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Experimental Evidence of Large-Scale Unicoloniality in the Tramp Ant *Wasmannia auropunctata* (*Roger*)

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We examined intraspecific colonial aggressiveness in Wasmannia auropunctata *(Roger), a tramp species originating from the neotropics. By observing the results of one-on-one confrontations, we compared the behavioral responses of workers originating from six New Caledonian locations (introduced range) and four Brazilian cocoa plantations (original range). We recorded interindividual "aggressive" behavior on four levels ranging from physical contact, with no aggressive response, to prolonged aggressiveness, including stinging by one or both ants. In Brazil, we often observed high intraspecific aggressiveness between populations originating from distant locations, indicating that* W. auropunctata *may behave as a multicolonial species in its native range. In New Caledonia, paired encounters resulted in low agonistic behavior, as shown by the absence of "full attacks" (which include stinging by one or both opponents). Our results suggest that* W. auropunctata *behaves as a single supercolony throughout New Caledonia and that the scale of its unicoloniality (widespread colonies with interconnected nests without aggressiveness between workers originating from distant areas) is different in introduced and*

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native populations. According to the present study, it seems likely that differences in intraspecific aggressiveness between native and introduced populations of W. auropunctata *contribute to its invasive success.*

KEY WORDS: nestmate recognition; intraspecific interaction; unicoloniality; Formicidae; biological invasion; tramp species.

INTRODUCTION

Biological invasions by ants are a severe threat to biodiversity and human activity in areas where they occur, with unicoloniality being one of the main attributes thought to facilitate their success (Holway *et al.*, 2002; Tsutsui *et al.*, 2003). Unicolonial species typically form spatially vast and competitively dominant supercolonies that lack territorial boundaries; they are polygynous, reproduce by colony budding, and exhibit high interspecific aggressiveness (Wilson, 1971; Passera, 1994). While large-scale unicoloniality has often been suggested as a main factor in the success of invasive ants, it has only been demonstrated for one species, the Argentine ant *Linepithema humile* (Suarez *et al.*, 1999; Tsutsui *et al.*, 2000; Giraud *et al.*, 2002).

In this study, we focus on the unicoloniality of the neotropical myrmicine *Wasmannia auropunctata* (Roger), considered one of the most ecologically destructive ants in areas where it has been introduced (Lowe *et al.*, 2000). To date, this species has been considered unicolonial based on observations in the Galàpagos Islands (Clark *et al.*, 1982; Ulloa Chacón and Cherix, 1990), but to the best of our knowledge, no one has published the results of behavioral assays conducted over a wide spatial scale to support this hypothesis. Here, we present results from behavioral tests performed among populations in New Caledonia where *W. auropunctata* has been introduced and among populations in Bahia state (Brazil), part of its native range.

MATERIALS AND METHODS

Origin and Collection of Ant Colonies

Scientists estimate that the native range of *W. auropunctata* encompasses most of Central America and much of South America down to northern Argentina (Jourdan *et al.*, 2002). Given the size of this area, it is unclear how extensive the native neotropical range was before populations of the ant were spread by humans. In our study, we considered populations from a cocoa-growing region in Bahia state in Brazil, where it is typically found (Delabie, 1990; Delabie *et al.*, 1994). Several concordant elements confirm

the native status of *W. auropunctata* in this part of Brazil. First, it occurs in Atlantic rain forest, which is the native vegetation in the Bahia area (Majer *et al.*, 1997; Majer and Delabie, 1999, Delabie *et al.*, 2000), and where it is less likely to have been introduced by human activity. It is also generally accepted that plantation ant fauna derive from Atlantic rain forest fauna, as the canopy was kept for shade in the early stages of the establishment of the cocoa plantations (Delabie *et al.*, 2000).

In Bahia, we collected specimens from four cocoa plantations: Itabuna (Ceplac/Cepec plantations), Itajuipe, Uruçuca, and Santa Luzia (Fig. 1a). Each cocoa plantation covers several square kilometers. Several nests of *W. auropunctata* were collected from separate plots inside the perimeter of each plantation and tested in August 2000.

In New Caledonia, *W. auropunctata* was recorded for the first time in the 1970s (Fabres and Brown, 1978). Formerly confined to human-modified ecosystems, it now spreads over a wide range of natural habitats and occurs throughout most lowlands (Jourdan, 1997; Jourdan *et al.*, 2001, 2002; Le Breton *et al.*, 2003). In January 2001, several colony fragments (nests) were collected within a few meters from each other, in six sites representative of the entire New Caledonian range (Fig. 1b). In the lab, for each locality, every colony fragment was kept isolated.

Voucher specimens of *W. auropunctata* collected during this project were deposited in the ant collection at the *Centro de Pesquisas do Cacau* (CPDC), Ceplac, Itabuna, Brazil.

One-on-One Confrontation Tests

As unicoloniality has been well studied in the Argentine ant, we used a standard behavioral assay commonly employed in such studies (Holway *et al.*, 1998; Suarez *et al.*, 1999; Tsutsui *et al.*, 2003). We paired two individual workers together in a neutral arena (ϕ, 4.5 cm; height, 1 cm) whose walls were coated with Fluon to prevent the ants from climbing out. During 5 min we scored interactions between the workers on a scale from 1 to 4: 1 = touch (physical contact but no aggressive response; may include antennation or trophallaxis), 2 = avoidance (the ants touch, and one or both recoils and runs in the opposite direction), 3 = aggressiveness (a physical attack by one or both of the workers, including lunging, biting, and pulling legs or antennae), and 4 = fighting (prolonged aggressiveness, including prolonged biting and pulling and the use of the sting by one or both ants). For each confrontation, we conducted 10 replications and used each worker only once.

In New Caledonia, we tested workers coming from the same sites, gathered from areas separated by a distance of 50 m (intra-area tests), and

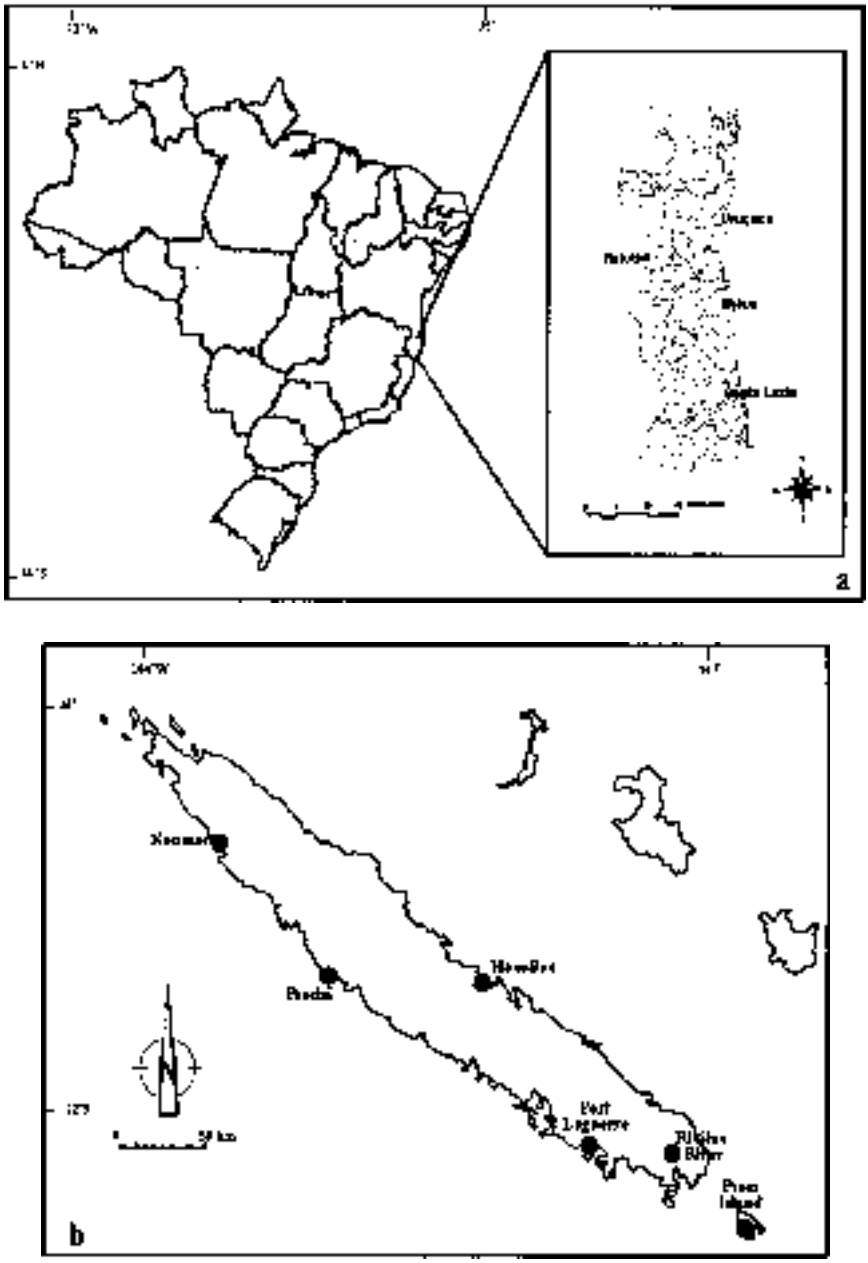

Fig. 1. Maps of study areas within the native (Brazil; a) and introduced (New Caledonia; b) ranges of *Wasmania auropunctata*.

workers coming from different locations separated from each other by between 60 and 410 km (inter-area tests). In Brazil, we tested workers coming from the same plantation, gathered from areas separated by a distance of between 0.05 and 3 km (intra-area tests) and workers coming from different plantations 16 to 118 km from each other (inter-area tests).

Statistics

Levels of aggressiveness between colony pairs were compared using the Kruskal–Wallis test. A *post hoc* test (Dunn's test) was then performed to isolate the groups that differed from the others. All statistical analyses were performed using SPSS 11.0 (SPSS Inc.).

RESULTS

In Brazil, we recorded two different patterns of aggressiveness (Kruskal–Wallis test: $H = 74.44$; $df = 10$; $P < 0.001$). During intra-area experiments, all but one colony pair showed no aggressiveness (Fig. 2a). The workers which exhibited a high level of aggressiveness came from Uruçuca and were gathered from sites separated by 3 km. Conversely, during inter-area experiments, all but one colony pair showed a high level of aggressiveness. Most pairings resulted in reciprocal full attacks with escalation reaching "stinging between workers" (i.e., level 4 of aggressiveness) and even the death of one of the opponents. The workers which did not exhibit aggressiveness came from Ilhéus and Itajuipe, two areas separated by 20 km.

In New Caledonia, the third level of our aggressiveness scale was sometimes reached, but we never recorded level 4 of aggressiveness during one-on-one encounters, resulting in a weak average escalation for all the colony pairs (Fig. 2b). A significant difference was obtained between the colony pairs (Kruskal–Wallis test: $H = 26.10$; $df = 12$; $P = 0.01$). Nevertheless, multiple comparisons did not permit us to distinguish which groups differ from the others, indicating that there is a weak difference in aggressiveness between short- and long-distance scales.

DISCUSSION

In New Caledonia, its introduced range, *W. auropunctata* workers showed no aggressive intraspecific behavior even when their nests were separated by up to several hundred kilometers (or the length of the island, ca.

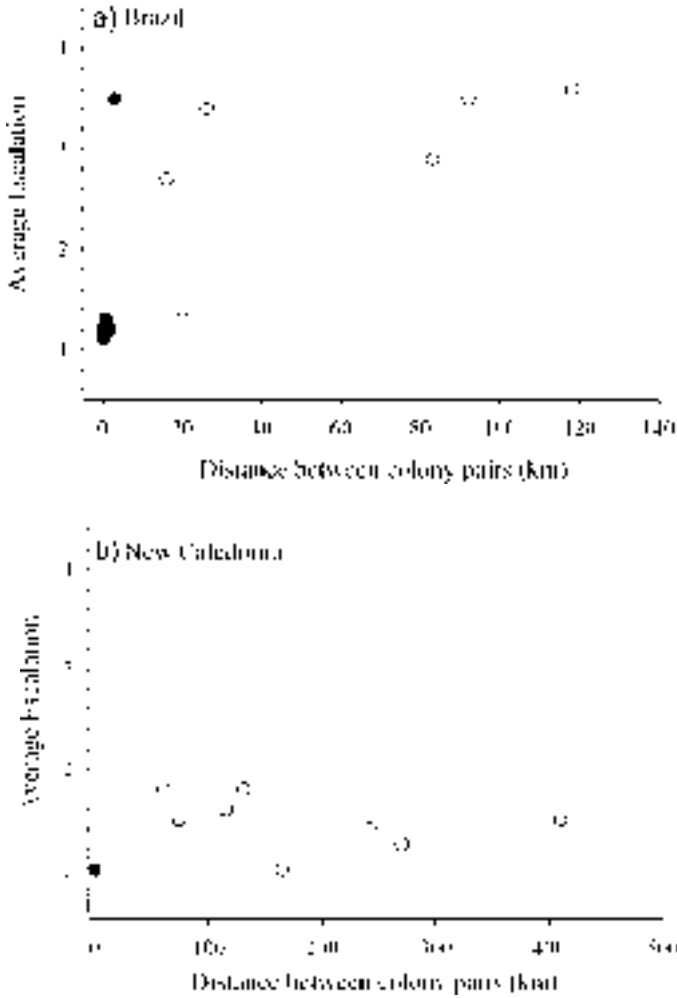

Fig. 2. Influence of the distance between localities on average escalation values during one-on-one confrontations of *Wasmannia auropunctata* workers, in Brazil (a) and New Caledonia (b). Dots indicate pairs of nests collected from the same location in New Caledonia and from the same plantation in Brazil. Circles indicate pairs of nests collected from different locations.

450 km), suggesting that *W. auropunctata* behaves as a single supercolony on the island. This is the first experimental evidence of unicolonial behavior in *W. auropunctata* on a large geographical scale. Similar supercolonies spreading over a wide geographic scale have been described for the Argentine ant

in southern California (Tsutsui *et al.*, 2000; 2003) and in southern Europe (Giraud *et al.*, 2002).

In Brazil, we noted aggressiveness between populations from different cocoa plantations. It seems that *W. auropunctata* forms relatively large colonies as shown by the absence of aggressiveness between workers belonging to nests separated by several kilometers (i.e., the size of the cocoa plantations). Nevertheless, aggressiveness was not directly related to distance: the shortest distance for which we observed high aggressiveness was 3 km, inside the perimeter of a cocoa plantation. Surprisingly, although separated by 20 km (Ilhéus and Itajuipe), the workers of one colony pair showed no agonistic behavior during confrontations. We later discovered that this absence of aggressiveness probably results from the fact that one plantation was created from cocoa plants originating from the other, with *W. auropunctata* colonies likely to have been transported between the two plantations (Delabie, personal observation). This observation illustrates that even within its native range *W. auropunctata* can be displaced. In this case, confrontations between workers from the original and the introduced areas show a low level of aggressiveness. Finally, a cross-range comparison shows that in *W. auropunctata* native populations appear "more multicolonial" compared to populations introduced in New Caledonia. Thus, even though we only examined one introduced population and a small part of Wasmannia's native range, it seems likely that differences in intraspecific aggressiveness between native and introduced populations of *W. auropunctata* contribute to its invasive success.

In terms of social organization, unicoloniality results in low intraspecific competition, which is one of the most important regulating factors in ant community equilibrium (Ryti and Case, 1988). In the Argentine ant *L. humile*, Holway *et al.* (1998) have already emphasized the loss of intraspecific aggressiveness in its invasive success: it allows high-density populations to be built on a local scale. The numerical dominance of *L. humile* in California appears then as a process resulting from unicoloniality: it helps to break ant community equilibrium by offering a numerical advantage against the entire ant guild (Holway, 1999; Human and Gordon, 1999). According to these studies, such behavior on a wide scale may be a decisive advantage and would contribute to *W. auropunctata*'s success as an invader. This also reinforces the hypothesis that unicoloniality is a key factor (though not the only one) in the ecological success of invasive ants in both their native and their introduced ranges.

Our results emphasize the ability of *W. auropunctata* to build high-density populations that rely on low intraspecific aggressiveness in both its native and its introduced ranges. In any case, some questions about the scale of the phenomenon remain. At what spatial scale is heightened intraspecific aggressiveness likely to lead to lower *W. auropunctata* density?

If intraspecific aggressiveness only manifests itself at relatively large spatial scales (e.g., several kilometers), then are intraspecific competition and territoriality really that likely to lead to decreased densities? This is a difficult empirical problem. As pointed out by Majer and Delabie (1999), when disturbance occurs, *W. auropunctata* outbreaks may be observed, so that this ant species is considered to be a disturbance specialist in its native range. In native natural environments, one might suspect that aggressiveness would be more frequent at shorter ranges. With this in mind, it would be interesting to study situations in undisturbed areas compared to those we studied in human modified areas (with more short-distance comparisons). Further studies on the invasive success of *W. auropunctata* should also focus on how nestmate recognition varies between native and introduced populations and should include analyses of cuticular hydrocarbons and genetics, in order to investigate the proximate causes of invasive success.

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