



Selection and sharing of sheltered nest sites by ants (Hymenoptera: Formicidae) in grasslands of the Australian Capital Territory

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Abstract In this study, it was investigated whether ants nesting under artificial rocks in a mesic south-eastern Australian grassland showed preference for nest sites with different temperature regimes. The study also allowed evaluation of competition between species for nest sites and observations of seasonality in brood and alate production in the nests of four common ant groups. On every sampling occasion more than 90% of nests were either *Iridomyrmex* spp., *Rhytidoponera* 'metallica', *Paratrechina* sp. or *Pheidole* spp. Soil underneath thinner artificial rocks had higher average temperatures and warmed up earlier in the day and *Iridomyrmex* spp. and *R. 'metallica'* showed preference for establishing nests under these. While all ant nests had summer peaks in brood production, *Iridomyrmex* spp. and *R. 'metallica'* had brood observed throughout the year. Winged reproductives were commonly encountered in *Iridomyrmex* spp., *R. 'metallica'* and *Paratrechina* sp. nests, but only occasionally *Pheidole* spp. nests. Alates were present in the nests from February but released by all taxa after spring rains and were scarcely recorded in November, December and January when brood production was observed in most nests. Nest sites that offer protection from predators are an obvious advantage, but improved reproductive success can be gained in cool regions such as the mesic grasslands of the Australian Capital Territory by choosing nest sites with an optimal thermal regime.

Key words competition, *Iridomyrmex*, nest selection, *Rhytidoponera metallica*, temperature.

INTRODUCTION

Ants nesting in the soil take advantage of the fact that soil temperature and humidity vary minimally at depths below a few centimetres and at least some ant species have preferred temperatures for nesting (Banschbach *et al.* 1997). Within the nest, ants are able to manipulate the development of their brood by moving the eggs and larvae to areas of optimal temperature and moisture (Hölldobler & Wilson 1990). While some species prefer open areas, many species of soil-nesting ants commonly build their nests underneath rocks or logs, gaining defence from large myrmecophagous predators and protection from the elements, such as high temperatures (e.g. Dean & Turner 1991; Fernández Escudero & Tinaut 1999; Thomas 2002). Rocks are known to affect microclimatic in general and may also offer low temperature relief in some environments (Cloudsey-Thompson 1956). The high-altitude ant species *Proformis longiseta* showed preference for small- or medium-sized rocks when selecting suitable nest sites in Spain (Fernández Escudero *et al.* 1993). On the other hand, the widespread Australian species *Rhytidoponera 'metallica'*

avoided nesting under small rocks (<200 cm²) in mesic south-eastern Australia (Thomas 2002).

The total number of pupae reared is higher in some ants when nest temperatures are higher (Lopatina & Kipyatkov 1993) and ants nesting in warmer microhabitats also have the advantage of being able to initiate egg-laying and brood development earlier (Hölldobler & Wilson 1990). The occurrence of eggs and larvae in some ant nests may be seasonal (Haines & Haines 1978; Hasegawa 1992) or related to climatic events (Haines & Haines 1978). Studies into seasonality of ant brood production in Australia are rare however with only two published studies of note. Some species of *Monomorium* (= *Chelaner*) and *Pheidole* (Briese & Macauley 1980) and *Rhytidoponera 'chalybea'* (Ward 1976) are noted to have immatures present virtually all year round. Some rocks, especially those that are thin and shallowly embedded, are able to raise the temperature of the underlying soil faster than the surrounding open soil and therefore should allow earlier and greater brood production.

In this manipulative field-based study I investigated the preference of ants to nesting under rocks with different temperature regimes in Australian Capital Territory (ACT) grasslands. I monitored nesting activity through time to investigate interspecific competition for nest sites, the ability of ants to colonise new nest sites in different seasons, and the seasonal production of brood and alates by ants.

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METHODS

Two grassland sites of approximately 0.4 ha (120 m × 33 m) in the Lower Molonglo Valley, ACT, with few surface rocks present, were chosen for the study. One site was above and one site was below the ACT Electricity and Water company Lower Molonglo Sewerage treatment plant and they are hereafter referred to as the Above site and the Below site, respectively. Each site was divided into 15 264 m² plots (Fig. 1) of which eight were allocated as potential treatments and four as controls. Two of the treatment plots at each site were randomly allocated for treatment at each of three time periods. A 9 × 5 grid of points 1.5 m apart was laid out in the centre of each treatment and control plot (Fig. 1). Five pitfall traps of 4.2 cm diameter and 10 cm depth were placed in a fixed formation among the grid points within each of the treatment plots and in the same formation in the control plots (Fig. 1). Each of the pitfall traps was partly filled with 70% ethanol and a trace of glycerol solution (Greenslade & Greenslade 1971). The pitfall traps were positioned 10–12 days before opening to overcome digging-in effects (Greenslade 1973) and had all vegetation within a diameter of 12 cm cleared using battery-operated grass shears 1 week before sampling. The foraging ant community structure in each plot was sampled by opening the pitfall traps for 72 h on 26 December 1994 and 21 February 1996. The treatment dates were 9 January 1995, 9 March 1995 and 8 August 1995. Two days prior to treatment, all surface vegetation within approximately 20 cm of every point on the 9 × 5 grid of the plots to be treated was removed with a spade. Two days later the bare soil was inspected for any evidence of ant nesting activity. In such cases the ants were identified to genus by recognition.

I used clay pavers as artificial rocks to offer the ants covered nest sites of varying temperature regimes. The temperature underneath rocks is dependent on the thickness and colour of the rock rather than the horizontal dimensions (Larmuth 1978). Hence, for consistency of colour and composition I used 'London Rustic' style clay pavers (230 × 110 mm).

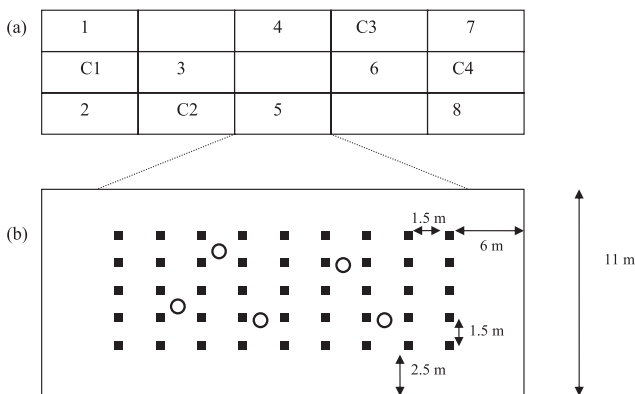


Fig. 1. Layout of the experimental plots used in the investigation of ant–nest site relations: (a) position of plots within each site (C designates control), and (b) layout of the 45 pavers and five pitfall traps (○) within each plot.

Pavers of either 30 mm, 75 mm or 150 mm thickness were firmly positioned level to the surface of the bare ground at each of the grid points. The 150 mm pavers were formed by joining two 75 mm pavers using adhesive.

Temperatures were recorded immediately underneath two pavers of each thickness: 20 cm below surface level underneath a 75 mm paver; 20 cm below the surface under no paver; air temperature in the shade at 40 cm; and surface temperature. All temperatures were measured at half hourly intervals during June and July 1995 and from November 1995 through to February 1996 using platinum resistor temperature devices.

Each paver was gently lifted and inspected for evidence of ant nesting activity after 1 day and then approximately 7, 14, 21, 28 days then monthly for the remainder of the experiment. Some ant species are known to evacuate nest sites when disturbed (Ward 1976), but in this study the gentle lifting and replacing of the pavers during each observational period was not considered to disturb the ants enough to force them to evacuate the nests. When an ant nest was discovered the ants were identified to genus and the presence of brood and alates was recorded. Two *Pheidole* species groups were identified, 'Golden' being small honey-coloured ants with minor workers less than 2 mm long and 'Common' being all other *Pheidole* species, generally with minor workers about 4 mm in length. *Iridomyrmex* were predominantly *I. rufoniger* with just a few *I. anceps* and are grouped as *Iridomyrmex* spp. for this analysis. To moderate any ambient temperature effect on nest activity, field observations were made between 8 and 12 AM in the summer months and between 1 and 4 PM in the winter months.

It is possible that new nests were sometimes observed but counted as being an old nest of the same taxa, hence the analyses was restricted to considering only the number of pavers colonised per taxa. When it appeared possible that there were two nests of the same taxa under a paver the observation was treated as a single nest.

Analyses

The daily mean, maximum and minimum temperatures were calculated as the average of the two temperature probes for each of the three different paver sizes in each of the 6 months temperatures were recorded. The daily constant temperature equivalent (CTE) (Georges *et al.* 1994) for each size of paver was calculated using the bisection method, which is based on the intermediate value theorem (Hille 1964). The CTE incorporates the mean and the daily range of temperatures experienced by each resistance temperature detector. The CTEs were compared between the different paver thicknesses using a repeated measures design ANOVA with the days a repeated measure for the fixed factor paver thickness. The pair-wise mean differences in CTE between paver thicknesses (i.e. 30–75 mm, 30–150 mm, 75–150 mm) were then calculated for each month of the experiment and tested using Wilcoxon signed rank test.

As the number of nests was expected to follow a Poisson distribution, a generalised linear model was used to compare the number of nests recorded underneath the pavers in the

treatment plots on 23 January 1996 against the fixed factors: thickness of paver, site, laying date and all associated second- and third-order interactions. Significance was determined by comparing the change in deviance after the inclusion of each term in the model against the chi-squared distribution. A separate model was used for each of the common taxa. The analysis was repeated for the observations on 4 April 1996 and results were compared.

Observations where more than one taxon was simultaneously nesting underneath a paver were recorded and tabulated. To investigate whether the occurrence of joint nests between taxa was random, chi-squared tests for goodness of fit were applied on the observed and expected number of joint nest observations for each combination of taxa. The number of nests expected to be shared among pairs of taxa was calculated using $Nests_{(AB)} = N_A \cdot P_{i(B)}$, where $Nests_{(AB)}$ = number of nests of taxa A expected to be shared with taxa B, N_A = total number of nests shared by taxa A, $P_{i(B)}$ = proportion of all nests that belonged to species B.

Nests lost by another taxon taking over were observed and tabulated. A log-linear model was used to determine whether the likelihood of the taxa losing a nest was determined by the thickness of the paver being shared.

RESULTS

Twenty discrete ant taxa were identified in the pitfall traps. The composition of ant taxa collected in both sites was similar; however, *Meranoplus* sp. were not observed in the Above site and *Tapinoma* sp. were not observed in the Below site. Overall the number of ants collected was similar in the two pitfall sample runs with 3981 and 4525 ants collected before and after the paver manipulations, respectively. Ten discrete taxa were observed nesting under pavers and of these only *Heteroponera imbellis* were not recorded in the pitfall traps. *Monomorium* spp. and *Notoncus ectatomoides* made up 29% and 10% of all ants trapped in the pitfalls but only made up 3% and 0.3% of nests under pavers, respectively. *Iridomyrmex*

spp., *R. 'metallica'*, *Paratrechina* sp. and Common *Pheidole* spp. consistently made up more than 90% of all nest observations, but only made up 63% of individuals caught in pitfall traps and 73% of trap records.

A total of 973 discrete ant nests were recorded under pavers throughout the study, with a sample maximum of 475 individual nests observed on 23 January 1996. There was a steady increase in the number of nests observed from the first laying in January until May 1995. The 180 pavers laid on 9 March were only barely colonised during the subsequent winter period and there was a decrease in nest observations until September 1995 (Fig. 2). There was a sharp increase in the number of nests observed in September 1995 (following the laying of the pavers in August), with more than 400 nests being observed through until the final observation period in April 1996 (Fig. 2).

On every sampling occasion more than 90% of nests were either *Iridomyrmex* spp., *R. 'metallica'*, *Paratrechina* sp. or Common *Pheidole* spp. (Fig. 3). *Iridomyrmex* spp. and Common *Pheidole* spp. were observed in roughly the same numbers throughout the entire study and overall made up 18% and 15% of nests observed, respectively (Table 1). Briefly after the first laying date, *Paratrechina* sp. were numerically dominant whereas *R. 'metallica'* were observed only in low numbers. However the relative number of nests from these two taxa reversed over the duration of the study (Fig. 3). By the final observation period in April 1996, they tended to occur in similar proportions, with *Paratrechina* sp. 23% and *R. 'metallica'* 26% of all nests observed in the whole study.

Soil directly beneath the thinner pavers had higher maximum temperatures and heated up earlier in the day, but the deeper pavers tended to retain their heat slightly longer overnight and these differences were moderated in winter but unambiguous in November to February (Fig. 4). The CTE was significantly different in the soil beneath pavers of the three thicknesses ($F = 354$, d.f. = 2, 281, $P < 0.0001$). All three paver thicknesses had higher CTEs in February than any other times of the year and the lowest temperatures in June and July (Fig. 5). Wilcoxon signed rank tests confirmed the 30 mm pavers had a significantly higher CTE than both 75 mm and

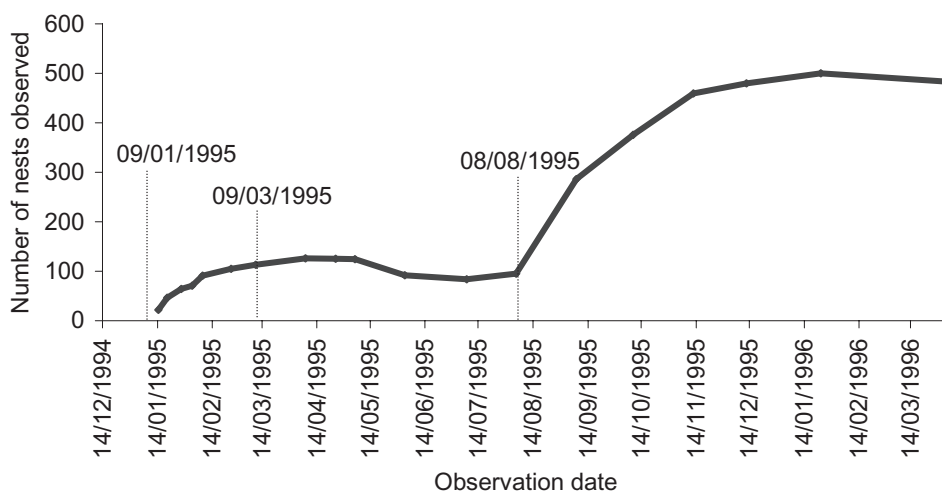


Fig. 2. Number of ant nests observed underneath artificial rocks per sampling period. Data are from both sites combined. Vertical lines indicate dates when artificial rocks were placed.

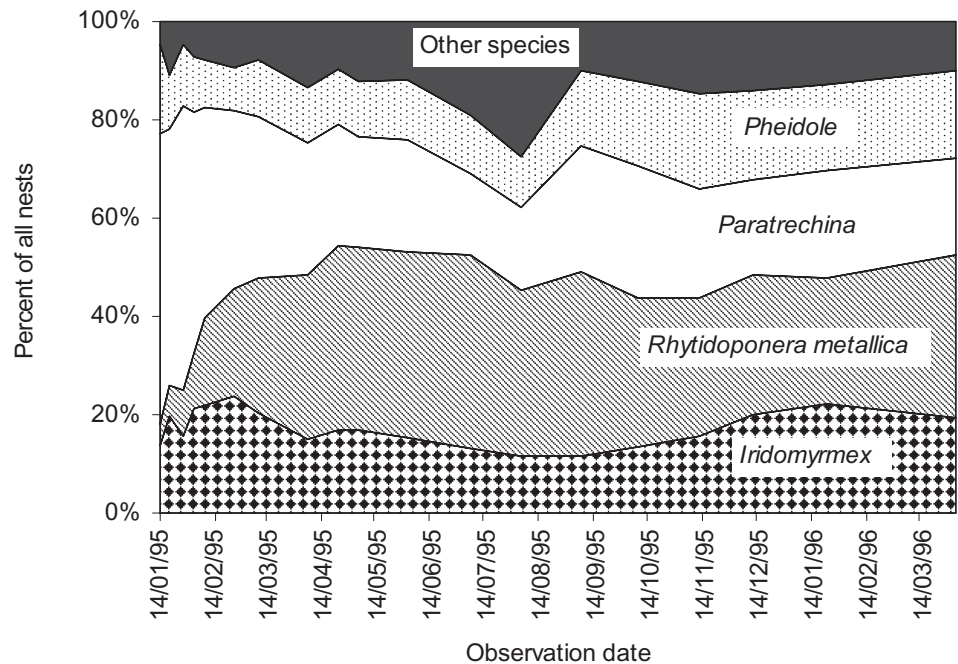


Fig. 3. Proportion over time of ant nests observed under pavers in the Lower Molonglo Valley that were of the four most common taxa.

Table 1 Observed shared nest sites for ants and termites underneath artificial rocks at Lower Molonglo Valley

Taxa	Rocks colonised at least once	Rocks shared at least once	Taxa sharing rock with					
			<i>Iridomyrmex</i>	<i>Rhytidoponera 'metallica'</i>	<i>Paratrechina</i>	Common <i>Pheidole</i>	<i>Heteroponera</i>	Termites
<i>Iridomyrmex</i>	180	85						
<i>Rhytidoponera 'metallica'</i>	255	126	29					
<i>Paratrechina</i>	229	127	27	56**				
Common <i>Pheidole</i>	145	85	24	36	26			
<i>Heteroponera</i>	37	18	2	3	5	5		
Golden <i>Pheidole</i>	64	39	7	7	11	10	2	3
<i>Monomorium</i>	26	11	3	3	2	1		2
<i>Camponotus</i>	2	1		1				
<i>Amblyopone</i>	7	1	1		1		1	
<i>Sphinctomyrmex</i>	2	2		1	1			
<i>Notoncus</i>	3	0						
<i>Meranoplus</i>	3	0						
Termites	24	22	0*	12	7	6	2	

Significantly different observed-to-expected comparisons are noted by * $P < 0.05$ and ** $P < 0.001$.

150 mm pavers and the 75 mm pavers had a significantly higher CTE than the 150 mm pavers in every month of the year ($P < 0.005$). The magnitude of the difference in the CTE was dependent on the month, with the mean difference between the 30 and 150 mm pavers ranging from 2°C in June to 7°C in February.

At the end of the study, *Iridomyrmex* spp. and *R. 'metallica'* had most nests under the thinner pavers and least nests under the thickest pavers (Fig. 6). *Iridomyrmex* spp. had considerably more nests at the site Below than the site Above while this effect was opposite for *R. 'metallica'* and *Paratrechina* sp. while Common *Pheidole* spp. showed no difference in nest numbers between either site or thickness (Fig. 6). There were no significant interactions between nest numbers and the time

of year the pavers were laid or whether the observation date was the 23 January 1996 or 4 April 1996 ($P > 0.05$).

The sharing of pavers by more than one taxon was observed 294 times including 271 pavers with two nests, 22 pavers with three nests and one paver with four nests. All the common taxa as well as *H. 'imbellis'* and Golden *Pheidole* sp. shared approximately 50% of their pavers at some stage during the study (Table 1). Termites colonised only 24 pavers but shared 22 of these and were observed in 32 nest sharing arrangements with ants (Table 1). The expected number of nest sites shared between taxa was extremely close to the observed number in almost all cases (Table 1). The only significant exceptions were that *Paratrechina* sp. shared 56 nests with *R. 'metallica'* when 35 were expected and termites shared no nests with

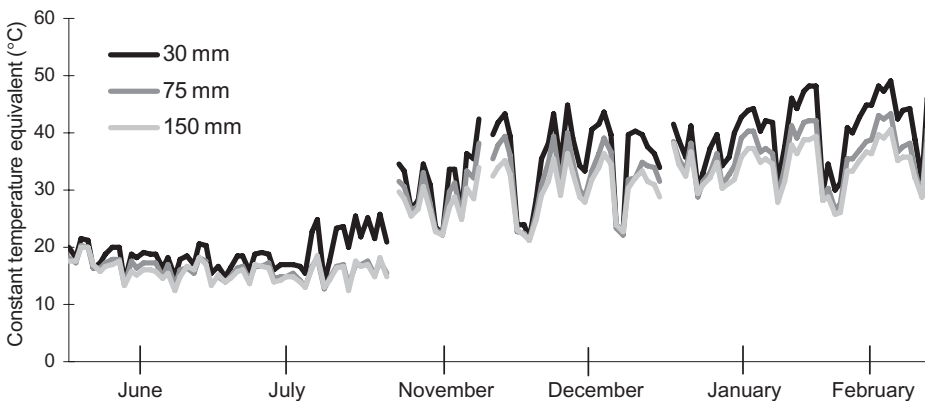
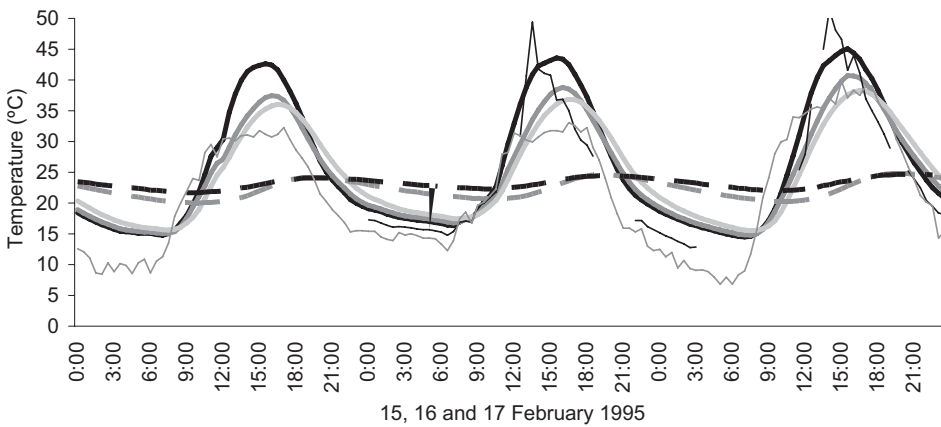
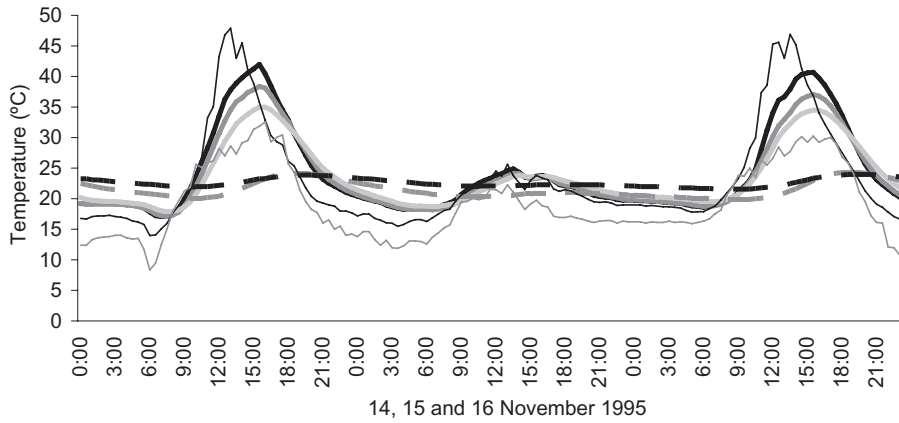
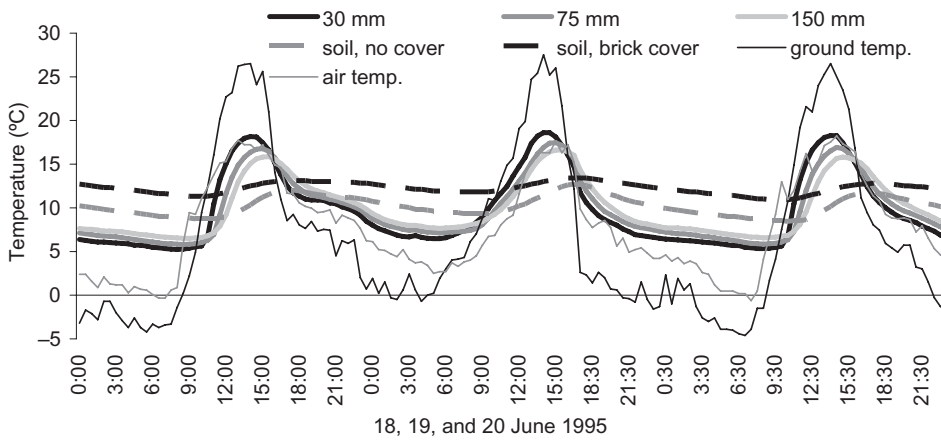


Fig. 4. Typical temperatures recorded in plots during various months in the study of ant-nest site relations in the Lower Molonglo Valley, Australian Capital Territory. Note that some ground temperatures were not recorded and are missing from the February graph.

Fig. 5. Constant temperature equivalent (CTE) recorded underneath pavers of three different thicknesses at various times of the year. The CTE incorporates the daily mean and the temperature range recorded at half hourly intervals.

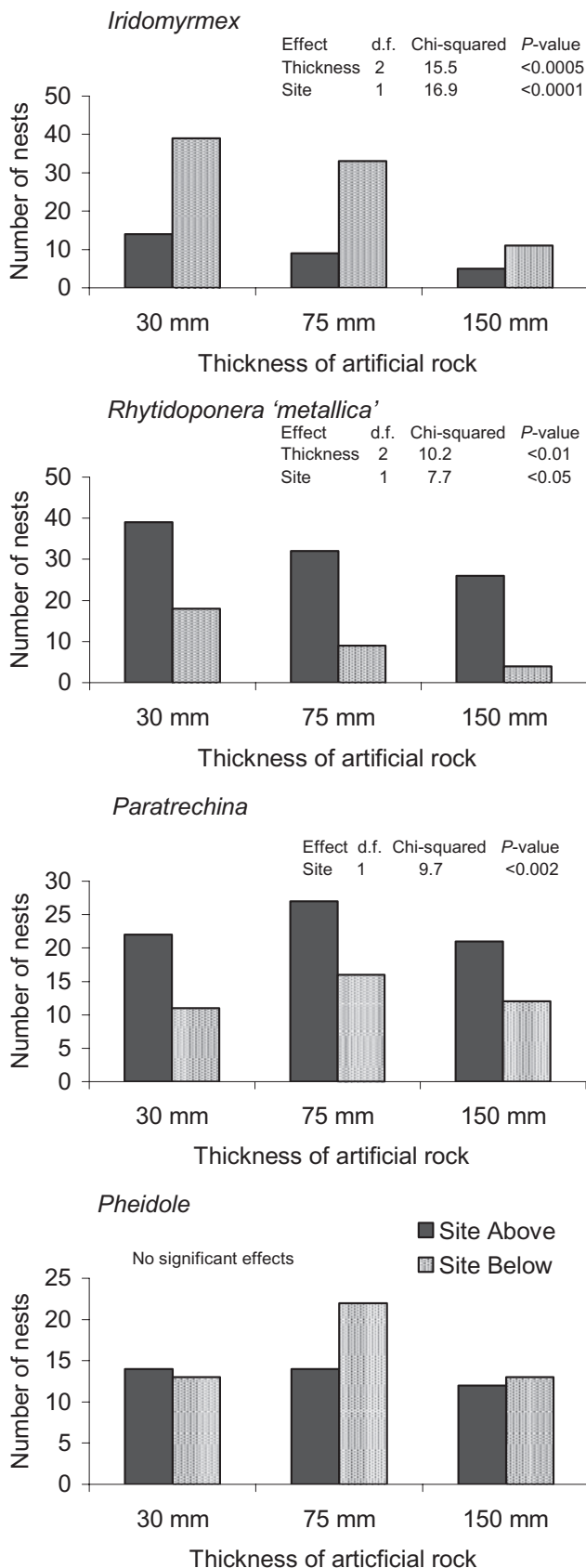


Fig. 6. Ant nests recorded under pavers at Lower Molonglo Valley on 23 January 1996.

Iridomyrmex spp. when they were expected to share six (Table 1).

Only six individual nests were observed to be active throughout the entire study and many nests were observed for only a 1- or 2-month period. A number of these nest losses may have been caused by competition with centipedes that on occasions were extremely common under the pavers and appeared able to cause ants to evacuate their nest (WA Robinson pers. obs. 1996). Thirty-nine pavers were affected by outside agencies during the study but only nine nests were definitely lost to driving, flooding or moving.

Many nest sites were lost when other taxa colonised a paver (Table 2). *Rhytidoponera 'metallica'* and Common *Pheidole* spp. were the most successful at taking over nest sites from other taxa, both gaining 1.87 and 1.79 as many nest sites from takeovers than they lost. *Iridomyrmex* spp. and *Paratrechina* sp. were not as successful, gaining only 80% and 73% of the nest sites that they lost, respectively. *Heteroponera 'imbellis'* (36%) also lost more nest sites than they gained, but these percentages should be treated cautiously as they are based on low numbers of observations (Table 2). Golden *Pheidole* spp. 11% also appeared to be big losers of nest sites, but these observations must also be treated cautiously as the observations could be distorted because of the cryptic nature of this taxon (WA Robinson pers. obs. 1996). Termites only gained 40% of nests compared with what they lost. The thickness of the paver did not significantly influence whether or not a species became the sole inhabitant of a brick they had previously shared ($G_{Iridomyrmex} = 0.39$, $G_{R. 'metallica'} = 1.81$, $G_{Paratrechina} = 3.68$, $G_{Common Pheidole} = 2.12$, d.f. = 2, all $P > 0.05$).

Iridomyrmex spp. and *R. 'metallica'* showed the most consistent brood production throughout the year, with 30–80% of nests having brood present on all sampling occasions. *Paratrechina* sp. and both *Pheidole* groups showed definite seasonality of brood production in comparison with the other taxa, having fewer brood observations in winter and maximum production observed from September to January.

Winged reproductives were commonly encountered in *Iridomyrmex* spp., *R. 'metallica'* and *Paratrechina* sp. nests, but only occasionally in Common *Pheidole* spp. or Golden *Pheidole* spp. nests. All taxa had released all of their reproductives by November, with many being released before the observations on 9 October. Alates were in low numbers or scarcely recorded for all taxa in November, December and January when brood was most abundant. Winged reproductive numbers had increased again by April and were expected to be held until favourable environmental conditions for release were encountered in September–October 1996 (WA Robinson pers. obs. 1996).

DISCUSSION

It was expected that more taxa be collected in the pitfall traps than those actually nesting under the pavers as some taxa prefer open nest sites Greenslade (1979). In this study the number of

Table 2 Ant and termite nest losses and changeovers observed during the study of ant-nest site relations in the Lower Molonglo Valley, Australian Capital Territory

Taxa losing nest	Taxa gaining nest						Nests lost to other taxa
	<i>Iridomyrmex</i> spp.	<i>Rhytidoponera</i> 'metallica'	<i>Paratrechina</i> sp.	Common <i>Pheidole</i> spp.	<i>Heteroponera</i> 'imbellis'	Golden <i>Pheidole</i> sp.	
<i>Iridomyrmex</i> spp.							
<i>Rhytidoponera</i> 'metallica'	10	27	16	8	2	0	2
<i>Paratrechina</i> sp.	16	28	15	12	0	1	1
Common <i>Pheidole</i> spp.	10	7	7	14	2	1	1
<i>Heteroponera</i> 'imbellis'	1	4	3	3	0	0	0
Golden <i>Pheidole</i> sp.	6	4	4	5	0	0	0
<i>Monomorium</i> spp.	1	2	0	1	0	0	0
<i>Sphinctomyrmex</i> sp.	0	1	0	0	0	0	0
Total nests gained	44	73	45	43	4	2	4
Nests gained/nests lost	0.80	1.87	0.73	1.79	0.36	0.11	1.00

20 taxa in pitfall traps and 10 under pavers is comparable to a similar study using fallen cocoa pods rather than pavers (Fowler 1993). The four common foraging taxa, *Iridomyrmex* spp., *R. 'metallica'*, *Paratrechina* sp. and Common *Pheidole* spp., were well represented under the pavers and appear to either be better opportunists, have a competitive advantage or have a preference for covered nest sites relative to the other taxa. All four taxa are widespread in ACT grasslands (Melbourne 1993; W Robinson unpubl. data 1995) and appear unaffected by most disturbances except severe decreases in insolation.

The importance of the CTE is well studied in the embryonic development of reptiles (e.g. Georges *et al.* 1994; Shine 1999, 2004), and more recently grasshoppers (Hao & Kang 2005) but little is known for ants. Ants can avoid excessive temperatures by moving the brood to areas of optimal temperature and moisture (Hölldobler & Wilson 1990) but there is a minimum critical temperature for brood development for ants (Lopatina & Kipyatkov 1993). While the critical temperatures are unknown for the taxa it can be assumed that ants nesting underneath the shallower pavers in this study were able to place their brood in more favourable conditions than those under the deeper pavers. Typically, many Australian ant species have few or no brood during winter and increase brood production in spring and early summer (Greenslade 1979). The resultant larger worker force in spring and summer allows for numerous nurse stages to look after the brood and large worker armies that compete for and bring food (Greenslade 1979). Therefore a competitive edge from larger worker numbers (Morrison 2000) could be enhanced by being able to produce brood earlier in the season and particularly if the rate of development of the brood can also be increased by warmer nests (Kipyatkov *et al.* 2002). Hence, it was not surprising that *Iridomyrmex* spp. and *R. 'metallica'* showed a distinct preference for the shallower pavers in both sites and were the most prolific brood producers observed in the study.

Larger rocks promote larger colony growth in *R. 'metallica'* (Thomas 2002); however, temperature regimes between the rocks of interest were not compared in that study. Incorporating Thomas's (2002) findings with the current study results I suggest larger and shallower rocks may provide optimal conditions for colony growth in *R. 'metallica'*.

The Below site appears more open in ground cover and may be more suitable for *Iridomyrmex* in general as they tend to prefer open habitats (Greenslade 1976, 1979; Andersen 1990, 1991; Abensperg-Traun 1992; Andersen & Patel 1994; Gibb & Hochuli 2003). However, the majority of *Iridomyrmex* in this study were smaller individuals from the *I. 'rufoniger'* group, which have been described as opportunistic (Abensperg-Traun 1992) and ubiquitous (Lobry de Bruyn 1993). In south-eastern Victoria, *Rhytidoponera 'tasmaniensis'* showed ability to numerically dominate sites when interspecific competition with *Iridomyrmex* spp. was reduced (Andersen & Mckay 1987). In the current study, *R. 'metallica'* showed a similar response, by being numerically dominant in numbers of nest sites at the Above site where the small *Iridomyrmex* spp. were in lower abundance. However without experimental evidence the opposite may also be possible and the significant

difference in the number of nests between sites is probably a consequence of the inherent differences in relative abundance of foundresses available before the study began.

The pavers were only a relatively small size (surface area 253 cm²) and the size of the nesting cavity can constrain colony size (Thomas 2002) so it was surprising that most species shared up to 50% of nests. *Iridomyrmex* spp. nests for example become highly active in a short period of time and they tended to excavate the entire soil area beneath the paver, leaving minimal room for other taxa to build nests. Common *Pheidole* spp. and Golden *Pheidole* spp. however tended to use smaller portions of the paver and used many smaller trails and burrows between slightly larger excavations. A few authors mention sharing of other resources such as foraging trails (Wilson 1965) and food sources (e.g. Abe 1971, 1976; Kloft 1983). There are also records of some species of *Solenopsis* as scavengers in other species nests (Bates 1985), parasitic queens of some *Teleutomyrmex*, *Anergates*, *Epimyrma* and *Leptothorax* species (Buschinger 1985) and slave-making ants such as *Polyergus* and *Protomognathus* (Savolainen 1992; Herbers & Foitzik 2002). None of these genera or traits were observed in this study. There is minimal literature on the frequency of just sharing of or competition for nests sites by ants and a longer observation period may have found competitive exclusion. However the current results concur with the common observations of nest sharing by ants in small nest sites in cocoa pods by Fowler (1993).

The higher than expected number of nests shared between *Paratrechina* sp. and *R. 'metallica'* may be influenced by the fact that both taxa had more nests at the Above site and hence had more likelihood of sharing simply by chance. To repeat the analysis for both sites separately would however reduce the power of the test and was not considered. *Rhytidoponera 'metallica'* were the most abundant nesting taxa and they also took over significantly more nests than other taxa. These numbers may not be generalised because *R. 'metallica'* nests occurred in higher numbers at the Above site where *Iridomyrmex* spp. were less abundant.

Some ant species move nest sites regularly (Smallwood & Culver 1979; Smallwood 1982a; Herbers 1989), often stimulated to do so by nest site suitability or competition (Smallwood 1982b) or nest fractionisation (i.e. dispersion from one nest without necessarily releasing foundation queens) (Herbers 1989). Of particular importance to this study, *Paratrechina* sp. are known to be nomadic, regularly moving nests (A Andersen pers. comm. 1996). It was therefore not surprising to find that these ants lost more nests than any other taxa. They were able to colonise the pavers laid in January quicker than any other taxa but gradually became replaced by *R. 'metallica'*. The same trend was not observed after the other laying dates however and it may have been a chance occurrence that *Paratrechina* sp. happened to be able to colonise the first lot of pavers so effectively. *Rhytidoponera 'metallica'* took over more nests from *Paratrechina* sp. than any other taxa (Table 2), but also shared with them more (Table 1). Thomas (2002) found that *R. 'metallica'* frequently abandoned nests under rocks in summer but there was no evidence

of this in the current study. Because Common *Pheidole* spp. lost very few nests (4) to other taxa when they were not previously observed sharing (Table 2) it is possible they are less likely than the other taxa to move nests without external influence. It is also likely that some of the taxa in this study moved nest sites before the old site was taken over by another species. Such data are not included in these analyses.

The observations of brood and winged reproductives must be treated cautiously because the position in the nest of these castes may be influenced by ambient temperatures (Briese & Macauley 1980; Hölldobler & Wilson 1990), and lack of observation may not mean lack of presence. However because observation times were changed to minimise variation in ambient temperature, these effects should be moderated. It is known that there are between-species differences in the extent to which brood can be found in ant nests during winter periods (Greenslade 1979).

Alate larvae and pupae in the nests produced at the same time as the worker brood and were held in the nests until the warmer months. These findings are typical of Australian ant species (Greenslade 1979) and are similar to *R. 'chalybea'* brood and alate production described in wet sclerophyll and rainforest from Victoria to southern Queensland (Ward 1976). In more extreme climates, ants only have reproductive effort during the warmer months, ceasing or severely reducing production of both worker and alate brood during the colder periods (Gamanilov & Kipyatkov 2000) and this generally applies to the majority of Australian taxa (Greenslade 1979). Some nests appeared to become dormant for periods of up to 4 months during the study, becoming active again in the warmer months. The sharp increase in nest numbers in September and October (Fig. 2) however also coincided with the release of winged reproductives, and for this reason the majority of the new nests observed in the warmer months, even those in the older plots are assumed to be new nests. It is reasonable to assume that the foundation of new nests was minimal during winter.

Rhytidoponera 'metallica' and *Iridomyrmex* spp. preferred the shallower pavers and had more brood observed year round. This may mean they produced more brood because they had more shallow pavers or because the warmer temperature of the narrower pavers allowed them to bring brood to the surface earlier in the day. This reason cannot be elucidated by this study, but it is recognised that these taxa both produce brood year round, while all taxa produced brood with seasonal peaks in summer.

There is a maximum critical temperature for brood development and this has been described for some species (Porter 1988; Lopatina & Kipyatkov 1993), but ants are known to move the brood to chambers of preferred temperature (Greenslade 1979; Briese & Macauley 1980; Hölldobler & Wilson 1990). Hence the effect of high temperature is independent of the advantages of minimum critical temperature. The temperatures 20 cm below the surface were almost identical whether under a 75 mm paver or under bare ground in summer and slightly warmer in winter (Fig. 4). Therefore nest architecture may play a role in which ant species could use the thermal advantages of

rocks; however, that is beyond the scope of this study. Other future work could be to use exclusion experiments to determine which rocks ants choose if they have choice and which species are able to outcompete the others.

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