Insect. Soc. 50 (2003) 355–360
0020-1812/03/040355-06
DOI 10.1007/s00040-003-0685-1

Insectes Sociaux

Research article

An experimental study of the relative humidity preference and survival of the Argentine ant, *Linepithema humile* (Hymenoptera, Formicidae): comparisons with a native *Iridomyrmex* species in South Australia

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Received 29 January 2003; revised 27 May 2003; accepted 6 June 2003.

Summary. The Argentine ant, *Linepithema humile* (Mayr), is a widespread invasive ant species that commonly displaces native ants and other ground-dwelling invertebrates in its introduced range. Previous studies have documented a relationship between the spread of Argentine ants and abiotic conditions (particularly water availability) in invaded areas, suggesting that the invasion success of Argentine ants may be related to specific abiotic factors. This study describes the relative humidity preferences and survival of Argentine ants and a dominant native ant, *Iridomyrmex* '*rufoniger*' sp. group, in the laboratory. In a preference experiment, Argentine ant workers showed a significantly greater propensity than *Iridomyrmex* to locate themselves in containers with the highest relative humidity. A series of survival trials revealed that the survival of both species was related to the relative humidities within experimental containers. The survival of Argentine ant colonies was reduced in comparison with those of *Iridomyrmex* sp. after 4 h, however by 24 h both species displayed similar levels of survival in all relative humidity conditions. These findings confirm a relationship between the level of available moisture and the distribution and survival of Argentine ants, and may help to account for the current distribution and invasion success of Argentine ants in Australia.

Key words: Argentine ants; humidity; nest climate; preference; survival.

Introduction

One of the major objectives of invasion biology is to determine the specific conditions that limit or impede the spread of invasive species and to subsequently predict those areas that may be most susceptible to invasion. The invasion of a new habitat may depend on a number of factors. Such factors may include the initial colonising ability of the species, which may reduce its susceptibility to extinction and allow it to rapidly increase its range (Sax and Brown, 2000; Duncan et al., 2001), the abiotic environment (Blackburn and Duncan, 2001; Gabriel et al., 2001), the characteristics of the invader and the recipient community (Vitousek et al., 1996; Juliano, 1998; Naeem et al., 2000), and the relationship between these variables (Holway, 1998). Thus, predicting the invasion success of an exotic species may be extremely difficult, given the complexity of the factors involved.

There are two factors, in particular, that are commonly considered to be of fundamental importance in the invasion of a new habitat. Firstly, the abiotic environment may often play a crucial role in determining which areas are the most suitable for the invading species (Sax, 2001). Secondly, the biotic interactions that occur within the invaded range may also affect the invasion success of an introduced species. The 'biotic resistance hypothesis' predicts that areas maintaining high species richness will be less likely to experience biological invasion than areas with lowered species richness (Elton, 1958). For instance, Lyons and Schwartz (2001) concluded that the removal of rare native plant species was more likely to facilitate the invasion of the exotic grass, *Lolium temulentum*, in comparison with areas that sustained higher levels of diversity. However, other research has provided mixed support for this hypothesis (Robinson et al., 1995), with one study concluding that highly diverse communities are fundamentally unstable, resulting in a regular turnover of species (Stohlgren et al., 1999).

It is likely, however, that the outcomes of biotic interactions may be largely influenced by the abiotic conditions that are experienced in the invaded zone (Byers, 2002). For instance, several biologists have argued that differing tolerances to the physical environment coupled with variations in competitive ability may facilitate the coexistence of species in a given area (Anderson et al., 2001; Byers, 2002).

The Argentine ant is a widespread invasive ant species that has been introduced via human commerce to nearly every continent (Collingwood et al., 1999). It is generally restricted to temperate regions (Hölldobler and Wilson, 1990), and its distribution has been linked with various abiotic conditions, including low-elevation areas (Human et al., 1998), mesic scrub fragments (Holway et al., 2002), sand and clay loam soils (Way et al*.,* 1997), and arable habitats (Cammell et al*.,* 1996). Studies conducted in California have identified increased levels of soil moisture (Holway et al., 2002), and the presence of a permanent stream flow (Holway, 1998) as particularly important abiotic variables determining the distribution of Argentine ants in their introduced range. Thus, the availability of moisture may be a necessary pre-condition for the invasion of Argentine ants into an area, and may consequently determine their distribution in an introduced range. Given that the soil temperatures, evaporation rates, and levels of soil moisture are likely to influence the humidity within ant nests (Potts et al., 1984), we attempted to assess the preferences by Argentine and native ants for environments that varied in their relative humidity, as well as the impact of relative humidity on the survival of ant colonies. Preferences by ants for particular humidities were described by Roces and Kleineidam (2000) who found that the leaf-cutter ant, *Atta sexdens rubropilosa*, selected higher humidity conditions to accommodate themselves and their fungus gardens, but distributed randomly when fungus was not present. Similarly, the workers of four species of *Solenopsis* (*S. aurea, S. geminata, S. invicta, S. xyloni*) were observed to aggregate in the saturated end of a humidity gradient (50–100%) when their brood were also present (Potts et al., 1984).

We conducted laboratory trials to determine the relative humidity preferences of Argentine ant workers, and to evaluate the survival rates of Argentine ant colonies exposed to different humidity conditions. The results were compared with those obtained for the native ant, *Iridomyrmex* '*rufoniger*' sp. group, which shares similar behavioural and morphological characteristics with Argentine ants, and which may compete with Argentine ants for resources in Australia (A. Walters, unpublished data). In Adelaide, this species has been observed in areas adjacent to sites inhabited by Argentine ants, and workers have also been collected in pitfall traps placed at invaded sites (Walters and Mackay, in press). Ants from the genus *Iridomyrmex* have been identified as dominant ant taxa within Australian ant communities (Andersen, 1990), largely as a result of their widespread distribution, large colony sizes, and aggressive behaviour (Greenslade, 1976). Furthermore, it has been suggested that the presence of species of *Iridomyrmex* may impede the spread of Argentine ants in Australia (Majer, 1994).

Materials and methods

Ant colony collection

Argentine ant colonies were collected from invaded sites throughout metropolitan Adelaide. In this region, they are patchily distributed and are commonly restricted to areas that are frequently tended and watered, such as residential parks and gardens. Native ant colonies from the genus *Iridomyrmex* were collected from the campus of the Flinders University of South Australia. During collection, soil was removed from the ant nests, and placed in a fluon-coated container for transportation to the laboratory. The ants were then separated from the soil via aspiration and housed in plastic containers coated with fluon to prevent ant escape. Ants were kept in a temperature-controlled room at 25 °C for 24 to 72 h prior to experimental use, and were fed a standard laboratory diet (Hölldobler and Wilson, 1990).

Ant preference trials

Sets of five containers (250 ml, 630 mm diameter) that varied in their relative humidities were established in the laboratory at 25 °C using a series of saturated saline solutions according to the methods of Winston and Bates (1960). The salts, and the subsequent relative humidity in the container with that salt solution, were as follows: – $K_2Cr_2O_7$ (>90%), KCl (~80%), NaCl (75%), and $MgCl_2 \cdot 6\,H_2O$ (33%). The final container was partly filled with dry silica gel, which provided the lowest relative humidity (~7%). Test chambers were constructed by connecting the five plastic containers with 7 cm lengths of plastic tubing (3 mm diameter) in a linear arrangement of increasing humidity (Fig. 1). The saturated salt solutions were then poured into each container, and excess salt was added to the bottom. A stand covered with mesh was placed in each container to prevent ants having contact with the solution, and the containers were left to equilibrate. After a period of 2 h, the relative humidity in each chamber was measured using a Testo® 615 relative humidity sensor, and 10 ant workers were placed in each container (total of 50 workers in each trial). The numbers of dead and living ants in each container were recorded after 1, 2, 4, and 24 h. The containers and stands were washed at the conclusion of each trial, and the plastic tubing connecting the containers was discarded. Replicate trials were conducted in various places within the laboratory to reduce the effects of behavioural preference for relocation by ants to a specific area of the laboratory. Trials were replicated on 14 different occasions for Argentine ants and 13 times for *Iridomyrmex*.

A second series of preference trials was conducted to assess the effects of relative humidity without any of the odours associated with particular salts. Four plastic containers containing a mesh-covered stand (as described above) were connected via plastic tubing to create an increasing relative humidity gradient. The gradient was established placing silica gel in the container at one end of the series, followed by two empty containers (between 45–60% RH), and a final container partially filled with de-ionised water (>90% RH). Trials were conducted in different areas of the laboratory, and the order of the containers was reversed, to reduce the possible effects of behavioural preference for movement by ants to a specific location within the laboratory. The numbers of workers in each container was counted after 1, 2, 4, and 24 h. Trials were replicated 8 times for each species, with 10 workers placed in

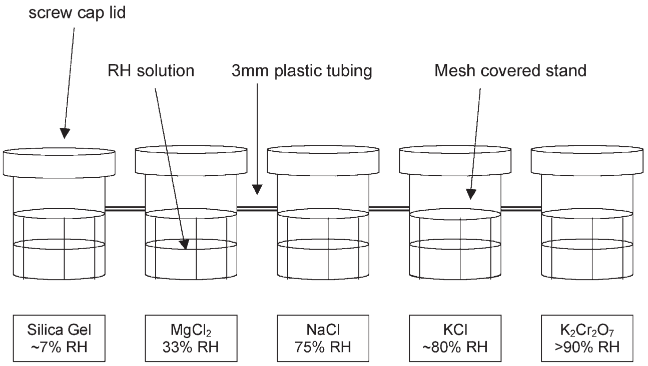

Figure 1. Diagrammatic representation of the increasing gradient established for the relative humidity preference trials

each humidity chamber, resulting in a total of 40 workers in each container set in each trial.

Statistical analysis of humidity preference trials

The proportion of living workers in each of the five containers after 1, 2, 4 and 24 h were calculated. If workers do not exhibit preferences for particular relative humidities at a particular time, it would be expected that these proportions would not differ significantly. A problem in analysing such data in the form of proportions is that the proportions must sum to one, and hence are not independent. This problem was dealt with by utilising compositional analysis (Aitchison, 1986) which transforms the raw proportions to "log-ratios", such that if initially we have a set of k proportions (p_1, p_2 … p_k), we create a set of k-1 log-ratios by dividing k-1 of the proportions by the remaining one, and then taking logarithms. Thus, if we use the kth proportion as the divisor, the ith log-ratio, $l_i = \log(p_i/p_k)$. The k-1 log-ratios are not constrained to sum to one and can therefore be more readily analysed using standard statistical techniques. (e.g. Aebischer et al. 1993; Griffin and Case, 2001).

In our analyses, the proportion of living workers in the container with the highest relative humidity ($K_2Cr_2O_7$ solution) was used as the divisor in calculating the log-ratios. The log-ratios were then analysed using a multivariate profile analysis to compare the distribution of Argentine ant and *Iridomyrmex* workers among the humidity containers.

For the second series of preference trials, we analysed the proportion of workers in the container with the highest relative humidity (that containing de-ionised water) after 1, 2, 4 and 24 h using a repeated-measures ANOVA.

Ant survival trials

To determine the survival of ant colonies in different humidity conditions, a series of trials was conducted using the aforementioned salt solutions ($K_2Cr_2O_7$, KCl, NaCl, and $MgCl_2 \cdot 6\,H_2O$) as well as a container partly filled with deionised water (>90% RH). A single 250 ml container was filled with a saturated salt solution and additional salt crystals, and a stand covered with mesh was placed in the container. Containers were positioned randomly within the laboratory to reduce the possible effects of location on the survival of the colony. The containers were left to equilibrate for 2 h, after which time the relative humidity within the container was measured, and an ant colony containing 100 workers and a queen was placed in the container. The number of live and dead workers was recorded after 1, 2, 4, and 24 h. At the conclusion of each trial the containers and mesh covered stands were washed and rinsed.

Using the counts of live and dead workers, the proportions of surviving workers were calculated for each time period. The data were analysed using a repeated measures analysis of variance on the arcsin-transformed proportions of surviving workers, using ant species and solution as between-subjects factors. The data for each relative humidity solution were analysed separately using a repeated-measures analysis of variance to compare the survival of the two species over time.

Results

Relative humidity preferences of ants

Workers of both species displayed a preference for particular relative humidity conditions, moving into the higher humidity treatment (>90%) over the course of the experimental period. The relative distributions of workers of the two species did not differ significantly after one or two hours. However, after 4 h, the responses of Argentine ants and *Iridomyrmex* to the relative humidity conditions differed significantly (Multivariate F-ratios for Solution * Species interaction, 4 h: $F_{3,23} = 3.21$, $P = 0.04$; 24 h: $F = 4.26$, $P = 0.02$) (Fig. 2). After 4 h, the log-ratios of the proportions of Argentine ant workers in the different relative humidity containers were significantly different ($F_{3,11} = 4.41$, $P = 0.03$), whereas those for *Iridomyrmex* workers did not differ significantly ($F_{3,10} = 2.56$, $P = 0.11$). After 4 h, a median proportion of approximately 50% of Argentine ant workers had located themselves in the highest humidity containers, whereas a median of only 20% of the *Iridomyrmex* workers had done so after 4 h. By 24 h, a median percentage of more than 80% of Argentine ant workers were located in the highest humidity containers, whereas the corresponding figure for the *Iridomyrmex* workers was only 60%.

Similar trends were observed in the preference trials that were designed to avoid any possible effects of the odour of the chemical solutions on the preferences of ants. After 1, 2, 4 and 24 h, an average of 55%, 53%, 63% and 80% of the Argentine ant workers were located in the highest-humidity container, whereas the corresponding figures for *Iridomyrmex* were 25%, 34%, 29% and 64%. The average proportion of Argentine ant workers in the highest-humidity container was thus greater than that for *Iridomyrmex* at each time (Between-species $F_{1,14} = 5.87$, $P = 0.03$). These results suggest that the possible effects of odour associated with the use of different saturated salt solutions were negligible.

Effects of relative humidity on ant survival

The survival of both ant species was strongly dependent on the humidity conditions that they were subjected to within the containers (Fig. 3). In the initial repeated-measures analysis, there was a highly significant interaction effect of time by solution by species, indicating that the two species reacted differently to the various humidity treatments over time ($F_{12,294} = 7.554$, $P < 0.001$). However, both species exhibited low worker survival in the 33%, 75%, and 80% RH containers, and the greatest worker survival in the moister treatments (>90% RH) after 24h.

Due to the significant interaction effect above, separate repeated-measures analyses were conducted on the survival data for each relative humidity solution. Significant Species * Time interaction effects were observed for the 2 solutions with the lowest relative humidities ($MgCl_2$ (33%) and NaCl (75%); $F_{3,23} = 22.66$, $P < 0.001$, and $F_{3,17} = 9.59$, $P = 0.001$, respectively). In both these treatments, the Argentine ant workers experienced a much greater decline in survivorship after 4 h than did the *Iridomyrmex* workers (Fig. 3). A significant Species * Time interaction effect was also observed in the $K_2Cr_2O_7$ (>90% RH) solution ($F_{3,17} = 4.50$, $P = 0.017$), where Argentine ant workers showed reduced survival rates between 4 and 24 h in comparison with *Iridomyrmex* (Fig. 3). In the containers with water (>90% RH), both ant species displayed high survival rates and the mean survival of both species (averaged over time) was not significantly different ($F_{1,15} = 0.65$, $P = 0.43$).

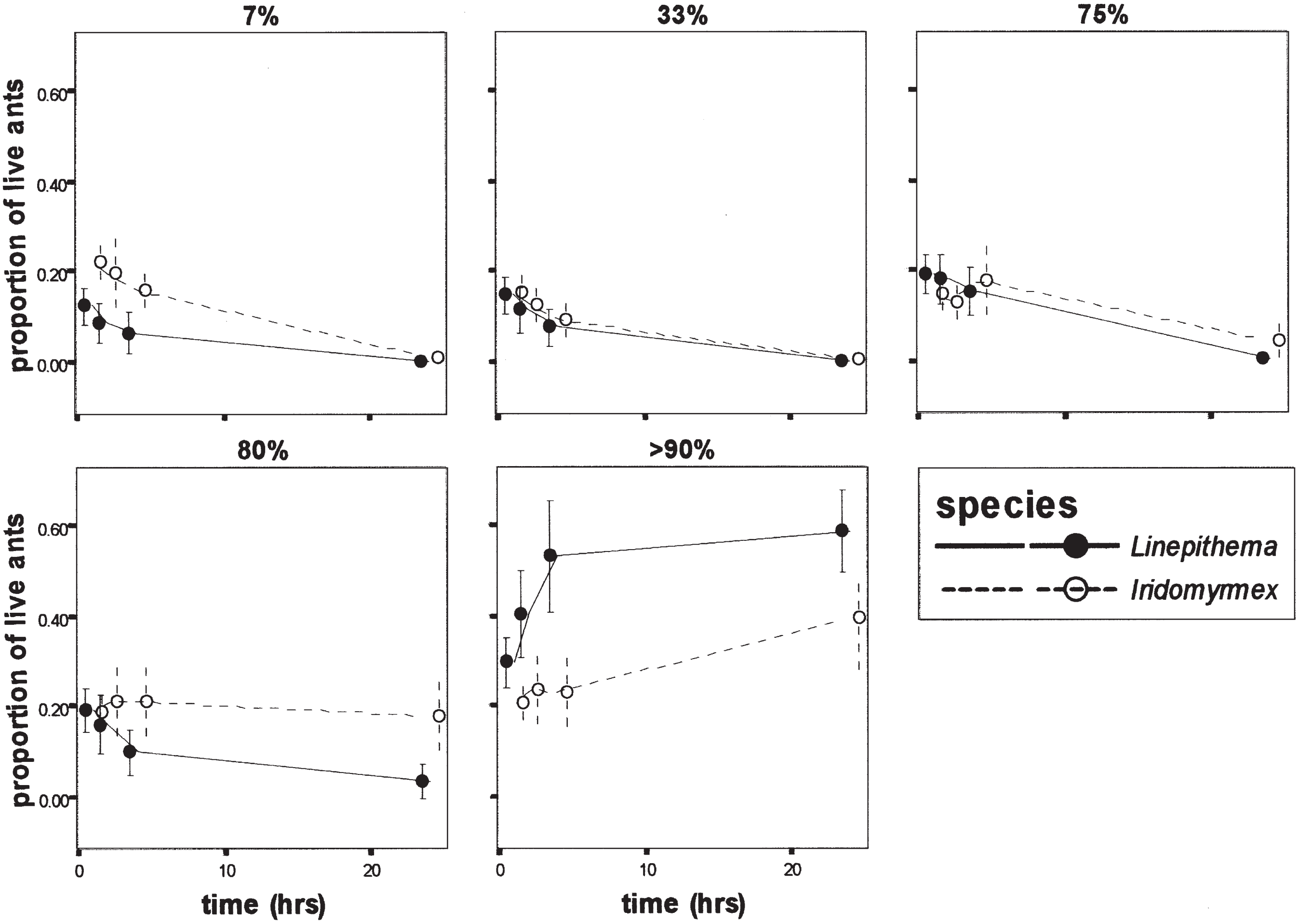

Figure 2. Relative humidity (%) preferences of workers of Argentine ants and *Iridomyrmex* sp. over 24 h (Silica gel = 7%, $MgCl_2$ = 33%, NaCl = 75%, KCl = 80%, $K_2Cr_2O_7$ = >90% RH). Error bars show 95% Confidence Interval of Mean

Discussion

The results of this study provide experimental support for the hypothesis that Argentine ants favour conditions with high levels of moisture. Individual Argentine ant workers preferentially selected conditions where the relative humidity exceeded 90%, while at the colony level, Argentine ant survival was greatest in the higher relative humidity treatments.

Previous research has documented a relationship between Argentine ant survival and water availability. For instance, Holway et al. (2002) found that laboratory colonies of Argentine ants suffered 100% mortality in treatments that received no water over a 6 week experimental period. In their study, Argentine ant worker survival failed to surpass 80% in conditions where less than 15 ml of water was added to the colony daily, whereas the survival of the native ant, *Forelius mccooki*, was independent of soil moisture (Holway et al., 2002). A similar trend has been observed in this study, with the native *Iridomyrmex* sp. displaying an increased tolerance to reduced levels of moisture in comparison with the introduced species.

Furthermore, Holway (1998) monitored the distribution of Argentine ants in the lower Sacramento River Valley in California over a period of four years. He estimated that Argentine ants spread at rates of 16.3 ± 3.5 metres per year at sites with a permanent stream flow, and retreated –5.9 ± 3.8 metres per year at sites with irregular stream flow (Holway, 1998). Other studies in California have also shown that Argentine ants fail to occur in the dry inland areas, despite being widespread in coastal regions and areas with a permanent water source (Ward, 1987; Holway, 1995; Holway et al. 2002).

Human et al. (1998) also observed a slightly significant interaction between the presence of Argentine ants and the distance to a water source. However, they concluded that while there was a slight tendency for Argentine ants to be present close to the water, they argued that colonies were also established in areas without a water source, suggesting that other factors may be responsible for the invasion success of Argentine ants at their field site (Human et al., 1998). This study also found a link between the presence of Argentine ants and the relative humidity of a given area. Both Argentine and native ants were found to be less active in areas where the

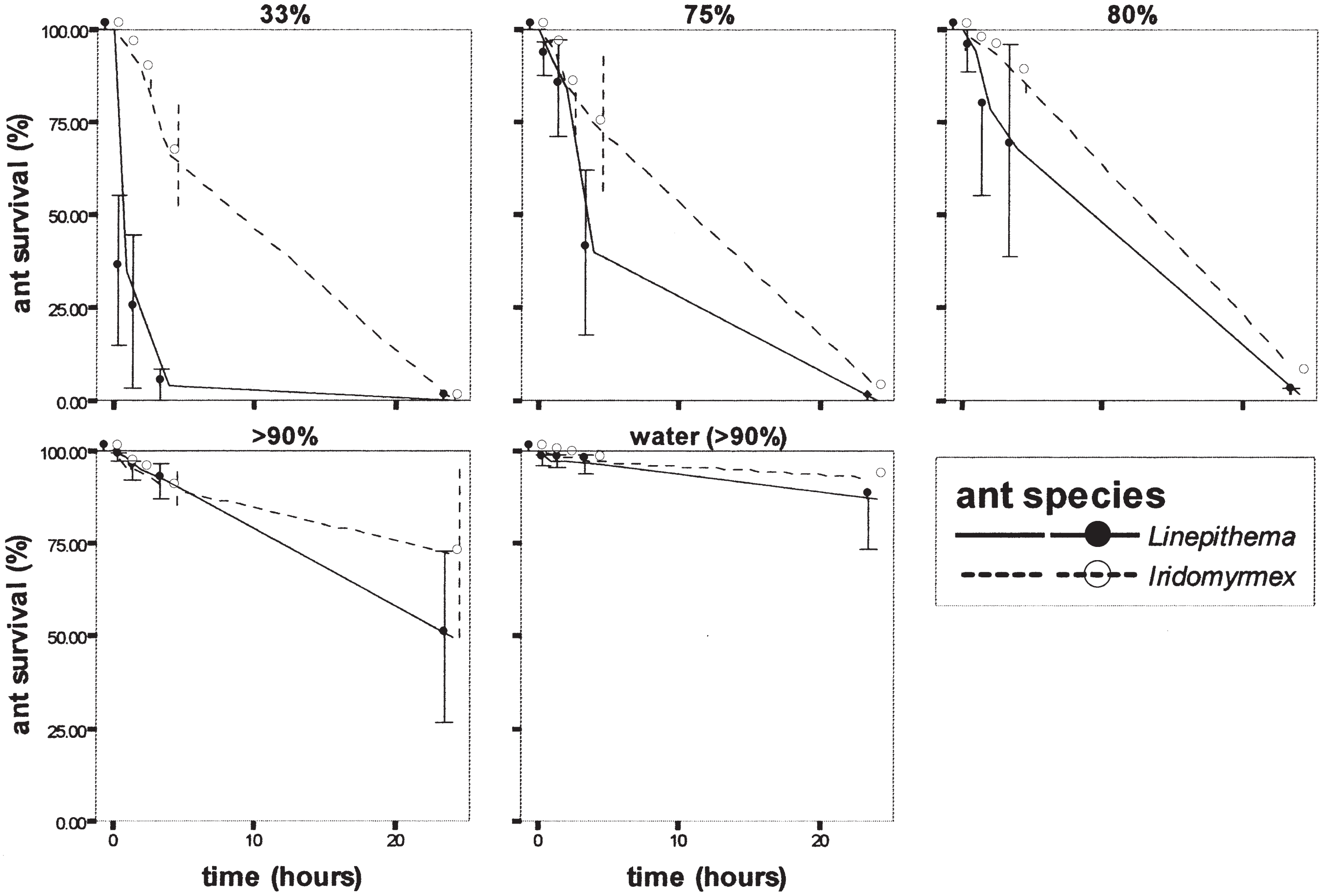

Figure 3. Ant survival (%) in closed containers under different relative humidity conditions over the 24 h experimental period ($MgCl_2$ = 33%, NaCl = 75%, KCl = 80%, $K_2Cr_2O_7$ = >90%, H_2O= >90% RH). Error bars display 95% CI of the mean.

relative humidity was less than 40%, and Argentine ants were marginally more likely to be active at higher relative humidities in comparison with native ant species.

The results obtained in this study may have implications for the invasion success and consequent dispersal of Argentine ants in their introduced range for several reasons. Firstly, this study reveals that Argentine ant preference and ultimate survival may be heavily reliant on relative humidity conditions, and as such, suggests that Argentine ants may be limited to areas with high levels of soil moisture, where the relative humidity levels in the nest may be elevated. Additionally, in comparison with native ants, Argentine ants may be more vulnerable to desiccation in the natural environment due to the structure of their nests, which are often located near the soil surface (Newell and Barber, 1913), where they may encounter greater fluctuations in abiotic conditions. For instance, Edney et al. (1978) found that dictyoperan nests located near the soil surface experienced greater variability in both temperature and humidity. Secondly, the relative humidity preferences of these two ant species indicate that, given the choice, both Argentine ants and *Iridomyrmex* will preferentially inhabit moister conditions. This result may have consequences for the distribution patterns of these species in areas where they may be located in close proximity to one another. For instance, in such areas, it is likely that the two species will compete for nesting sites that retain high levels of soil moisture. Recent surveys of the distribution patterns of *Iridomyrmex* and Argentine ants within metropolitan Adelaide (A. Walters, unpublished data) show that the two genera rarely co-occur at fine spatial scales, e.g. within the same park or garden area. However, on a number of occasions both genera have been recorded within the same suburb or locality, implying that they are both able to tolerate similar environmental conditions. Additionally, Argentine ants have been recently located near to the site of the collection of the *Iridomyrmex* colonies used in this study, suggesting that competition may occur between these two species. Consequently, the patchy distribution patterns of Argentine ants in South Australia may be a result of the biotic interactions that occur between species of *Iridomyrmex* and Argentine ants over areas that are desirable to both.

In this study, we found that the native ant, *Iridomyrmex*, was able to tolerate lower relative humidities for significantly longer than Argentine ants. *Iridomyrmex* may have evolved morphological or behavioural characteristics that enable it to cope with the effects of desiccation in the typically dry conditions of the Australian environment. Furthermore, it has been suggested that the size and colour of Argentine ants may lead to their more rapid desiccation in comparison with other ant species (Tremper, 1976 cited in Human et al., 1998). The slightly larger size of *Iridomyrmex* workers, relative to those of Argentine ants, may also marginally increase the survival of *Iridomyrmex* in the dry Australian conditions.

Acknowledgments

This project was supported through funding from the Wildlife Conservation Fund, and from the Flinders University of South Australia. We are grateful to Steve Shattuck for identification of voucher specimen and are indebted to Mike Bull, Tom Chapman, and two anonymous referees for comments on the manuscript.

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