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Non-native Ants Are Smaller than Related Native Ants

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ABSTRACT: I compare the sizes of non-native and native ants to evaluate how worker size may be related to the ability of a species to invade new habitats. I compare the size of 78 non-native ant species belonging to 26 genera with the size of native congeneric species; native ants are larger than non-native ants in 22 of 26 genera. Ants were sorted by genera into fighting and nonfighting groups, based on observations of interspecific interactions with other ant species. In all of the genera with monomorphic worker castes that fight during competition, the non-native species were smaller than the native species. The genera that engage in combat had a higher frequency of significantly smaller size in non-native ants. I selected *Wasmannia auropunctata* for further studies, to compare native and non-native populations. Specimens of *W. auropunctata* from non-native populations were smaller than conspecific counterparts from its native habitat. I consider hypotheses to explain why non-native ants are smaller in size than native ants, including the role of colony size in interspecific fights, changes in life history, the release from intraspecific fighting, and climate. The discovery that fighting non-natives are smaller than their closest native relatives may provide insight into the mechanisms for success of non-native species, as well as the role of worker size and colony size during interspecific competition.

Keywords: exotic species, invasive species, tramp ants, body size, fighting, Lancheater's laws.

Non-native plants and animals that have established populations outside their native habitat are often successful invaders that thrive at the expense of native species living off the same resources (Moller 1996; Williamson 1996). In this article, I use *native* to describe species that have not established non-native populations. Many researchers have directed effort toward discovering traits associated with non-native ant species (Vander Meer et al. 1990; Williams 1994; Yamauchi and Ogata 1995; Human and Gor-

don 1996; Holway et al. 1998). Common attributes of non-native ants include polygyny, a monomorphic worker caste, unicoloniality, a high degree of interspecific aggression, and intranidal mating (Hölldobler and Wilson 1990; Passera 1994; McGlynn 1999a). Bernstein (1979) and Passera (1994) suggest that species with traits common to non-native ants are characteristically small in size. Several authors have reviewed the biogeography and life histories of non-native ants (Vander Meer et al. 1990; Brandão and Paiva 1994; Passera 1994; Reimer 1994; Van Schagen et al. 1994; Moller 1996; McGlynn 1999b), but none provides an analysis of body size. In this study, I focus on the size differences between non-native ants and their native relatives.

Fights are common during intra- and interspecific interactions in ants (Crowell 1968; Torres 1984; Gordon 1988; Andersen and Patel 1994; Gordon and Kulig 1996). Non-native ants often use aggressive interactions at food items to exclude native ants (Lieberburg et al. 1975; Clark et al. 1982; Ward 1987; DeKock and Giliomee 1989; Brandão and Paiva 1994; Holway 1995; Holway et al. 1998). Non-native ants also typically arrive in higher numbers than native ants at bait items (Haskins and Haskins 1965; Lieberburg et al. 1975; Clark et al. 1982; Majer et al. 1984; DeKock and Giliomee 1989; Porter and Savignano 1990; Human and Gordon 1996; Jourdan 1997; Holway 1999). Even if the non-native species are not the first to arrive at a food item, they may competitively exclude native species by recruiting many workers, which engage in interference competition (Clark et al. 1982; Human and Gordon 1996; Holway 1999).

Worker size interacts with foraging strategy and competitive ability in ants. Within and among species, ants that differ in size often employ different foraging strategies (Davidson 1978; Bernstein 1979; Herbers 1980; Detrain and Pasteels 1991; Cerda and Retana 1997). When many ants fight in large groups, numerical superiority is important for winning the battle. Even though a single large ant will often defeat a single small ant, small ants can win battles by recruiting large numbers of workers (Franks and Partridge 1993, 1994). Ant colonies experience a trade-off between worker size and colony size; colonies can produce more workers by making them smaller (Oster and Wilson

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1978; Bourke and Franks 1995). Franks and Partridge (1993, 1994) applied combat models, called “Lanchester battles” (Lanchester 1917), to describe the importance of numerical superiority when small ants are engaged in fighting. Whitehouse and Jaffe (1996) supported the Franks and Partridge (1993) hypothesis by provoking intraspecific combat in a leaf-cutting ant species; colonies employed small workers in fights against conspecific colonies. Although small size often lends an advantage during direct competition with other ants, large ants can carry more food, tolerate foraging in harsher microclimates (Kaspari 1993), and are more successful in one-on-one combat with other ants (Franks and Partridge 1993, 1994).

In this article, I directly compare specimens of non-native and native congeneric species, testing the prediction that non-native ants will be smaller than their native congeners. Once I establish that non-native ants are smaller in size than native ants, I group ants into categories, indicating whether they engage in interspecific fighting during foraging behavior. Because fighting is affected by worker size and colony size, I examine how size differences between native and non-native ants vary among the fighting groups. Size differences among native and non-native ants may also occur intraspecifically. I selected *Wasmannia auropunctata* to observe differences in size among native and non-native populations.

Methods

Are Non-native Ant Species Smaller than Their Native Relatives?

I measured representatives of known (McGlynn 1999b) non-native ant species at the Los Angeles County Museum of Natural History, Smithsonian National Museum of Natural History, and University of São Paulo Museum of Zoology (table 1). I did not measure ants with a polymorphic worker caste because in these species the size of individuals may reflect biases in the methods of collection, as well as flexibility associated with environmental heterogeneity (Oster and Wilson 1978). While a minority of non-native species have polymorphic worker castes (T. McGlynn, unpublished data), some important non-native ants such as *Anoplolepis gracilipes* and *Solenopsis* spp. are not included in this study because they have polymorphic worker castes.

To measure each species, I used 10 specimens from a variety of localities when available. Because the status of ant systematics does not provide data on degrees of relationship within a genus, I arbitrarily selected 10 native congeners of non-native ant species, from the same biogeographic region when possible. In the instances when <10 species were available (see value labels in fig. 1), I used all of the species within the collections.

Table 1: Non-native species measured for size comparison with native congeners

Subfamily and non-native ant species	Mean head width (mm)	<i>n</i>	SE
Dolichoderinae:			
<i>Linepithema humile</i>	.634	10	.009
<i>Linepithema iniquum</i>	.580	10	.017
<i>Linepithema melleum</i>	.488	10	.008
<i>Ochetellus glaber</i>	.602	10	.015
<i>Ochetellus itoi</i>	.564	9	.014
<i>Tapinoma melanocephalum</i>	.388	10	.006
<i>Technomyrmex albipes</i>	.600	10	.010
Formicinae:			
<i>Brachymyrmex minutus</i>	.322	10	.015
<i>Brachymyrmex musculus</i>	.368	10	.011
<i>Brachymyrmex obscurior</i>	.422	10	.007
<i>Paratrechina bourbonica</i>	.690	10	.023
<i>Paratrechina clandestina</i>	.607	3	.027
<i>Paratrechina fulva</i>	.686	10	.018
<i>Paratrechina guatemalensis</i>	.488	10	.013
<i>Paratrechina longicornis</i>	.498	10	.007
<i>Paratrechina pubens</i>	.694	20	.009
<i>Paratrechina vaga</i>	.556	5	.020
<i>Paratrechina vividula</i>	.546	10	.013
<i>Plagiolepis alluaudi</i>	.320	10	.008
<i>Plagiolepis exigua</i>	.322	6	.010
Myrmicinae:			
<i>Cardiocondyla ectopia</i>	.449	10	.003
<i>Cardiocondyla emeryi</i>	.353	10	.003
<i>Cardiocondyla nuda</i>	.356	10	.003
<i>Cardiocondyla venustula</i>	.459	10	.006
<i>Cardiocondyla wroughtoni</i>	.395	10	.005
<i>Crematogaster lineolata</i>	.802	10	.025
<i>Crematogaster sordidula</i>	.585	10	.008
<i>Eurhopalothrix floridana</i>	.685	10	.006
<i>Leptothorax luciliae</i>	.618	10	.005
<i>Monomorium chinense</i>	.307	3	.012
<i>Monomorium destructor</i>	.562	10	.030
<i>Monomorium ebeninum</i>	.401	10	.002
<i>Monomorium floricola</i>	.324	10	.012
<i>Monomorium latinode</i>	.625	10	.010
<i>Monomorium minimum</i>	.435	10	.031
<i>Monomorium monomorium</i>	.310	10	.003
<i>Monomorium orientale</i>	.290	1	<i>n</i> = 1
<i>Monomorium pharaonis</i>	.426	10	.004
<i>Monomorium sechellense</i>	.353	3	.003
<i>Monomorium subopacum</i>	.475	2	.025
<i>Myrmica rubra</i>	1.018	10	.005
<i>Smithistruma margaritae</i>	.389	10	.007
<i>Strumigenys eggersi</i>	.354	10	.005
<i>Strumigenys godeffroyi</i>	.433	10	.010
<i>Strumigenys gundlachi</i>	.368	10	.009

Table 1 (Continued)

Subfamily and non-native ant species	Mean head width (mm)	<i>n</i>	SE
<i>Strumigenys languinosa</i>	.465	10	.010
<i>Strumigenys lewisi</i>	.464	10	.006
<i>Strumigenys perplexa</i>	.447	3	.012
<i>Strumigenys rogersi</i>	.439	10	.005
<i>Strumigenys silvestrii</i>	.351	10	.004
<i>Strumigenys solifontis</i>	.560	1	<i>n</i> = 1
<i>Tetramorium bicarinatum</i>	.793	10	.739
<i>Tetramorium caldarium</i>	.510	10	.009
<i>Tetramorium caespitum</i>	.823	10	.025
<i>Tetramorium grassii</i>	.761	10	.025
<i>Tetramorium guineense</i>	.730	3	.015
<i>Tetramorium languinosum</i>	.587	10	.004
<i>Tetramorium pacificum</i>	.757	10	.008
<i>Tetramorium simillimum</i>	.506	10	.010
<i>Tetramorium tonganum</i>	.571	7	.014
<i>Wasmannia auropunctata</i>	.417	10	.005
Ponerinae:			
<i>Anochetus mayri</i>	.823	10	.017
<i>Gnamptogenys porcata</i>	1.069	10	.023
<i>Hypoponera eduardi</i>	.613	6	.021
<i>Hypoponera opaciceps</i>	.656	10	.007
<i>Hypoponera punctatissima</i>	.496	5	.024
<i>Hypoponera zwaluwenburgi</i>	.320	1	<i>n</i> = 1
<i>Leptogenys falcigera</i>	1.491	10	.010
<i>Odontomachus haematodus</i>	1.854	10	.099
<i>Odontomachus ruginodis</i>	1.990	10	.296
<i>Odontomachus simillimus</i>	1.900	10	.039
<i>Pachycondyla luteipes</i>	.815	10	.020
<i>Pachycondyla stigma</i>	1.075	10	.029
<i>Ponera coarctata</i>	.580	10	.015
<i>Ponera leae</i>	.370	6	.004

Note: A summary of the 233 native congeneric species measured is available on request. Generic averages for native and non-native ants are presented in figure 1.

I use head width, which is highly correlated with body length and a standard measure for ant size (Hölldobler and Wilson 1990; Kaspari 1993), as a general measure of size for all specimens. Measurements were of mounted and identified museum specimens; I used an ocular micrometer calibrated with a stage micrometer to an accuracy of 0.01 mm.

I compared how often non-natives were smaller than natives, using the mean of native species and mean of non-native species for each genus (table 2). To determine genera with more pronounced differences between natives and non-natives, I used an ANOVA to compare the non-native and native members of each genus, using the mean size of each species as a single data point. When a genus

contained only one non-native species, I compared the mean of the native congener head widths with the mean value of the non-native species head width. I used the single value of the non-native species mean head width as a single parametric value, referring to the *t* distribution for critical values (as in Sokal and Rohlf 1981, p. 231). To find the most significant differences, a Bonferroni correction was used within each fighting group to lower the alpha level.

Is the Small Size of Non-native Ants Associated with Fighting Behavior?

I designated ant genera into one of three groups based on their fighting behavior. The fighting groups are derived from observations by several researchers (Torres 1984; Savolainen and Vespalainen 1988; Hölldobler and Wilson 1990; Vander Meer et al. 1990; Dejean 1991; Tennant 1994; Williams 1994; Andersen 1995; Yamauchi and Ogata 1995; Bestelmeyer and Weins 1996; Morrison 1996; Andersen 1997a; McGlynn 1999b). Fighters have documented observations of interspecific fighting in the field. Nonfighters do not participate in interspecific combat at bait items (e.g., Andersen 1995). One of two conditions was satisfied to classify a nonfighter: either the species repeatedly avoids confrontation at bait items, or the species does not recruit workers to food. For ant genera that cannot be classified as fighters or nonfighters, I have designated them as unknown. Ants of unknown fighting status have received no appropriate field observations, or the consensus on their fighting behavior is questionable. Because this study examines ants at the global scale, the assignment of fighting groups must be considered in a global context; a localized occurrence of fighting behavior in one site is not sufficient to designate a species as a fighter on the worldwide scale (Andersen 1997b).

In table 2, I break down the occurrence of smaller size in non-native ants among fighting groups. I used binomial tests and Fisher's exact tests of association to determine whether the frequency of smaller-sized non-natives was associated with fighting groups.

Do the Non-native Populations of Wasmannia auropunctata Contain Smaller Workers than Native Populations?

I selected a non-native species that is well collected and whose native distribution is known. *Wasmannia auropunctata* is native to continental Latin America and is a non-native wherever else it is established (Lubin 1985; Tennant 1994; McGlynn 1999b). I measured the sizes of museum specimens of *W. auropunctata* from native and non-native sites. While colony sizes were not reported for

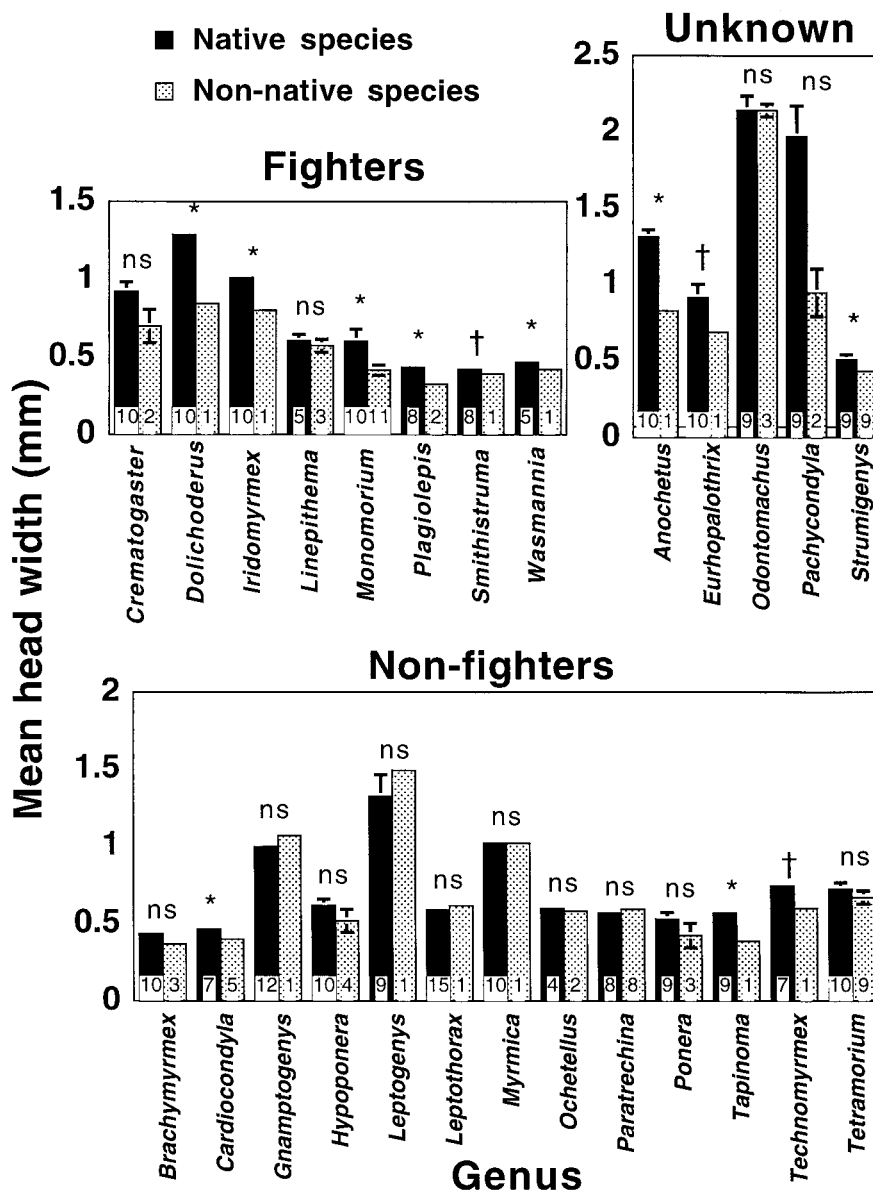


Figure 1: Relative sizes of native and non-native species by genus. The number of species in each sample is indicated by the value at the base of each column. Error bars are \pm SEs. Results of comparison by ANOVA are as follows: ns indicates $P > .05$; asterisk indicates $P < .05$; dagger indicates $P < .05$ but not significantly different after Bonferroni correction in each fighting group. See “Methods” for designation of fighting groups.

the museum specimens, colonies were probably mature because young nests of *W. auropunctata* are difficult to locate while collecting (T. McGlynn, personal observation). I excluded specimens of the *W. auropunctata* “black form,” which may be a different undescribed species (L. Alonso, personal communication). I analyzed these data using a hierarchical ANOVA, grouping the non-native and native populations of *W. auropunctata*, to determine whether there is a significant group effect.

Results

Are Non-native Ant Species Smaller than Their Native Relatives?

In 22 of 26 genera, the non-native species were smaller than the native species (binomial test among genera, $P < .01$; fig. 1; table 2). Twelve of the 22 genera were statistically significant by ANOVA, and nine were significant after Bonferroni correction.

Table 2: The frequency of smaller-sized non-native species among fighting groups

Fighting group	Number of genera	Non-natives smaller than natives	Non-natives significantly smaller	Non-natives significantly smaller after Bonferroni
Fighters	8	8	6	5
Nonfighters	13	9	3	2
Unknown	5	5	3	2
Total	26	22	12	9

Note: Of 26 genera, 22 have small-sized non-native species (binomial test, $P < .01$). After determining which genera have smaller non-natives after ANOVA comparisons, I found that the fighting group has a higher proportion of significantly smaller non-natives compared to the nonfighters (Fisher's exact test, $P < .05$).

Is the Small Size of Non-native Ants Associated with Fighting Behavior?

The disposition for non-native ants to be small in size is associated with the fighting groups. In all of the eight fighting genera, the non-native ants were smaller than the native ants, while nine of the 13 non-native nonfighters were smaller than the native nonfighters (table 2). Using statistically significant differences to find the more pronounced differences, there was a higher proportion of small-sized non-native ants in the fighting group (Fisher's exact test, $P < .005$; table 2).

*Do the Non-native Populations of *Wasmannia auropunctata* Contain Smaller Workers than Native Populations?*

The localities of native specimens (and the numbers of samples measured) were as follows: Brazil (19), Colombia (43), El Salvador (78), and Peru (18). Non-native specimens came from the Bahamas (9), Florida (44), Jamaica (10), and the Solomon Islands (29). Ants from non-native populations of *W. auropunctata* were significantly smaller than native ants of the same species (fig. 2; hierarchical ANOVA, $F = 15.61$; $df = 1, 6$; $P < .0001$). The mean head width of the specimens from non-native populations was 0.401 mm (SE ± 0.05), and the mean head width of specimens from native populations was 0.436 mm (SE ± 0.04). The intraspecific differences in the size of *W. auropunctata* were relatively small compared to interspecific size differences presented in the earlier comparison.

Discussion

Why are non-native ants smaller in size than native ants, among and within species? The likely explanations will emerge from the behavioral and ecological characteristics that are unique to non-native ants. Unfortunately, these

data are missing in most ant taxa (Tschinkel 1991), including most non-native ants. Nonetheless, using existing theories on the biology of non-native ants, I consider four hypotheses that may explain the striking trend for non-native ants to be smaller than native ants.

Hypothesis 1: Smaller Ants Belong to Larger Colonies; Large Colonies Are More Successful at Interspecific Combat

Large colony size is an important component of interspecific competition in non-native ants. Having many workers allows non-native ants to win battles with colonies that have fewer ants. By producing smaller workers, non-native ant colonies increase the number of workers. Non-native ants often use fighting to spread into new areas, as I established in the introduction. Lanchester battles (Franks and Partridge 1993, 1994) describe how having a large colony with small ants is more important than having a small colony with large ants. This hypothesis can be true only if Lanchester battles correctly model fighting ants. To date, two manipulative field experiments support the application of Lanchester's laws to ant biology (Whitehouse and Jaffe 1996; T. McGlynn, unpublished manuscript), while I know of no experiments that refute the application of Lanchester battles to fighting ants. The importance of fighting is supported by the results in table 2, as fighting non-native ants are more different in size from congeneric native species, compared to nonfighting non-native ants. If Lanchester battles are not responsible for the difference between fighting and nonfighting non-native ants, then other variables correlated with fighting must be at work.

In general, larger colonies of ants produce larger workers (Johnston and Wilson 1985; Tschinkel 1988, 1998; Beshers and Traniello 1994; I. Billick, unpublished data). However, the published studies on the relationship between colony size and worker size have been performed on large, monogynous, monodomous colonies, while non-native ants

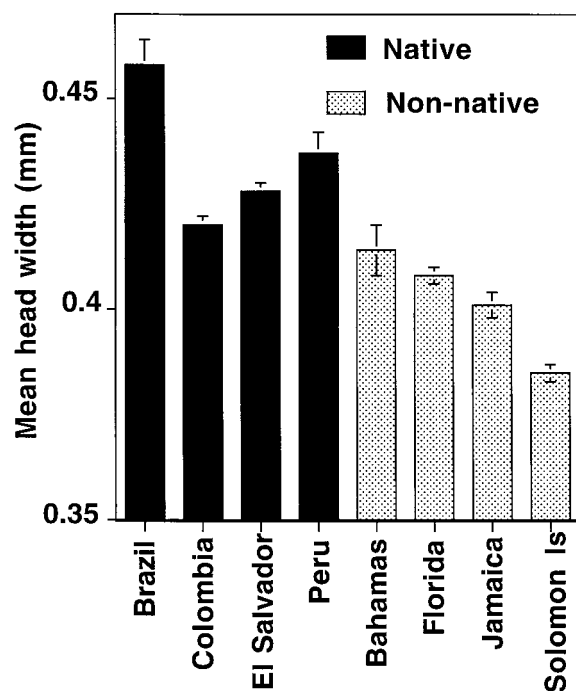


Figure 2: Sizes of workers in non-native and native populations of *Wasmannia auropunctata*. Error bars represent \pm SEs. The non-native populations contain smaller workers than the native populations (hierarchical ANOVA, $P < .0001$).

tend to be polygynous and have polydomous colonies with small nests (see "Hypothesis 2"). The rules that govern efficiency of worker production in colony ontogeny may be drastically different in species with life histories similar to those of non-native ants.

Colonies with smaller ants can produce many individual workers quickly because such colonies can produce ants more quickly (Bourke and Franks 1995). Small ants have a distinct advantage in terms of colony growth because colonies with a higher number of workers can produce an even greater number of workers. Modular growth is advantageous to the growth of colonies with small ants; the rate of exponential growth is increased as the size of ants becomes smaller (Bourke and Franks 1995). The number of existing workers is a positive feedback on the production of workers, such that making smaller-sized ants will result in even more workers. While these colonies may have the same efficiency and growth rate in terms of total worker mass, the increase in the individual number of fighting units is a key variable in interspecific fights. Because large numbers of small fighting units are necessary to overcome larger-sized competitors, rapid colony growth may be an important contributing factor in the establishment of reproducing populations in new areas.

Hypothesis 2: The Life Histories of Non-native Ants Result in Smaller Worker Sizes

The most successful non-native ants have a suite of life-history characteristics that may enable them to out-compete native species (Hölldobler and Wilson 1990; Passera 1994; McGlynn 1999a). Many non-native ant species are polygynous, with many queens within a single colony (Keller and Vargo 1993; Passera 1994). The degree of polygyny may be generally associated with smaller worker size, as has been demonstrated in the polymorphic species *Solenopsis invicta* (Goodisman and Ross 1996). In addition to higher queen numbers, colony organization of non-native ants can increase interspecific competitive ability. Some non-native ants are uniclonal, indicating that there are no colony boundaries and that neighboring conspecific nests share resources rather than fight with one another (Passera 1994; Holway et al. 1998). Uniclonal ant colonies commonly reproduce by budding (Passera 1994), such that queens move a short distance from a parental colony with a complement of workers. This mechanism reduces the mortality of new queens because they are invested with a large and developed workforce.

Non-native ants may be small in size as a result of their uniclonality. While there is no direct link yet established between worker size and uniclonality, the extreme polygyny found in uniclonal ants (Keller and Passera 1992) may result in smaller workers as queen number can be negatively correlated with worker size (Goodisman and Ross 1996). Many widespread non-native ants are uniclonal, including *Linepithema humile* (Holway et al. 1998), *Wasmannia auropunctata* (Fabres and Brown 1978; Clark et al. 1982; Jourdan 1997), *Pheidole megacephala* (Haskins and Haskins 1965; Lieburburg et al. 1975), and *Tapinoma melanocephalum* (Passera 1994).

The difficulty in evaluating the effects of uniclonality on size in non-native ants is that frequencies of uniclonality among taxa are unknown. As published studies of most native ants show clear colony boundaries (reviewed in Hölldobler and Wilson 1990), it is more than mere coincidence that the most widespread non-native ants are uniclonal (McGlynn 1999b). However, most other non-native ants are also smaller in size than native ants, and they are not yet known to be uniclonal because there are no published field observations.

Hypothesis 3: Non-native Ants Are Small in Size as a Release from Intraspecific Competition

While hypothesis 1 invokes Lanchester's laws of fighting, the comparative roles of fighting in native and non-native habitats are unknown. J. Wetterer (personal communication) proposed that non-native ants fight less in non-

native habitats, as they often flourish in areas with reduced interspecific competition. Under this hypothesis, small worker size is not a mechanism for the success of non-native ants but instead a result of the lack of fighting between ants. A reduction in fighting can be associated with the ability of a non-native ant to invade new areas. Holway et al. (1998) demonstrated that the lack of intraspecific fighting in unicolonial populations of *Linepithema humile* in California is responsible in part for their success.

Non-native ants are most successful on oceanic islands, where there are fewer native ants (Brandão and Paiva 1994; Yamauchi and Ogata 1995; Jourdan 1997; McGlynn 1999b). J. Wetterer (personal communication) argues that there is less competition on oceanic islands because of the reduced native ant fauna. Other authors have also suggested that the widespread success of non-native ants may result from less "biotic resistance" from the depauperate ant faunas on oceanic islands (Haskins and Haskins 1965; Reimer 1994; Jourdan 1997; but see Simberloff 1995). On the one hand, island ant faunas have a greater fraction of non-native species than continental areas, and a disproportionate number of small-sized non-native ant species were described from islands by systematists (McGlynn 1999a). On the other hand, non-native ants compete intensely with one another on islands, despite the small number of native species (Wilson and Taylor 1967; Lieburburg et al. 1975).

If there is less competition on islands, then fighting by non-native ants may be less frequent than in native habitats. This hypothesis is supported by the comparison of native and non-native *W. auropunctata*, in which the island populations have smaller workers than the continental populations (fig. 2). As is the case with most non-native ants, the native populations are continental, and many non-native populations are on islands with reduced or absent native ant faunas (Wilson and Taylor 1967; McGlynn 1999b). In the absence of data showing the impact of competition on size in workers, this hypothesis remains an attractive alternative to invoking the effects of Lanchester battles to explain the small size of non-native ants.

Hypothesis 4: Climate Regulates Worker Size

In light of the fact that social insects are colonial organisms, it is possible that non-native ants have smaller workers in non-native habitats as a buffer against harsher climates. Kaspari and Vargo (1995) found that colony size, rather than worker size, of social insects increases as a buffer for the greater climatic variation associated with high latitudes. Many non-native species, including *W. auropunctata*, have tropical origins and are transported into subtropical climates at higher latitudes (McGlynn 1999b).

Because an increase in colony size may be associated with the reduction of worker size, the small size of non-natives transported to higher latitudes may be explained by climate as well as by interspecific interactions.

Explanations for Intraspecific Size Differences

It is intriguing to find intraspecific size differences between the native and non-native habitats of *W. auropunctata*. There are three nonexclusive explanations for the smaller size in non-native populations. First, the smaller non-native ants that arrived in new habitats could have been more successful than propagules with larger sizes. The origins of the non-native populations could be determined using similar molecular techniques to those of a previous study on a widespread beetle pest (Williams et al. 1994). The second possibility is that small size is the product of selection after ants were introduced into non-native habitats. The third explanation keys into the observation that size in monomorphic worker castes, on a small scale, varies with life history: life histories may be variable among non-native and native populations of the same species. However, the relationship between colony size and worker size is not well understood for *W. auropunctata* and even less so for other non-native ants.

Finding the Right Answers

The existing studies on non-native ants are not equipped to deal with the interacting effects of biogeography, colony size, worker size, and fighting behavior. Discovering which mechanisms are responsible for the fact that non-native ants are small in size will entail a series of observational and manipulative experiments. Support for hypothesis 1, large colonies winning Lanchester battles, can come from two avenues. First, additional support for Lanchester battles as a general rule for ant competition will support this theory. Second, comparative observations among native and non-native species at the site of an invasion will show whether non-native ants have a colony size advantage over native species.

Hypothesis 2, the role of a unique life history in the success of non-native ants, can be tested by comparing populations of non-native ants that represent different life histories. So far, Holway et al. (1998) have shown that intraspecific aggression reduced the success of non-native Argentine ants (*L. humile*), and polygynous fire ants (*S. invicta*) are more effective ecological invaders than monogynous fire ants (Porter and Savignano 1990; DeHeer and Tschinkel 1998). Much of the evidence for Lanchester battles can be applied to hypothesis 3, decreased worker size in the response to a lack of competition. In addition, laboratory experiments comparing isolated and cohabiting

colonies should demonstrate whether the disappearance of competition affects worker size. Hypothesis 4, associations between climate and worker size, can be supported by further macroecological studies (e.g., Kaspari and Vargo 1995) with field collections of colony sizes and worker sizes. Future experiments on the application of Lanchester battles to real-world systems and the effects of biogeography and competition on worker size distributions will determine whether small worker size is an important factor in the spread of non-native ants.

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