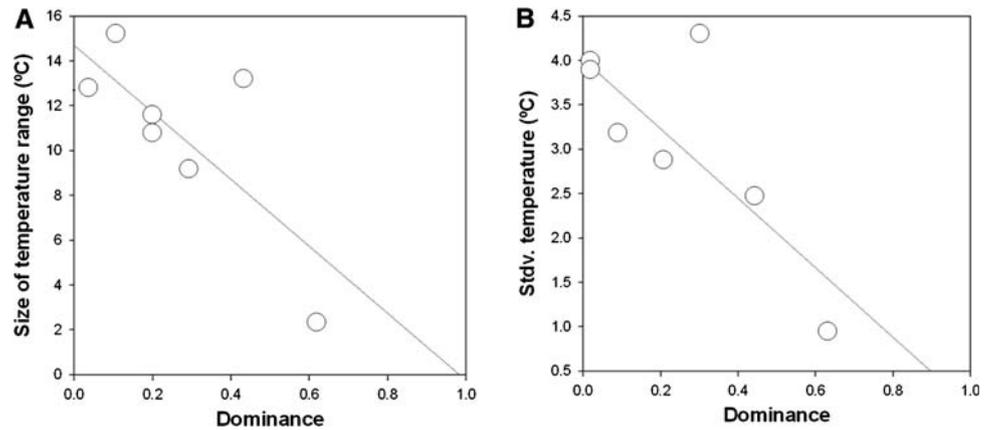


Fig. 3 Foraging temperature ranges of the seven most common ground-dwelling ant species in this system. The horizontal line in the box plots shows the median temperature (\pm SEM) for each species. The lower limit of the box plots shows the 25th percentile and the upper limit shows the 75th percentile. The organization of the bars is such that species on the left are the most dominant and species on the right are the most subordinate. Dominance is estimated using a modified version of Fellers's dominance index as described in the text. Different letters indicate significant difference ($P < 0.05$) between means, based on a Tukey test

dominant species, contrary to what a discovery-dominance tradeoff would predict.

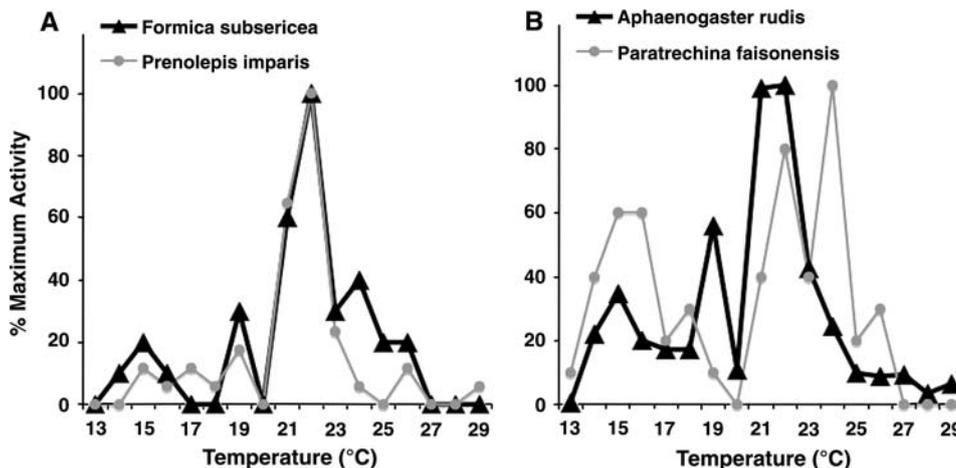
Cerdá et al. (1997; 1998) documented a dominance-thermal tolerance tradeoff in Mediterranean ant communities and suggested that it was this tradeoff that allowed the coexistence of dominant and subordinate ant species. Whereas in the study region examined by Cerdá et al. (1997; 1998) high temperatures were limiting, in the current study low temperatures were. Subordinate species in our system foraged at lower temperatures than did

dominant species. In addition, they exploited a greater range of temperatures during foraging. In contrast to the results documented by Cerdá et al. (1998) we did not observe clear temporal segregation in foraging regime, perhaps because fluctuations in daily temperature are not nearly as extreme in the temperate forests of southern Appalachia as they are in the desert shrublands of Spain. But taken together, our results support the hypothesis that temperature plays a role in promoting coexistence between dominant and subordinate species.

A key question that emerges from our results is why subordinate ants forage at lower temperatures than do dominant species. Subordinate species may have greater thermal tolerance than dominant species (Fellers, 1989; Cros et al., 1997), perhaps due to character displacement or to niche conservatism. Alternatively, subordinate and dominant species may have similar thermal tolerance, but dominant species forage only at near optimal temperatures (or risk-free temperatures, see Cerdá et al., 1998), whereas subordinate species are competitively excluded from those temperatures and forced to forage at a wider range of temperatures to attain resources. We cannot distinguish between these two possibilities yet, but the example of *P. imparis* (which foraged at high temperatures in our study sites during the summer, but also forages during the coolest months of the year) suggests that competitive exclusion, rather than intrinsic metabolic limitations, may account for the observed patterns.

A priori it might be predicted that dominance-thermal tolerance tradeoffs allow coexistence not only in space and during a given day but also through the season. However, at least in this project's study region, this does not appear to be the case. Dunn et al. (2007) showed that the seasonal activity periods of ant species are either random or more clustered in the warm months of the year than expected by chance. Further, species studied here that forage at significantly colder temperatures during the warmer months of the year do not necessarily also forage in colder months than do other species (and vice versa). For example,

Fig. 4 Foraging temperature regime measured as a percent of maximum activity. Activity is the sum of baits occupied and maximum activity is the maximum number of baits occupied in any given temperature bracket. The figure shows standardized activity for the two most abundant **a** dominant and **b** subordinate species



Prenolepis imparis, often called the winter ant, foraged at relatively warmer temperatures in our study period (Figs. 3, 4) and was behaviorally dominant, but its season of peak activity is actually during much cooler months than any other ant species in the region (Dunn et al., 2007).

Our results are consistent with a dominance-thermal tolerance tradeoff, but they do not support the hypothesis that a discovery-dominance tradeoff promotes species coexistence. Adler et al. (2007) proposed that subordinate ant species might be able to coexist with dominant species because of the ability of subordinate species to rapidly discover and exploit food resources. But here, species that discovered many baits were not any more submissive in aggressive encounters than were species that discovered fewer baits. In addition, species that were subordinate did not discover baits faster than did dominant species. Similarly, Santini et al. (2007) found no evidence for the discovery-dominance or the dominance-thermal tolerance tradeoff in a Mediterranean ant assemblage, though such tradeoffs likely promote coexistence in other Mediterranean ant assemblages (Cerdá et al., 1997; 1998a).

Fellers (1987) found evidence of the discovery-dominance tradeoff in other temperate forest ant communities. Surprisingly, the ant communities studied by Fellers were very similar in species composition to those studied here. Perhaps the most striking difference in community composition between Fellers's study and ours is the presence of *Tapinoma sessile* (Say), which was common at Fellers's study site in Maryland, but not at Coweeta LTER and the absence of *Paratrechina faisonensis* (Forel), which was absent from Fellers's study site but present in the communities studied here. In fact, a close look at the discovery-dominance relationship in our study shows that the poor discovery ability of the subordinate *P. faisonensis* partially explains why the discovery-dominance tradeoff does not hold in our system. Contrary to the prediction of the discovery-dominance tradeoff, *P. faisonensis* was behaviourally subordinate and discovered few baits relative to its

local abundance. Overall, these results suggest that the importance of tradeoffs in shaping ant communities may vary not only with habitat, but also with assemblage specific characteristics, including the presence or absence of a single species.

The dominance index we used could also explain the lack of a discovery-dominance tradeoff. One problem with assessing dominance rank is that not every species pair interacts in nature. In a recent study, LeBrun and Feener (2007) used a mathematical algorithm developed for rating American college football teams which takes into consideration non-interacting species to assess ranks in transitive dominance hierarchies (because not every football team plays every other football team). Although using a different dominance metric could slightly alter the order of dominance ranks, it is unlikely to make species such as *A. rudis* and *P. faisonensis* appear dominant, since both of these species are almost always submissive in interspecific encounters.

Previous studies have shown that the dominance-thermal tolerance tradeoff could account for coexistence of species within local communities. Our results suggest that these tradeoffs may also explain patterns of variation among sites because sites with more variation in temperature also had more species. It is now well established that temperature strongly affects broad-scale patterns of ant species richness (Kaspari et al., 2004; Sanders et al., 2007) and local community structure in a number of systems (Bestelmeyer, 2000; Cerdá et al., 1997; 1998). Much of the focus on the effect of temperature on ant diversity has been on mean annual temperature, but variation in temperature is also clearly important, especially if it promotes coexistence among dominant and subordinate species. It may be generally true that sites with many thermal niches may also tend to have many species, as we found here. Within communities, the dominance-thermal tolerance tradeoff can account for species coexistence. Subordinate species tend to forage at a wide array of temperatures, which might

allow them to forage while dominants are not active and thus, avoid aggressive encounters. Taken together, our results add to a growing number of studies indicating that temperature, either directly or indirectly, plays a key role in shaping the structure and dynamics within, and among, ant communities.

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