Research Note

Role of Propagule Size in the Success of Incipient Colonies of the Invasive Argentine Ant

JASON J. HEE, DAVID A. HOLWAY,* ANDREW V. SUAREZ, AND TED J. CASE

Department of Biology, 0116, University of California at San Diego, 9500 Gilman Drive, La Jolla, CA 92093–0116, U.S.A.

Abstract: *Factors that contribute to the successful establishment of invasive species are often poorly understood. Propagule size is considered a key determinant of establishment success, but experimental tests of its importance are rare. We used experimental colonies of the invasive Argentine ant (*Linepithema humile*) that differed both in worker and queen number to test how these attributes influence the survivorship and growth of incipient colonies. All propagules without workers experienced queen mortality, in contrast to only 6% of propagules with workers. In small propagules (10–1,000 workers), brood production increased with worker number but not queen number. In contrast, per capita measures of colony growth decreased with worker number over these colony sizes. In larger propagules (1,000–11,000 workers), brood production also increased with increasing worker number, but per capita brood production appeared independent of colony size. Our results suggest that queens need workers to establish successfully but that propagules with as few as 10 workers can grow quickly. Given the requirements for propagule success in Argentine ants, it is not surprising how easily they spread via human commerce.*

El Tamaño de Propágulos como Factor en el Éxito de Colonias Incipientes de la Hormiga Invasora Argentina

Resumen: *Los factores que contribuyen al establecimiento exitoso de especies invasoras son frecuentemente poco entendido. El tamaño del propágulo es considerado un factor clave del éxito del establecimiento, pero se han realizado pocas pruebas experimentales para determinar la importancia de este factor. Para estudiar cómo influyen estos atributos en la supervivencia y el crecimiento de colonias incipientes utilizamos colonias experimentales de la hormiga invasora argentina (*Linepithema humile*) distintas en cuanto al número de hormigas obreras como de reinas. Hubo mortalidad de reinas en todos los propágulos sin obreras y, en contraste, en solo 6% de los propágulos con obreras. En propágulos pequeños (10–1,000 obreras) la producción de crías incrementó con el número de obreras, pero no con el número de reinas. En contraste, las mediciones per capita del crecimiento de la colonia disminuyeron para estos tamaños de colonia. En propágulos grandes (1,000-11,000 obreras), la producción de crías también incrementó con el número de obreras, pero la producción de crías per capita parece ser independiente del tamaño de la colonia. Nuestros resultados sugieren que las reinas necesitan obreras para establecerse exitosamente, pero los propágulos con tan poco como 10 obreras pueden crecer rápidamente. Dado que son los requerimientos para el éxito de los propágulos de hormigas argentinas, no nos sorprende la facilidad con la cual estas hormigas se dispersan como resultado del comercio humano.*

**Address correspondence to D. A. Holway; email dholway@biomail.ucsd.edu*
Paper submitted January 22, 1999; revised manuscript accepted July 23, 1999.

Conservation Biology, Pages 559–563
Volume 14, No. 2, April 2000

Introduction

Biological invasions cause severe ecological and economic problems. Invasive species carry diseases, disrupt ecosystem processes, reduce biodiversity, and impose large economic costs (Vitousek et al. 1996; Wilcove & Chen 1998). Given these concerns, it is important to understand the proximate factors responsible for the success of harmful invasive species. One attribute commonly believed to influence the probability of establishment is propagule size (Ehrlich 1989; Lodge 1993). Despite its recognized importance, however, research on this topic has focused mainly on avian introductions (Case 1996; Duncan 1997) and biological control programs (Simberloff 1989); experimental studies of propagule size and establishment success are rare.

We investigated the role of propagule size as a determinant of establishment success in incipient colonies of the Argentine ant (*Linepithema humile* [Mayr]), a widespread invasive species. Now common throughout the world in areas with Mediterranean climates (Williams 1994), Argentine ants cause many ecological problems; perhaps most notably, they displace native ants (Hölldobler & Wilson 1990; Williams 1994). Because ants are important components of most ecosystems, the replacement of entire guilds of native ants by a single introduced species generates a variety of effects. These include the disruption of mutualisms (Bond & Slingsby 1984), declines in other arthropod taxa (Cole et al. 1992; Bolger et al. 2000), and reductions in vertebrate populations, such as those of the coastal horned lizard (*Phyronosoma coronatum*; Suarez et al. 2000).

Like other tramp ants (Passera 1994), Argentine ants possess several characteristics that make them proficient colonists. First, this species has general nesting and dietary requirements, allowing it to associate closely with humans (Newell & Barber 1913). Second, although workers are sterile, Argentine ant colonies typically have many queens (Newell & Barber 1913). Compared to single-queened colonies, this extreme polygyny increases the likelihood that a colony fragment will be reproductively viable. Finally, rather than occurring through nuptial flights, colony reproduction occurs primarily if not entirely by budding. This process entails queens leaving an established nest on foot with a group of workers to found a new nest elsewhere. Budding—and nest relocation more generally—allows Argentine ants to establish new nests opportunistically. Although these characteristics explain in part how Argentine ants have spread throughout the world via human commerce, the factors contributing to the survival of propagules following colonization are unknown.

We sought to determine the role of propagule size in the success of incipient Argentine ant colonies. By establishing laboratory colonies that differed in numbers of both queens and workers, we tested whether queens can successfully establish new colonies without the help of workers and how queen and worker numbers influence propagule growth.

Methods

We collected Argentine ants from Marian Bear Memorial Park, San Diego, California. We divided colony fragments into experimental colonies differing in numbers of queens and workers and reared experimental colonies in plastic nest containers lined with Fluon and Tanglefoot to prevent ants from escaping. Nest containers contained nest chambers (10-mL test tubes half filled with water and plugged with cotton) covered with aluminum foil. Colonies were fed sugar water ad libitum. Temperature was maintained at approximately 25° C throughout the experiment.

To determine the effect of queen and worker number on propagule survivorship and growth, we used a fully crossed two-way design. Experimental colonies contained 1, 3, or 5 queens and 0, 10, 100, or 1000 workers. Every treatment category was replicated four times. Each experimental colony occupied a plastic container (30 × 14 × 8 cm) with three nest chambers. We fed all colonies either one cricket or approximately 0.1 g of scrambled egg daily. We monitored colonies for queen mortality on an approximately daily basis. At the end of 2 months, we counted queens, workers, and brood. We used Fisher's exact test and multiple logistic regression to assess how worker number and queen number affect queen mortality. The dependent variable in the multiple logistic regression was whether queen mortality occurred in a replicate. We also used two-way analysis of variance (ANOVA) to compare total brood production, per capita brood production, and per capita growth rate across treatments; these data were log-transformed prior to analysis. We defined per capita brood production as the final number of brood (eggs, larvae, pupae) divided by the number of workers alive at the end of the experiment and per capita growth rate as final worker number divided by initial worker number.

In a second experiment, we investigated the effect of propagule size on brood production for colonies differing in size from 1000 to 11,000 workers. For each of eight experimental colonies, we added one queen for every 1000 workers. We reared these experimental colonies in plastic containers (31 × 46 × 28 cm) furnished with one nest chamber for every 1000 workers. Using 3 m of plastic tubing, we connected each nest container to a foraging container (30 × 14 × 8 cm) in which we placed food. Each day, we fed colonies either one cricket or approximately 0.3 g of scrambled egg for every 1000 workers. After 2 months, we counted the number of brood and surviving workers. We used simple linear regression to determine the relationship between colony size and final brood production. We also used simple linear regression to investigate the relationship between per capita brood production and colony size; this analysis is suspect, however, because the dependent variable contains the independent variable in its denominator. For all regressions, variables were log-transformed prior to analysis. The colonies of 1000 workers and one queen from our experiment on propagule success were included in these analyses, raising the total sample size to 12 experimental colonies.

Results

Queens in propagules without workers were more likely to die than those in propagules with workers (Fig. 1). Of propagules without workers, 100% (12/12) experienced some degree of queen mortality during the experiment, in contrast to only 6% (2/36) queen mortality in propagules with workers (Fisher exact test: $p < 0.0001$). Although the presence of workers influenced queen survival, the number of queens did not (Fig. 1; multiple logistic regression, $n = 48$: whole-model test $\chi^2 = 24.211$, df = 2, $p < 0.0001$; worker number Wald $\chi^2 = 5.999$, df = 1, $p < 0.014$, queen number Wald $\chi^2 = 0.945$, df = 1, $p = 0.33$). Moreover, queens from workerless propagules that survived failed to raise any new workers during the experiment.

Worker number positively influenced brood production, but queen number did not have a significant effect (Fig. 2; two-way ANOVA: worker number $F_{2,27} = 22.331$, $p < 0.0001$; queen number $F_{2,27} = 0.418$, $p > 0.50$; worker number × queen number interaction $F_{4,27} = 0.431$, $p > 0.50$). Both measures of per capita colony growth, however, decreased with increasing worker number (Fig. 3). Per capita brood production decreased with worker number but not queen number (Fig. 3a; two-way ANOVA: worker number $F_{2,27} = 22.047$, $p < 0.0001$; queen number $F_{2,27} = 0.418$, $p > 0.500$; worker number × queen number interaction $F_{4,27} = 0.431$, $p > 0.50$). Per capita growth rate also decreased with worker number but not queen number (Fig 3b; two-way ANOVA: worker number $F_{2,27} = 3.308$, $p = 0.052$; queen number $F_{2,27} = 1.891$, $p > 0.15$; worker number × queen number interaction $F_{4,27} = 1.185$, $p > 0.30$).

Brood production increased linearly with final colony size (Fig. 4; linear regression: $F_{1,10} = 13.43$, $p < 0.005$). The slope of this regression included a slope of one (95% confidence interval: 0.357–1.466), indicating that the per capita brood production and final colony size were independent of each other. Moreover, the regression of per capita brood production versus final colony size revealed no relationship between these two variables (linear regression: $y = -0.123 - 0.117x$, $F_{1,10} = 0.230$, $p > 0.50$, $r^2 = 0.02$).

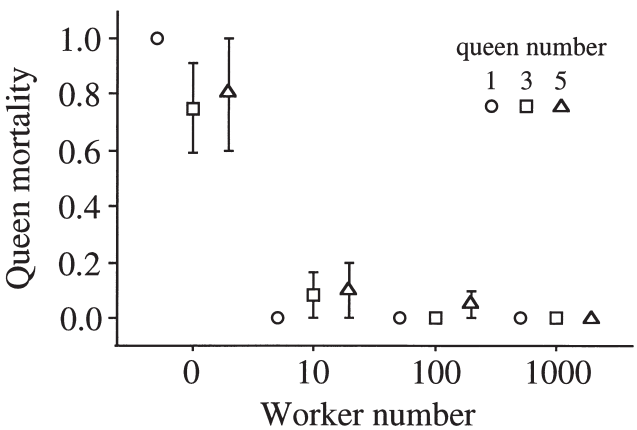

Figure 1. The effect of initial numbers of workers and queens on proportional queen mortality (mean ± SE) in Argentine ant propagules.

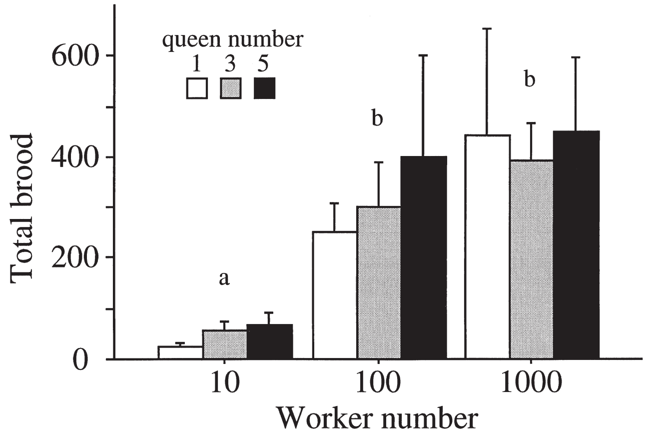

Figure 2. The effect of worker number and queen number on mean (±SE) brood production in experimental propagules of Argentine ants. Sets of bars with different letters indicate significantly different amounts of brood for the three categories of worker number (p < 0.05; Fisher's protected least-square difference). Queen number had no significant effect on brood production.

Discussion

Our results provide insight into the relationship between worker number, queen number, and brood production in incipient Argentine ant colonies. Queens were unable to produce new workers on their own, and most did not survive in the absence of workers, despite favorable laboratory conditions. This finding probably reflects the low fat content of Argentine ant queens, typical of ants that (like *L. humile*) undergo dependent colony founding (Keller & Passera 1989). Queens with as

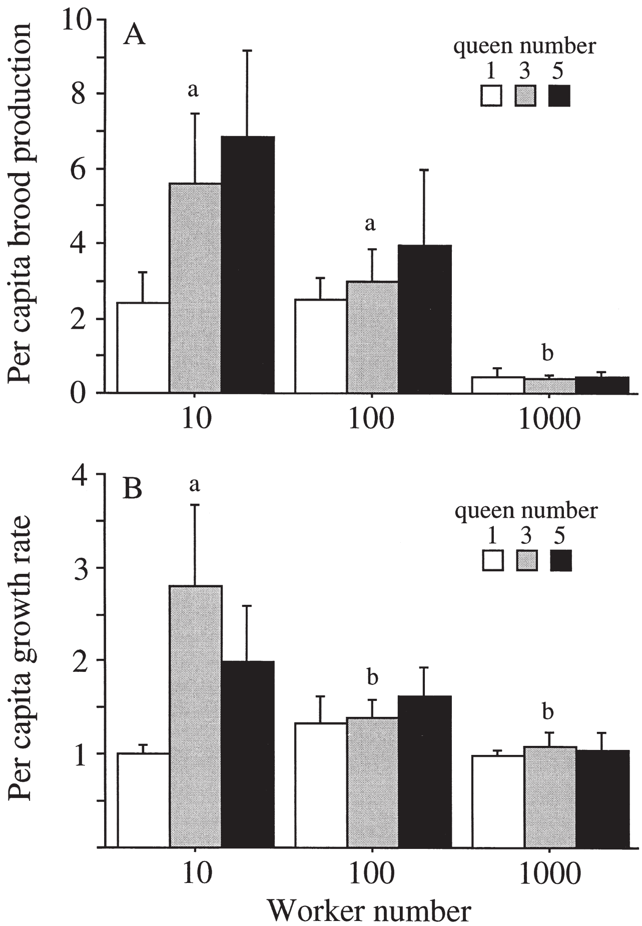

Figure 3. The effect of initial worker number and queen number on (a) mean (±SE) per capita brood production and (b) mean (±SE) per capita growth rate in experimental propagules of Argentine ants. Sets of bars with different letters indicate significantly different per capita measures of production for the three categories of worker number ($p < 0.05$; Fisher's protected least-square difference). Queen number had no significant effect on either per capita measure of production.

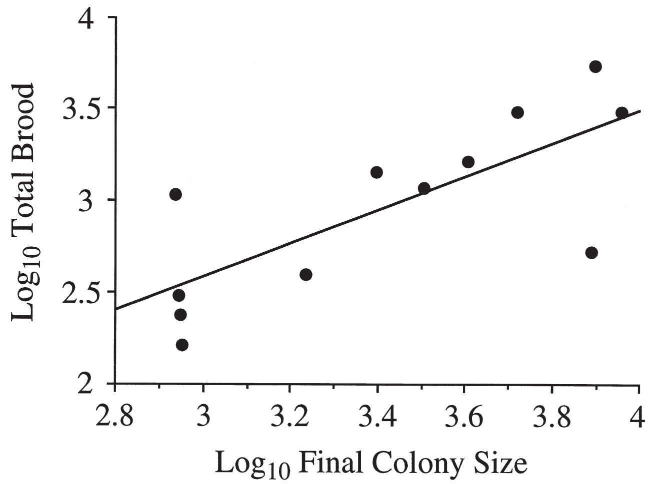

Figure 4. Relationship between colony size and brood production for incipient laboratory colonies of Argentine ants. Brood production scales log-linearly with colony size ($y = -0.149 + 0.912x$, $r^2 = 0.573$).

few as 10 workers, however, experienced high survivorship, and these propagules grew rapidly, in some cases tripling in size. These results provide insight into the minimum requirements for the establishment of this species and help explain why it is such a successful colonist. Given that the invasion dynamics of Argentine ants are driven by human-mediated dispersal, the success of small propagules as seen here illustrates how easily the transport of just a few individuals can result in the establishment of new foci.

Increasing the number of queens in small propagules did not increase overall brood production. The reduction of brood produced per queen in polygynous colonies has been documented in several ant species and could be the result of food limitation or queen suppression of reproduction (Hölldobler & Wilson 1990). In our propagule success experiment, worker number had a greater effect on brood production than did queen number. This is consistent with the hypothesis that brood production is limited by worker provision rather than the egg-laying capacity of queens. Multiple queens may be able to lay more eggs than single queens. If food is limiting, however, there may be only enough resources to feed a fixed amount of brood. Therefore, the egg-laying capacity of a colony may not be as important as the capability of a colony to provision the brood. Colonies in our second experiment were fed an amount of food proportional to their colony size and showed a linear increase in brood production. In addition, it is possible that queens are suppressing one another's reproduction. Queen suppression of reproduction is common in polygynous species (Hölldobler & Wilson 1990; Tschinkel 1998), although it has not been well investigated in Argentine ants.

Although per capita measures of colony growth decreased with worker number in small propagules (i.e., 10–1000 workers; Fig. 3), per capita brood production appeared unrelated to worker number among small colonies (i.e., 1,000–10,000 workers). The decline in per capita brood production with increasing worker number (Fig. 3a) is reminiscent of the "reproductivity effect" (Michener 1964). This negative trend disappears at larger colony sizes, similar to the result reported by Cole (1984) for *Leptothorax allardycei.* It is important to note that although our results apply over the span of colony sizes used in this study, the size of individual nests in nature can greatly exceed those used here (Newell & Barber 1913). Moreover, at least in their introduced range, Argentine ants form supercolonies made up of many interconnected nests and typically lack intraspecific aggression over many kilometers (Holway et al. 1998; Suarez et al. 1999).

We examined the intrinsic factors that influence establishment success in Argentine ants. Extrinsic factors, such as physical conditions and the competitive environment, must also influence the probability of establishment. Abiotic factors commonly influence establishment success in ants (Johnson 1998). This may be particularly true for Argentine ants because their distribution appears limited by moisture availability (Tremper 1976; Ward 1987). Although biotic resistance does not appear to influence the rate of spread of established populations (Holway 1998), it may influence the success of incipient Argentine ant colonies because numerical advantages appear key to their competitive ability (Tremper 1976; Holway 1999). More generally, it seems probable that factors determining establishment success are often different from those promoting spread. We advocate experimental approaches to test the relative importance of factors determining success at different stages of invasion.

Acknowledgments

We thank T. Walker of the San Diego Parks and Recreation Department for allowing us to collect Argentine ants in Marian Bear Memorial Park. This work was supported by U.S. Department of Agriculture postdoctoral fellowship 97-35302-4920 (D.A.H.), the Canon National Parks Science Scholars Program (A.V.S.), National Institutes of Health Cellular and Molecular Genetics training grant GMO 7240 (A.V.S.), National Science Foundation grant DEB-9610306 (T.J.C.), and a Research Experiences for Undergraduates supplement to DEB-9610306. The manuscript was improved by comments from R. Carroll, R. Johnson, and E. Main.

Literature Cited

Bolger, D. T., A. V. Suarez, K. R. Crooks, S. A. Morrison, and T.J. Case. 2000. Effects of habitat fragmentation and Argentine ants on arthropods in southern California. Ecological Applications **10:**in press.

Bond, W., and P. Slingsby. 1984. Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. Ecology **65:**1031–1037.

Case, T. J. 1996. Global patterns in the establishment and distribution of exotic birds. Biological Conservation **78:**69–96.

Cole, B. J. 1984. Colony efficiency and the reproductivity effect in *Leptothorax allardycei* (Mann). Insectes Sociaux **31:**403–407.

Cole, F. R., A. C. Medeiros, L. L. Loope, and W. W. Zuehlke. 1992. Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. Ecology **73:**1313–1322.

Duncan, R. P. 1997. The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. American Naturalist **149:**903–915.

Ehrlich, P. R. 1989. Attributes of invaders and the invading processes: vertebrates. Pages 315–328 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. Wiley, New York.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Harvard University Press, Cambridge, Massachusetts.

Holway, D. A. 1998. Factors governing rate of invasion: a natural experiment using Argentine ants. Oecologia **115:**206–212.

Holway, D. A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. Ecology **80:**238–251.

Holway, D. A., A. V. Suarez, and T. J. Case. 1998. Loss of intraspecific aggression in the success of a widespread invasive social insect. Science **282:**949–952.

Johnson, R. A. 1998. Foundress survival and brood production in the desert seed-harvester ants *Pogonomyrmex rugosus* and *P. barbatus* (Hymenoptera, Formicidae). Insectes Sociaux **45:**255–266.

Keller, L., and L. Passera. 1989. Size and fat content of gynes in relation to the mode of colony founding in ants (Hymenoptera; Formicidae). Oecologia **80:**236–240.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution **8:**133–137.

Michener, C. D. 1964. Reproductive efficiency in relation to colony size in Hymenopterous societies. Insectes Sociaux **11:**317–342.

Newell, W., and T. C. Barber. 1913. The Argentine ant. Bulletin **122.** Bureau of Entomology, U.S. Department of Agriculture, Washington, D.C.

Passera, L. 1994. Characteristics of tramp species. Pages 23–43 in D. F. Williams, editor. Exotic ants: biology, impact, and control of introduced species. Westview Press, Boulder, Colorado.

Simberloff, D. 1989. Which insect introductions succeed and which fail? Pages 61–75 in J.A. Drake, H.A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. Wiley, New York.

Suarez, A. V., N. D. Tsutsui, D. A. Holway, and T. J. Case. 1999. Behavioral and genetic differentiation between native and introduced populations of the Argentine ant. Biological Invasions **1:**43–53.

Suarez, A. V., J. Q. Richmond, and T. J. Case. 2000. Prey selection in horned lizards following the invasion of Argentine ants in southern California. Ecological Applications **10:**in press.

Tremper, B. S. 1976. Distribution of the Argentine ant, *Iridomyrmex humilis* Mayr, in relation to certain native ants of California: ecological, physiological, and behavioral aspects. Ph.D. thesis. University of California, Berkeley.

Tschinkel, W. R. 1998. The reproductive biology of fire ant societies. BioScience **48:**593–605.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist **84:**468–477.

Ward, P. S. 1987. Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the lower Sacramento River Valley and its effects on the indigenous ant fauna. Hilgardia **55:**1–16.

Wilcove, D. S., and L. Y. Chen. 1998. Management costs for endangered species. Conservation Biology **12:**1405–1407.

Williams, D. F., editor. 1994. Exotic ants: biology, impact, and control of introduced species. Westview Press, Boulder, Colorado.