Comparisons of Upper Thermal Tolerances Between the Invasive Argentine Ant (Hymenoptera: Formicidae) and Two Native Australian Ant Species

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ABSTRACT The Argentine ant, Linepithema humile (Mayr), is a significant pest species, having become established on almost every continent, particularly in areas with a Mediterranean climate. In its introduced range, the Argentine ant has been associated with reductions in the abundance and diversity of native ant and nonant invertebrate fauna, as well as the interruption of ant-plant mutualisms. The distribution of Argentine ants has been correlated with particular abiotic factors, including soil moisture, relative humidity, disturbance, and particular soil and vegetation types. This study assessed the importance of temperature on the survival of Argentine ants and two native ant species (Iridomyrmex "rufoniger" and Rhytidoponera "convexa") in the laboratory. Workers were placed in incubators of varying temperatures (25, 32, 40, 45, 47, and 50°C), and counts of the numbers dead and alive were recorded after 1, 2, and 3 h. The results showed that all species displayed almost 100% survival at 25, 32, 40, and 45°C, but at 47°C the mortality rate of all species increased, with Argentine ants experiencing 100% mortality after 3 h. At 50°C, Argentine ants displayed no survival at 1 h, whereas the Iridomyrmex exhibited ~50% survival after 3 h. These results may have significant implications in Australia, where the ground surface temperatures may become very high during the summer, potentially limiting the spread of Argentine ants.

KEY WORDS temperature, abiotic conditions, survival, biological invasion

The introduction of non-native species into areas outside their native range has received increasing attention because of their potential negative effects, such as the loss of native species (Vanderwoude et al. 2000) and the interruption of ecological processes (Woodward and Hildrew 2001). Abiotic conditions may influence the establishment and spread of invasive species. The identification of such abiotic conditions may assist ecologists in better understanding the physiology and tolerances of invading species and may aid in identifying climatically suitable areas for focusing control and eradication efforts (Weber 2001).

The Argentine ant, Linepithema humile (Mayr), is an invasive ant species that has spread globally, typically into areas with a Mediterranean climate (Suarez et al. 2001). In its introduced range, the Argentine ant is associated with losses of resident ant (Holway 1998, Suarez et al. 2001) and nonant invertebrates (Cole et al. 1992, Bolger et al. 2000, Walters and Mackay 2003a), and disruption of ant-plant mutualisms (Bond and Slingsby 1984, Christian 2001). The distribution of the Argentine ant has been associated with available water sources (Holway 1998, Holway et al. 2002), increased relative humidity (Walters and Mackay 2003b), enhanced disturbance regimes (Suarez et al. 1998), and specific vegetation and soil types (Way et al. 1997).

High soil temperatures negatively influence the foraging behavior of a number of ant species (Ruano et al. 1999), including Argentine ants for which activity has been reported to be highest at temperatures between 15 and 19°C (Witt and Giliomee 1999), with activity ceasing at temperatures of 32°C (Markin 1970), 40–44°C (Witt and Giliomee 1999), and 45°C (Human et al. 1998). In the laboratory, mortality of 50% of workers was found to occur between 45 and 46°C (Tremer 1976), suggesting that foraging by Argentine ants ceases 1–2°C before the critical survival maximum of this species. Because it has been suggested that thermal tolerances may vary with location and population (Orr and Seike 1998), this study increases our knowledge of the temperature tolerances of invasive populations of Argentine ants across continents and may highlight those factors that may limit the spread of Argentine ants in invaded areas.

The aim of this study is to determine whether the thermal tolerances of Argentine ants differ from those of selected native ant species in South Australia. We hypothesize that Argentine ants are less well adapted to hot conditions in Australia in comparison with native ant species and therefore suffer greater mortality under high temperatures.
Materials and Methods

Study Species and Study Site. We selected native ant species from the genera *Iridomyrmex* and *Rhytidoponera* because they are widespread (Andersen 1990) and are diverse in their behavior and morphology. In addition, these two species have been observed in areas adjacent to, or overlapping, areas occupied by Argentine ants (Walters and Mackay 2003a). Ants from the genus *Iridomyrmex* are dominant members of the Australian ant community, particularly in arid and semiarid localities, where they exhibit high activity levels and a strong capacity to recruit to resources (Andersen 1990). Their dominance in Australian ant communities is thought to be largely due to their extensive colony sizes (Greenslade and Halliday 1983), competitive ability (Fox et al. 1985, Andersen 1990), aggressive behavior (Hölldobler 1982), and strong associations with other invertebrates and plants (Davidson and Morton 1981, Eastwood and Fraser 1999). Workers from the species complex *I.* "rufoniger" were selected for these laboratory trials because they have been found to be proficient competitors with Argentine ants for resources, form large polygynous colonies, and are located in areas inhabited by Argentine ants in South Australia (A.W., unpublished data). Ants from the genus *Rhytidoponera* also were selected because they are locally abundant (Andersen 1986), particularly in disturbed locations (Andersen 1990), but differ from *Iridomyrmex* in that they are large, opportunistic (Andersen 1990), solitary foragers (Greenslade and Halliday 1983) that have small colony sizes (Shattuck 1999). Workers from the species complex *R.* "conexa" were used in the laboratory trials because they are much larger than both the Argentine ants and *I.* "rufoniger" and because they are active members of the ant community in areas with Argentine ants (A.W., unpublished data).

We collected at least 10 colonies of each species from locations in the Adelaide metropolitan region between December 2001 and February 2002. Native ant colonies were collected from areas at least 50 m from areas inhabited by Argentine ants. Colonies consisting of workers, queens, and larvae were placed in buckets and returned to the laboratory where they were separated from the soil by aspiration. Colonies were stored in plastic containers that were coated with flour to prevent ant escape. A “nest” consisting of a glass test tube filled partially with water and plugged with cotton wool was placed in each container. Ant colonies were provided with water daily and fed a standard laboratory food mixture (Hölldobler and Wilson 1990) every second day.

Experimental Design. Survivorship trials were conducted at temperatures of 25, 32, 40, 45, 47, and 50°C, and at least 10 replicates were conducted for each species at each temperature. In each replicate, colony fragments of 50 workers of *I.* "rufoniger," or *L.* *humile*, or 15 *R.* "conexa" workers, were placed in separate test tubes, which were sealed with moistened cotton wool. Test tubes were placed in an incubator, and the counts of the numbers of live and dead workers were recorded at 1, 2, and 3 h. Six different incubators were used over the course of the trials; and to minimize the possible confounding effects associated with different incubator models, incubators were assigned different temperatures over the course of the trials. Each ant colony was used on one occasion. Voucher specimens were lodged with Commonwealth Scientific and Industrial Research Organization (Northern Territory, Australia).

Statistical Analysis. Data on the proportions of ants surviving in the different temperature conditions over time were arcsine transformed to meet with the assumptions of normality and analyzed using a multivariate repeated measures analysis of variance (ANOVA) with two-between-subjects factors (species and temperature) and one within-subjects factor (time). The species*temperature*time interaction effect in this design tests whether the differences in the survival profiles of the different ant species do not vary among the temperature conditions. Pairwise Sidak post hoc tests also were conducted to compare the survivorship of the three ant species at each time at 47 and 50°C.

Results

All three species showed high survivorship at temperatures up to 45°C (Fig. 1). However, at 47°C, there was a pronounced effect of temperature on mortality, with no Argentine ants surviving after 2 h and *Rhytidoponera* experiencing 100% mortality after 3 h, at which time the mean survival of the *Iridomyrmex* was reduced to 35%. At 50°C, the Argentine ants experienced 100% mortality after 1 h, whereas the *Rhytidoponera* displayed 100% mortality after 2 h. The survival of the *Iridomyrmex* at this temperature showed a more gradual decrease, and at the conclusion of the experimental period, an average of 50% of the ants in the replicate colonies remained alive.

These differences in the survival profiles of the three ant species across the different temperatures were statistically significant, as demonstrated by a highly significant species by temperature*time interaction effect ($F_{50, 396} = 5.389; P < 0.001$) in the repeated measures ANOVA. Pairwise post hoc comparisons of the three species at temperatures of 47°C showed that after 1 h, there were no differences between the survival of the three species; however, after 2 and 3 h, the survival of *L.* *humile* differed significantly from that of *Iridomyrmex* but not *Rhytidoponera*. At 50°C, the survivorship of *L.* *humile* was significantly lower than that of *Iridomyrmex*, but it did not differ significantly from that of *Rhytidoponera*, at all three time intervals (Table 1).

Discussion

The results of this study indicate that the survival of Argentine ants and the native species *R.* "conexa" were significantly reduced in comparison with that of the highly competitive, native ant *I.* "rufoniger" under
Fig. 1. Proportion of live workers of I. "rufoniger" (▲), Argentine ants (▼), and R. "convexa" (□) after 1, 2, and 3 h. Trials were conducted for each species at temperatures of 25, 32, 40, 45, 47, and 50°C. Error bars display 95% C.I. of mean.

Elevated temperatures. Such findings may have implications for the distribution and subsequent spread of Argentine ants in arid and semi-arid parts of Australia, including parts of South Australia where air temperatures of 48.9°C have been recorded in areas inhabited by both Argentine ants and native ant species (A.W., unpublished data).

The results of this study show that 100% mortality of Argentine ant workers occurs at temperatures between 45 and 47°C after 3 h, whereas the native species of I. "rufoniger" displays ~50% mortality at 50°C. The native species R. "convexa" exhibits intermediate survival; however, like Argentine ants, 100% mortality occurred at 47°C after 3 h. These findings agree with those of other studies that also have found reduced survival and activity of Argentine ants under increasing temperature conditions relative to native ant species. In North America, laboratory trials showed that native ants were able to survive higher temperatures than Argentine ants, with 100% Argentine ant mortality occurring at ≥46°C (Holway et al. 2002). Holway et al. (2002) also found that Argentine ants reached maximum numbers at baits at significantly lower temperatures (~35°C) than the native ant dormyrmex insanus (Buckley) (~39°C), concluding that Argentine ants are less tolerant of higher temperatures than native species. Similarly, in Africa, the maximum activity of Argentine ants was reached at temperatures between 40 and 44°C, at lower soil surface temperatures than three of the four native ants that also were tested in the study (Witt and Giliosee 1999).
Table 1. Pairwise Sidak post hoc results based on the arcsine transformed data for the survival of Iridomyrmex, L. humile, and Rhytidoponera at temperatures of 47 and 50°C after 1, 2, and 3 h

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. humile</td>
<td>--0.16** (0.16)</td>
<td>--0.69** (0.11)</td>
<td>--0.59** (0.10)</td>
</tr>
<tr>
<td>L. humile</td>
<td>--0.24** (0.16)</td>
<td>--0.25** (0.10)</td>
<td>0.09** (0.03)</td>
</tr>
<tr>
<td>Iridomyrmex</td>
<td>--0.08** (0.17)</td>
<td>0.44*** (0.11)</td>
<td>0.83*** (0.10)</td>
</tr>
<tr>
<td>Rhytidoponera</td>
<td>--1.23*** (0.11)</td>
<td>--0.83*** (0.08)</td>
<td>0.83*** (0.08)</td>
</tr>
<tr>
<td>Iridomyrmex</td>
<td>--0.25** (0.10)</td>
<td>0.00** (0.07)</td>
<td>0.00** (0.08)</td>
</tr>
<tr>
<td>L. humile</td>
<td>0.91*** (0.11)</td>
<td>0.83*** (0.08)</td>
<td>0.80*** (0.08)</td>
</tr>
</tbody>
</table>

The mean pairwise difference is given for each time and the standard error is given in parentheses (**P < 0.001; ns, P > 0.05).

The reduced survival experienced by Argentine ants under high temperatures, coupled with the presence of the dominant ant genera Iridomyrmex, may limit their spread in Australia either to areas with a moderate climate or to locations that are protected against the heat. Given that Argentine ants tend to construct "satellite" nests that are located close to the soil surface (Newell and Barber 1913), they may be further exposed to hot conditions in comparison with native ants that tend to nest deeper in the soil. Moreover, the slightly smaller size and coloration of Argentine ant workers relative to some native ants has been associated with increased risk of desiccation (Treher 1976). The strong relationship between the presence of Argentine ants and the presence of water (Holway 1998) further suggests that they may suffer greater mortality under hot conditions.

The lowered survival of Argentine ants at heightened temperatures also may have implications for their foraging success, possibly leading them to alter their foraging strategies so that they increase foraging activity during cooler seasons of the year or times of the day. In California, Argentine ants were observed to forage for longer periods than other native ant species and were present at baits during the middle of the day, when native ant species had ceased foraging (Human and Gordon 1996). This suggests that different populations of Argentine ants may display varying temperature tolerances or that some populations experience plastic responses to their new environment.

In this experiment, Iridomyrmex were able to tolerate higher temperatures than Argentine ants, and their capacity to forage during warmer periods may exceed that of Argentine ants. Previously, it has been suggested that the invasion success of non-native ants in Australia may be hindered by the presence of competitive resident ants (Majer 1994, Andersen 1997). However, the results of this study suggest that abiotic conditions also may impact the survival of invasive ant species in Australia, reducing their ability to compete with heat-adapted native ants for resources. Given that the invasion success of Argentine ant depends on their large colony sizes (Holway and Case 2001, Tsutui and Suarez 2003), specific abiotic conditions may be required to allow them to attain numerical dominance over native ant species. This, coupled with the aggressive and competitive interactions with native ant species, may help to explain why, in Australia, Argentine ants are restricted to the cooler southern regions, whereas species of Iridomyrmex are found throughout Australia and are very common in the hot and arid zones.

Although we have shown that Argentine ant survival is significantly reduced under heightened temperatures in comparison with ants from two native Australian genera, the results should be interpreted with caution because under natural conditions, ants may alter their foraging behavior and nest structure in response to changes in temperature conditions, thus avoiding the negative effects associated with high temperatures. Moreover, because many abiotic conditions interact, it is possible that the interaction between temperature and some other abiotic factor or factors are more limiting to the spread of Argentine ants than temperature alone. Further research into the foraging activity of Argentine ants in Australia is required to determine whether Argentine ants forage predominantly during the cooler months or alter their foraging activity to nights or earlier times of the day to avoid high temperatures.

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