Some like it hot: effects of temperature and fine-scale resource distribution on ant community domination

L.D. STRINGER[1,2], J. HAYWOOD[3] and P.J. LESTER[1]

[1] School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington, New Zealand.

[2] Current address: The Horticulture and Food Research Institute of New Zealand, PO Box 51, Lincoln, New Zealand.

[3] School of Mathematics, Statistics & Computer Science, Victoria University of Wellington, PO Box 600, Wellington, New Zealand.

Correspondence: Phil Lester, School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington, New Zealand. E-mail: phil.lester@vuw.ac.nz

Abstract   In order to coexist in sympatry, subordinate species must somehow obtain resources that dominant taxa may generally control. We examined the response of an ant community to fine-scale variation in resource distribution, as a mechanism enabling resource acquisition by subordinates in the presence of dominant taxa. Food (6g) was partitioned as 1, 8, or 64 items in a $0.4m^2$ area, near nests of the dominant ant *Monomorium sydneyense* Forel, during a variety of temperatures.

As the number of food items increased, a significant increase in the number of species utilizing the food was observed, associated with an increase in the unutilized proportion of food items.

The changing occupation rates of food items by *M. sydneyense* and three other species was modelled against soil surface temperature and the varying dispersion rate of the food resource. We observed significant main effects of density, site, species, and temperature on the probability of food being occupied by a species. However, there were also significant interaction effects, making it impossible to interpret the main effects in isolation. *Monomorium sydneyense* dominated a smaller proportion of resources in trials with increased resource distribution and cooler temperatures, allowing more species to access resources.

There was considerable variation between species in their response to variation in temperature and food distribution. Though most species were able to respond to increasing resource dispersion, species that were in low abundance apparently could not. However, even species that could respond to increasing resource dispersion had a limit to the number of resources that they could secure.

Key words   Coexistence, sympatry, diversity, dominance, food, temperature, foraging, *Monomorium sydneyense.*

Introduction

Community theory predicts that species competing for the same resource should be spatially or temporally separated in order to allow for coexistence, and that subordinate species can coexist only when their niche is different from that in ecologically dominant species. This niche differentiation can arise when stochastic fluctuations in the environment, such as with

the distribution of resources or temperature variation, affect each species differently (Savolainen & Vepsäläinen, 1988). Temperature is considered to be a key factor for coexistence in some ant communities; so much so that resource partitioning based on thermal tolerance has been demonstrated in several studies (Andersen, 1995; Cerdá *et al.*, 1997; Albrecht & Gotelli, 2001). Ecologically dominant species can have limited thermal tolerance compared to that of subordinate species, enabling these subordinates to achieve a much higher density than would be otherwise expected (Cerdá *et al.*, 1998). In at least some communities there even appears to be a trade-off between temperature tolerance and behavioural dominance, wherein subordinate species are only able to forage at extreme low or high temperatures in the absence of the behaviourally dominant species (Bestelmeyer, 2000), thus escaping competitive interactions. However, in several of these studies, considerable niche overlap in temperature is observed between competing and coexisting ant species (e.g. Bestelmeyer, 2000; Albrecht & Gotelli, 2001). Additionally in habitats where there are small daily temperature fluctuations, such as those that are found on the equator, there are extremely diverse ant assemblages yet these sites have limited potential for niche differentiation based on temperature (Kaspari *et al.*, 2004). For such communities, other mechanisms of reducing niche overlap must be acting to allow species to obtain resources while living in sympatry.

One such mechanism enabling coexistence at a scale of tens or hundreds of meters is habitat partitioning. Greenslade (1979) demonstrated dominant species to be spatially separated with little overlap in their foraging range. This pattern in ant distribution has been described as 'ant mosaics' (Leston, 1973). Such regular dispersion in ant communities is often observed and is thought to result from neighbourhood competition, where competition between established colonies is often weak but can be intense for colonies attempting to establish within the territory (Ryti & Case, 1992). Subordinate species coexist in these mosaics by fitting between the boundary gaps of the dominant species (Greenslade, 1979). The size of the area that the dominant species occupies varies, but is generally of several meters or more (Greenslade, 1971, 1979). Consequently, perhaps it is not surprising that in studies examining ant coexistence in spatial scales encompassing tens of meters (e.g. Levings & Traniello, 1981; Albrecht & Gotelli, 2001; Thomas & Holway, 2005), considerable niche overlap is observed and the spatial segregation of species is considered a major factor enabling niche overlap and species coexistence.

For many ant species within communities coexistence occurs at much finer scales than that of meters. Individual traps rarely collect only an individual species, indicating a variety of species are foraging in the same local environment. One under-studied potential factor contributing to this result is variation in the number of and distribution of resources at fine spatial scales. Different ant species vary considerably in the way that they utilize resource patches in an environment. Some species will recruit on mass to individual resources, while others spread out over a wide area (Hölldobler & Wilson, 1990). There is considerable variation between species in their ability to find food in an environment, which has been suggested to contribute to coexistence in the dominance-discovery trade-off hypothesis (Davidson, 1998). In experiments on fly communities that utilize carrion resources, dominant competitors may be spatially aggregated creating spatial refuges for weaker individuals (e.g. Ives, 1991). Further, the size of the resource patch may enhance or decrease the potential for coexistence (Kouki & Hanski, 1995; Horgan, 2005). Such influences of resource distribution on coexistence in ant communities have generally been ignored, despite the knowledge that multiple food resources occur in small habitat patches ($<1m^2$) (Wehner, 1987) and not in one large patch as in most experimental studies (Albrecht & Gotelli, 2001; Thomas & Holway, 2005).

In this study, the role of fine-scale variation in food distribution and temperature enabling multiple species to utilize food resources in a small area ($0.4m^2$) was examined. Furthermore, the response of individual species to variation in food distribution and temperature, in comparison with *Monomorium sydneyense* Forel was investigated. This species is of Australian origin and is a recent invader to New Zealand (Lester, 2005). Previous work in this study system showed that *M. sydneyense* has significantly altered the composition of ant communities (Stringer & Lester, In Press). It was observed to compete for and dominate food resources in study plots, though it appeared not to have excluded other ant species from study areas (Stringer, 2005). Such a result is perhaps the norm for many invasions; a new species establishes and may dominate certain resources, and may alter the community composition, but with few or no species being extirpated from the invasion zone. The hypothesis was that other ant species are able to coexist with *M. sydneyense* by having different responses to changes in temperature and resource distribution, thereby reducing the amount of competition interactions with *M. sydneyense*. *Monomorium sydneyense* was used as

the reference species and comparisons were made on how other ant species are able to obtain resources in its presence.

Methods

Study site

The study was undertaken at Sulphur Point, Tauranga, New Zealand (37° 39'S, 176° 11'E) in 2003 and 2004. This area experiences a sub-tropical climate with warm humid summers and mild winters. Daily average temperatures range from 22-26°C in summer, with the hottest months being January and February, to 12-17°C during winter, with July being the coolest month (NIWA 2005). Annual precipitation ranges between 1250 to 1500 mm per year, with the monthly average increasing slightly during the winter months (de Lilse & Kerr, 1963). The food utilization experiments were conducted in a 70×40 m grassed area. Five *M. sydneyense* colonies were located along the edge of the grassed area where it came into contact with an asphalt road, as nests were easier to find by following workers returning to these colonies. Colonies were separated by ~10 m and did not interact with each other.

Resource utilization experiments

We examined the effect of food dispersion on the number of ant species accessing food resources, as well as differences in the proportion of foods occupied by co-occurring ant species due to a change in the dispersion of the food and temperature. Approximately 6 g of food was divided at three different rates within a known area simultaneously recording soil surface temperatures. Smooth, sugared peanut butter was used as a food resource, as it was found to be a preferred food type, highly attractive to the majority of ants in the area and retained its moisture and attractiveness for extended periods of time (Stringer, 2005).

Food items were placed in 50 cm radius half circles (total area ~0.40 m^2) from the edge of the asphalt centred on each of the five *M. sydneyense* colonies. The peanut butter was haphazardly placed within the trial areas at a dispersion rate of either '1' (n = 31), '8' (n = 31) or '64' (n = 30); one '64' trial was not completed due to rain. A dispersion rate of '1' meant

that all six grams of the peanut butter was clumped in one spot within the half circle, whereas a rate of '64' meant that the six grams of peanut butter was distributed between 64 spots within the 50 cm radius half circle. All of the food items were uniquely identified by placing numbered flags through the centre of the food so that the presence or absence of ant species at each individual food item could be assessed. Trials were deemed to have started once the first piece of food was placed on the ground. At the end of a 2 h period, the species present at each food item was recorded. Soil surface temperature was recorded using an electronic thermometer with a probe that was placed under grass next to the trial site. All foods in the trials were placed on grass and never on the asphalt. Ant species in this study were readily able to be distinguished in the field, but samples of all species were taken back to the laboratory to confirm identification.

To investigate whether there were differences in ant species richness during a trial due to the dispersion rate of the food comparisons were made on the number of species recorded for each dispersion trial (n = 92, with a total number of 2199 data points). Five sites were surveyed, which were sampled in March, August, October and December 2004. A Generalized Linear Model (GLM) quasi-Poisson regression was used to test for differences in ant species richness between food dispersion treatments.

The four most commonly occurring ant species were used to test for the effect of food dispersion and temperature on food utilization: *M. sydneyense, Pheidole rugosula* Forel*, Paratrechina vaga* (Forel) and *Iridomyrmex anceps* (Roger). These ants were observed co-occurring at the five sites. Predictions were made on the proportion of baits occupied by each species using a binary logistic regression (Agresti 2002). The dependent response variable was the presence or absence of an ant species at each of the individual food items at the end of the two hour trial modelled using four explanatory variables: ant species, food dispersion rate, site and temperature. Binary logistic regression fits the data to give predicted probabilities (odds) of presence at food, given particular values of the explanatory variables. The continuous explanatory variable temperature was centred about zero by mean-correction, making the mean temperature of 21.3°C a reference point. For the categorical explanatory variables of species, food dispersion rate and site, the reference categories, from which all other categories are fitted as deviations, are: species = *M. sydneyense,* dispersion rate = 1 and site = 1. The natural way to interpret a parameter estimate, β_i, in such models is via the direct effect that the

parameter has on the odds of presence at a food item. Those odds increase multiplicatively by exp(β_i) for every one unit increase in the corresponding ith explanatory variable, at fixed levels of the other explanatory variables. For example, if the predicted odds ratio, exp(β), is 15 for one of the ant species, when comparisons are made between the proportion of food items occupied with only species allowed to change, the odds that it is present at the food is 15 times as large as the odds of *M. sydneyense* being present. An exp(β) value of one implies that the predicted proportion of foods occupied by the species is not different from the reference species, *M. sydneyense*. Conversely, an exp(β) value of 0.5 means that the odds are half that of *M. sydneyense* being present at the food. However, when significant interaction effects occur (as they do in the selected model, below) it is impossible to interpret exp(β) directly, as the main effects cannot be considered in isolation.

To illustrate the calculation of food utilization probabilities, consider first the simplest logistic regression model with just a single explanatory variable, x. The odds of bait occupation would be calculated as $\exp(\alpha + \beta x)$; i.e., the logarithm of the odds depends linearly on x. The corresponding probability of food utilization is then given by the equation:

$$P(\textit{bait occupied}) = \frac{\textit{odds}}{1 + \textit{odds}} = \frac{\exp(\alpha + \beta x)}{1 + \exp(\alpha + \beta x)}.$$

In this analysis, however, there are several statistically significant explanatory variables and interactions between them (Table 1). Consequently the expressions for odds of bait occupation become more complicated, but the corresponding probabilities are still calculated using an equation of the form above. For example, the probability of *Ph. rugosula* occupying a food item at a high food dispersion rate located at site 2, at a temperature of 15°C is given by:

$$P(\textit{bait occupied}) = \frac{\exp(\alpha + \beta_1(15 - 21.3) + \beta_2 + \beta_3(15 - 21.3) + \beta_4 + \beta_5 + \beta_6 + \beta_7 + \beta_8)}{1 + \exp(\alpha + \beta_1(15 - 21.3) + \beta_2 + \beta_3(15 - 21.3) + \beta_4 + \beta_5 + \beta_6 + \beta_7 + \beta_8)},$$

where α represents the 'baseline' effect for species *M. sydneyense* at the lowest food dispersion rate, located at site 1 at the reference temperature of 21.3°C, while the remaining

parameters account for differences from those reference conditions. In particular, β_1 is the main effect of difference from the reference temperature, β_2 is the main effect of species *Ph. rugosula* rather than *M. sydneyense*, β_3 is the coefficient of the interaction between temperature and species *Ph. rugosula*, β_4 is the main effect of a high food dispersion rate, β_5 is the interaction between high food dispersion rate and species *Ph. rugosula*, β_6 is the main effect of site 2, β_7 is the interaction between high food dispersion rate and site 2, and β_8 is the interaction between site 2 and species *Ph. rugosula*. All analyses were performed in SPSS (SPSS, 2002).

Results

A significantly higher mean ant species richness was observed when the 6 g of food was distributed in 64 patches, compared to just in an individual patch (d.f.=2; Deviance= 9.430; *P*= 0.009) (Fig. 1a). There was a site effect on the number of ant species present (d.f.= 4; Deviance= 15.821; *P*= 0.003). Although it is difficult to specifically state the cause of this significant site effect, it is likely to be related to spatial variation in the distribution and size of ant colonies or microclimate differences between sites. No significant food dispersal rate × site interaction was observed (d.f.= 8; Deviance= 1.403; *P* = 0.994). A total of 9 ant species were observed foraging on the bait. These species were (in order of most to least observed over the entire study): *Pheidole rugosula, Monomorium sydneyense, Paratrechina vaga, Iridomyrmex anceps, Monomorium antarcticum* (F. Smith)*, Monomorium antipodum* Forel*, Tetramorium grassii* Emery*, Tetramorium bicarinatum* (Nylander)*, Cardiocondyla minutior* Forel. The following analysis will focus on the first four of these species, as only these provided sufficient data for the logistic regression analysis. At the time of choosing the study sites, all four species were observed to be present at all of the five study sites used below.

The proportion of foods occupied by ants declined with increasing food dispersion (Fig. 1b). An initial binary logistic regression model that contained only the main effects of food dispersion, site, species and temperature, was relatively poor at correctly classifying food occupation by ants (percentage correct classification= 88.3% overall; 9.5% for ants at food; 98.7% for ants not being present) (d.f.= 10; Deviance= 4911.7). The selected model included

all 2-way interactions of the main effects except temperature × site, and temperature × density (these factors were excluded from the analysis as they did not improve classification success). This selected model improved the correct classification rate relative to the initial model, particularly for ants present at food (percentage correct classification= 89.2% overall; 49.2% for ants at food; 94.5% for ants not being present) (d.f.= 39; Deviance= 4159.4). The change in deviance from the initial model of 752.3 on 29 d.f. ($P < 0.001$) is indicative of a substantial improvement in model fit. The addition of 3-way interactions did not improve classification success (and would have been difficult to interpret).

The binary logistic regression model indicated significant main effects of density, site, species, and temperature ($P \leq 0.029$). However, there were also significant interaction effects for these variables, making it impossible to interpret the main effects in isolation. For example, the model with 2-way interactions indicated that the odds, exp(β), that *Pheidole rugosula* would occupy a food item were 34 × greater than the odds for *M. sydneyense*, when other factors were fixed at reference levels ($P < 0.001$; Table 1). However, the odds ratios for *M. sydneyense* were higher at all four other study sites and the site × *Ph. rugosula* interaction terms were significantly negative at all other sites, indicating a relative reduction in the odds ratio for *Ph. rugosula* at all other sites (i.e. the odds ratios were less than 34 × that for *M. sydneyense* at the other sites).

As food dispersion was increased from 1 to 64 items, the odds of food being occupied decreased for all species (Fig. 1b). The food dispersion × species interaction terms indicated that both *Ph. rugosula* and *I. anceps* responded in a similar manner to increasing food dispersion as did *M. sydneyense*. However, the odds of food occupation by *Pa. vaga* declined significantly faster, being 33 × lower at a food dispersion of 64 per arena than for *M. sydneyense*. Thus, the probability of *Pa. vaga* occupying food at higher resource dispersion rates declined at a faster rate than for the other species.

For each degree of increase in temperature, the odds ratio of food occupation by *M. sydneyense* increased by 1.16 (Table 1). This result is demonstrated by increasing probability of foods being occupied by *M. sydneyense* with increasing temperatures (Figs. 2 & 3). At the highest temperature range (30-39.8°C), fewer species were observed on the food items at all dispersion rates and only *M. sydneyense* was observed on the food at a dispersal rate of 1 (Fig. 2). The influence of temperature on *M. sydneyense* foraging was exemplified over the course

of one of the 2h trials where *M. sydneyense* and *Ph. rugosula* were observed to repeatedly displace each other from baits when there was a change in the amount of insolation. With cloud cover *Ph. rugosula* quickly displaced *M. sydneyense* from the food, however, without cloud cover *M. sydneyense* rapidly returned to the foods that it occupied by displacing *Ph. rugosula.* In contrast, the regression model indicated that *Ph. rugosula* showed no significant change in the odds ratio for food occupation over the range of temperatures observed in this study (8.0 to 39.8°C). This result is apparent from the graphical analysis, as in all temperature ranges *Ph. rugosula* occupied approximately 50% of the baits in at least one of the dispersion treatments (Fig. 2). For the other ant species, the logistic regression model predicted an increase in odds ratio of food occupation by *I. anceps* as temperatures increased (1.08 per 1°C) but a decrease for *Pa. vaga* (0.94 per 1°C). Unfortunately, there were few replicate observations at the high temperatures (30-39.8°C) and a food dispersion rate of 1. These few replicates had only a small overall influence in the statistical model, which predicted other ant species being able to utilize the food under these conditions (Fig. 3) while none were actually observed that were able to do so (Fig 2c).

The logistic regression model also showed a significant effect of site and significant site × species interaction (Table 1), indicating a significantly variable odds ratio for *M. sydneyense* occupying a bait at different sites. These results are related to differences in the observed relative abundance of ants between sites (Table 2). For example, almost all observations of *I. anceps* were at site 3, where a nest of this species was observed close to the study arena. Similarly, almost all observations of *Pa. vaga* were at sites 2 and 5. *Ph. rugosula* was at all sites, but its relative number of baits occupied differed substantially between sites. With these differences in ant abundance between sites, it was not surprising to also observe a significant dispersion × site interaction term. The relative abundance of ants at each site seems likely to have influenced the number of baits any one ant species is able to control.

Discussion

Food dispersion, temperature, and site effects all influenced the utilization of food by different ant species. It seems likely that these factors are all major contributors to coexistence of species within the ant community. It appeared that there was a hierarchy of influencing factors

whereby site provided a base abundance for each species. Temperature further affected the presence or absence of ants, which appeared to influence their ability to secure resources. Results of our study show many small resources support a greater species diversity than the same amount of resource in one large clump. At the highest dispersion rate, the probability of a food item being occupied declined for the dominant species, allowing vacant resources to become available for subordinate species. Previous studies have found that coexistence can be achieved with resources being dispersed over wide spatial scales (>10 m) (e.g. Levings & Traniello, 1981; Albrecht & Gotelli, 2001; Thomas & Holway, 2005), but our study demonstrates that resource dispersion even at a fine spatial scale (<0.5 m) allows subordinate species to gain access to resources. A dispersed distribution of resources at such a relatively small spatial scale is likely to be a major mechanism allowing species coexistence in a wide variety of communities.

Not all ant species responded in a similar manner to variation in food dispersion and temperature. Differences between the thermal tolerances of different ant species is thought to be a strong force driving resource acquisition rates and competitive ability, thus is likely to promote ant coexistence (Cerdá *et al.*, 1997; Retana & Cerdá, 2000). Each of the species responded differently to increasing temperature. The statistical model predicted that as temperature increased, the probability of bait occupation increased for both *M. sydneyense* and *I. anceps* (though at a higher rate for *M. sydneyense*), but remained constant for *Ph. rugosula*, and declined for *Pa. vaga*. This result suggests that there is a change in the dominant ant species due to differences in foraging intensity because of differences in soil surface temperatures. Initially it was thought that *M. sydneyense* was the dominant ant in this system, but it appears that *Ph. rugosula* dominates resources in all but the higher temperature ranges. This species was the most abundant ant in the system and appeared to secure a higher proportion of foods than the other species tested. When surface temperatures increased *M. sydneyense* dominated food resources at warmer temperatures. These results are in accordance with similar studies that have indicated temperature to be a strong force acting on food utilization rates (Thomas & Holway, 2005; Cerdá *et al.*, 1997; Fellers 1989). That *M. sydneyense* had the highest rate of increase of bait occupation with increasing temperature from cool to warm (decreasing thermal stress) is typical for ecologically dominant ant species (Andersen, 1995). However, only during the warmer trials was *M. sydneyense* able to

dominate and occupy all the individual large resource clumps, when *Ph. rugosula* was forced to shift its foraging toward unoccupied smaller resource items (Fig. 2). Thus, it is likely that the influence of dominant species on subordinate foraging success is overstated in other studies which do not account for small scale variation in the spatial distribution of food resources.

The result that an increasing dispersion of a constant amount of food resources may promote coexistence is consistent with the resource concentration hypothesis, which states that species diversity is inversely proportional to spatial food concentration (Root, 1973). An increase in the spread of a resource increases the probability of a part of it being found by any organism (Cain *et al.*, 1985). Different ant species have different foraging strategies. Some species recruit a large number of foragers to discovered food resources and others forage singly (Andersen, 1995; Wilson, 1971). Within this study the probability of any ant species occupying a food item declined with an increasing dispersion of food, but most dramatically for *Pa. vaga*. Little is known about the foraging behaviour of *Pa. vaga*, however, this species had a low abundance within the study sites. It is likely that *Pa. vaga* was numerically limited in how it could respond to any change in the number of resources in any one environment. With higher numbers it may have been able to recruit to more baits, as was apparent for some of the other species. An alternative hypothesis is that *Pa. vaga* may not be as strongly attracted to the food that was used. As differing food preferences is thought to be another mechanism for species coexistence in ant communities (Ribas *et al.*, 2003; Sanders & Gordon, 2003), *Pa. vaga* may be more competitive on different food types.

A further mechanism promoting species coexistence between competing organisms is the spatial variation of species abundance between sites (Palmer, 2003; Morrison, 2000). This is especially the case for ant communities, in which interspecific competition is important and numerical dominance enables resource acquisition (Palmer, 2003). These data demonstrated considerable differences between sites and species in ant abundance, and in their utilization rates of food. Differences in ant abundance between sites may be driven by a variety of biotic and abiotic factors including nest availability (Armbrecht *et al.*, 2006; Hölldobler & Wilson, 1990), microhabitat variation (Palmer, 2003), differences in vegetation (Ribas *et al.*, 2003), and other food resources (Sanders & Gordon, 2003). The presence of existing nests of competing species also influences species abundance (Ryti & Case, 1992). Whatever the

mechanism for differences in ant abundance between sites, variation in the density of different species clearly influenced resource acquisition. Differences in the abundance of different ant species between sites must also aid species coexistence in this area. Thus there are within and between site factors that contribute to the acquisition of food and coexistence.

Perhaps the key result for this paper is that factors such as temperature and resource dispersion are important for species to obtain resources at small spatial scales, because different species respond differently to each of these factors. These processes are likely to jointly enable competing species to coexist in sympatry, in addition to aspects such as niche differentiation, though the relative contribution of each is unknown. This study highlighted the importance of studying ant competition over a large range of conditions. The hypothesis was focussed on *M. sydneyense* as it was thought to be the dominant ant in the Tauranga community when in fact it appears that *Ph. rugosula* is that species in the typical temperature conditions observed in this area. One criticism of this work might be that the experiment was somewhat artificial as resources were experimentally added at what may have been unnaturally high densities. A key area for future research is with spatial and temporal variability in the natural, fine-scale resource distributions within individual patches. The conclusions from this study are likely to be broadly relevant to a variety of systems wherein multiple resources and competing species occur within individual patches.

Acknowledgements

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Table 1. Primary results from the binary logistic regression on the predicted probability that bait would be occupied dependent on species, temperature, site and dispersion rate of the food item. Further results on differences between sites, and specific dispersion × site and site × species interactions, are not shown for brevity purposes.

Factor	β	S.E.	Wald	d.f.	*P*	exp(β)
Species			39.68	3	0.000	
Ph. rugosula	3.533	0.693	25.98	1	0.000	34.236
I. anceps	-1.442	1.322	1.19	1	0.275	0.236
Pa. vaga	-0.870	1.267	0.47	1	0.492	0.419
Dispersion			7.11	2	0.029	
Dispersion (8)	-0.147	0.937	0.02	1	0.875	0.863
Dispersion (64)	-0.976	0.902	1.17	1	0.279	0.377
Dispersion × Species			18.92	6	0.004	
Dispersion (8) × *Ph. rugosula*	-0.355	0.687	0.27	1	0.605	0.701
Dispersion (8) × *I. anceps*	-1.128	0.947	1.42	1	0.234	0.324
Dispersion (8) × *Pa. vaga*	-1.371	0.931	2.17	1	0.141	0.254
Dispersion (64) × *Ph. rugosula*	0.066	0.649	0.01	1	0.919	1.068
Dispersion (64) × *I. anceps*	-1.565	0.890	3.10	1	0.079	0.209
Dispersion (64) × *Pa. vaga*	-2.641	0.882	8.96	1	0.003	0.071
Dispersion × Site			18.39	8	0.018	
Temperature	0.152	0.013	135.29	1	0.000	1.164
Temperature × Species			102.77	3	0.000	
Temperature × *Ph. rugosula*	-0.150	0.016	91.53	1	0.000	0.860
Temperature × *I. anceps*	-0.075	0.029	6.78	1	0.009	0.928
Temperature × *Pa. vaga*	-0.214	0.038	32.43	1	0.000	0.807
Site			12.53	4	0.014	
Site × Species			339.44	12	0.000	
Constant	-2.585	0.917	7.95	1	0.005	0.075

Table 2. The number of baits occupied by each of the four ant species after two hours, at each of the five study sites. The total number of ants observed at each site is shown in brackets; however, counts for one of the four sampling periods are missing, when only presence-absence data were taken.

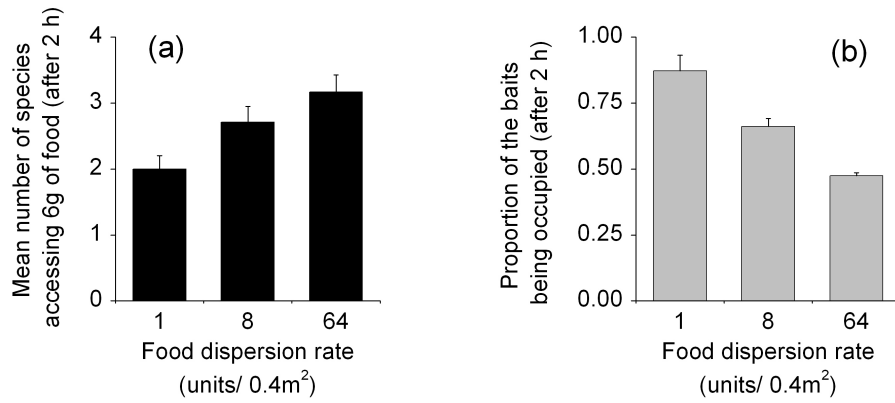| Species | Site | | | | | Total |
	1	2	3	4	5	
M. sydneyense	16 (12)	90 (465)	115 (423)	58 (323)	26 (89)	305 (1312)
Ph. rugosula	267 (1121)	63 (355)	69 (256)	204 (927)	35 (207)	638 (2866)
I. anceps	1 (0)	2 (0)	60 (20)	0 (0)	1 (0)	64 (20)
Pa. vaga	1 (1)	7 (56)	1 (0)	0 (0)	12 (14)	21 (71)
Total	285 (1134)	162 (876)	245 (699)	262 (1250)	74 (310)	1028 (4269)

Fig. 1. (a) Mean species richness of ants at the 6 g of bait, distributed in either 1, 8 or 64 patches (± S.E.; n= 31, 31, 30); and (b) the proportion of baits occupied by the four main species at different food dispersal rates (± S.E.; n=31, 248, 1920).
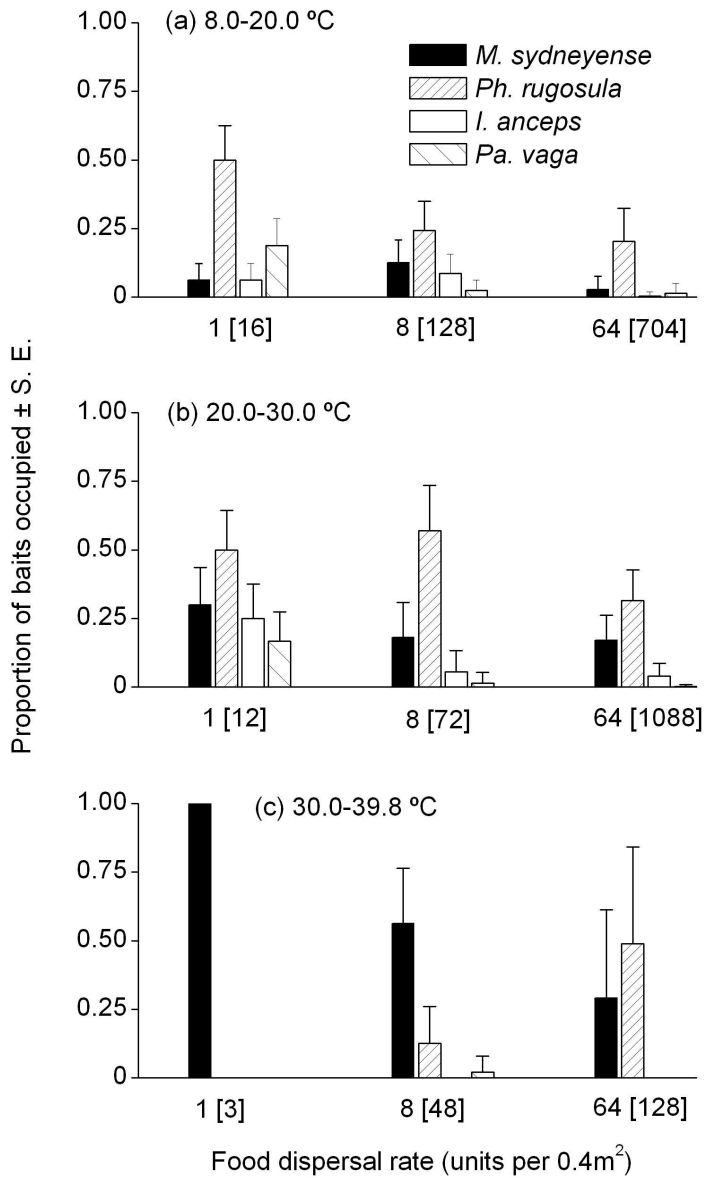
Fig. 2. Proportion of baits occupied by the four most abundant species at different temperatures and food dispersion rates (± S.E.; n varies, depending on recorded temperature, and is shown in square brackets). All trials have been combined for three ranges of temperatures recorded during the study.
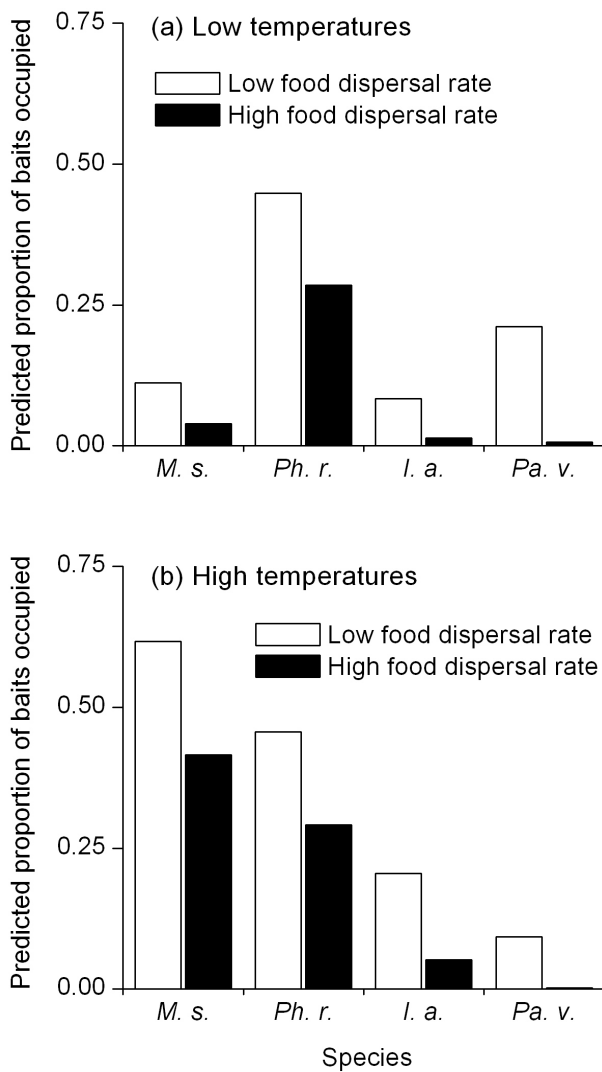
Fig. 3. The predicted proportion of baits occupied by the four most abundant species at a low (15°C) and high temperature (35°C), dependent on food spatial dispersal rates, and averaged over the five sites. Probabilities were calculated using equations of the form presented in Methods. *M. s.* = *Monomorium sydneyense*; *Ph. r.* = *Pheidole rugosula*; *I. r.* = *Iridomyrmex anceps*; and *Pa. v.* = *Paratrechina vaga.*