

Do Lanchester's laws of combat describe competition in ants?

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Lanchester's laws are mathematical models, originally designed to model military combat, that describe battle outcomes based on the sizes of armies and the potencies of individual fighting units. The "square law" describes a scenario in which small-sized competitors may use a numerical advantage to overcome large-sized competitors in simultaneous combat. The "linear law" describes how a competitor with large-sized fighting units may use one-on-one combat to favor victory when outnumbered. Lanchester's laws have been suggested as an important regulator of interspecific competition in social insects, but without experimental support. In this study, experimental platforms were designed to invoke the conditions of both Lanchester's laws in a community of ants in lowland tropical wet forest in Costa Rica. I measured behavioral dominance at the food platforms in two separate manners: an ordinal ranking of the number of workers present, and the monopoly of the food platforms. At the platform invoking simultaneous combat, satisfying the square law, small-sized ants were more behaviorally dominant by numerical superiority. At the platform invoking one-on-one combat, satisfying the linear law, larger ants were more behaviorally dominant by monopoly. These results suggest that Lanchester's laws explain, in part, the outcome of interspecific competition in ants. *Key words*: Lanchester battles, ant, fighting, competition, foraging behavior, leaf litter, *Ectatomma*, *Pheidole*, *Solenopsis*, *Wasmannia*. [*Behav Ecol* 11:686–690 (2000)]

Ants may fight with one another during competition (Andersen and Patel, 1994; Carrol and Janzen, 1973; Gordon, 1988; Gordon and Kulig, 1996; Torres, 1984). While competing ants may fight for a variety of reasons, fighting and shows of force among ants at naturally occurring and experimentally placed food items are common (Adams and Trianello, 1981; Andersen, 1992; Brian, 1955; Davidson, 1977, 1998; Perfecto, 1994). The outcome of fighting events between ant colonies may result in a loss of the entire colony, relocation of a colony, loss of brood, or the inability to exploit a food resource (reviewed in Hölldobler and Wilson, 1990). Lanchester's laws of combat may characterize interspecific interactions among ants involving fighting or shows of force (Franks and Partridge, 1993, 1994; Lanchester, 1917; Whitehouse and Jaffe, 1996).

Lanchester's laws originated as mathematical models to predict successful air battle outcomes during World War I (Lanchester, 1917). Since then, these models have been used in operations research (e.g., Taylor, 1984) in addition to military scenarios (e.g., Lepingwell, 1990). This decade, Franks and Partridge (1993, 1994) applied Lanchester's laws to describe the evolution of body size in army ants and slave-making ants, and Whitehouse and Jaffe (1996) found that these laws correctly predict outcomes of intraspecific competition among leafcutting ants. Lanchester's laws have also been implicated in the worker size of non-native ants. Ant species that have established populations outside their native habitat generally have smaller workers than related ants that have not established non-native populations (McGlynn, 1999). Moreover, the difference in size is more pronounced among the ants that engage in fighting during interspecific competition (McGlynn, 1999). If Lanchester's laws apply to ant competition, then the small size of non-native ants may assist in com-

petition with other species as they spread into non-native habitats as the cost of native species.

Lanchester's laws of combat, as applied to fighting social insects, use the variables worker size and number of workers to determine which style of combat is more likely to result in victory. Lanchester's square law predicts that small sized ants will be more successful in large battles in which many workers are simultaneously interacting with one another in a single arena. The linear law describes the situation in which large sized workers can win battles against numerically superior colonies of small ants by fighting in one-on-one confrontations, such as in raids by slave-making ants (Franks and Partridge, 1993) and on shoots of plants. Franks and Partridge (1993) provide a detailed review.

Here I present a manipulative field experiment designed to determine whether Lanchester's laws correctly predict the outcome of interspecific fights among ants. Two types of food platforms were created to force ants to interact with one another under the conditions of the mathematical models. The platform to invoke the square law had a large opening for simultaneous confrontations, while the platform imposing the linear law contained a single opening to permit one ant at a time. Lanchester's square law predicts that small ants will be dominant at baits with large openings, while the linear law predicts that large ants will be dominant at the baits with small openings.

METHODS

I tested Lanchester's laws by modifying standard 50 mm plastic petri dishes into enclosed bait platforms (see Figure 1). The platform designed to invoke the square law featured a 5 mm high opening cut across 180 degrees of the side of the bottom portion of the dish. To invoke the one-on-one combat, I created a 5 mm circular hole in the side of the petri dish bottom portion, which allowed all ground-foraging ants to pass. I used forceps to place baits of ≈ 5 g of oil-packed tuna into the petri dish, and replaced the lid such that no ant of any size could enter the petri dish without using the opening. Tuna is a standard bait used in ant foraging experiments, representing an ideal food high in fat and protein (Hölldobler

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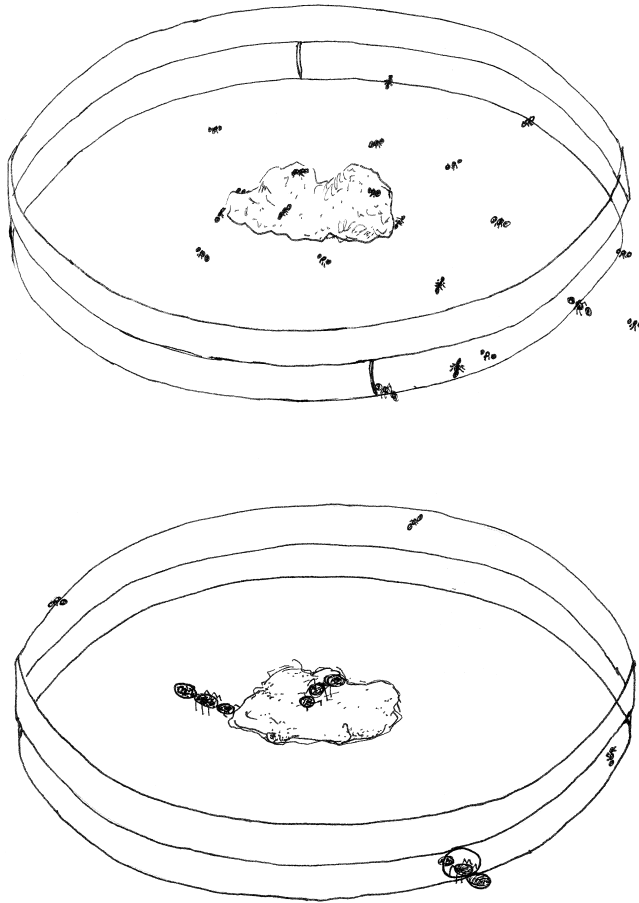


Figure 1
The modification of petri dishes into bait platforms creating interactions consistent with Lanchester's laws. The top dish with a 180 degree opening is consistent with the square law, and the bottom dish with a narrow entrance creates the conditions of the linear law.

and Wilson, 1990). I took precautions to assure that no oil residue would appear on the outside of the petri dish; when dishes were reused, they were washed with hot water and industrial cleanser. In addition, oil residue within the dish was kept to a minimum, so that small ants would not drown and remain in the petri dish prior to collection of the dish. When inclement weather reduced the number of foraging ants, I removed all of the baits without collecting data.

The experiment was conducted at La Selva Biological Station, located in a tropical wet forest located in the Caribbean lowlands of Costa Rica in Heredia Province, Sarapaquí Canton. La Selva receives approximately 4 m of rain annually, with the majority falling in the wet season between June and December (McDade and Hartshorn, 1994). The ecology of ants at this field site has been studied frequently (e.g., Alonso, 1998; Breed et al., 1990, 1992, 1999; Byrne, 1994; Kaspari, 1993, 1996a,b; McGlynn and Kelley, 1999; McGlynn and Kirksey, in press). This study was conducted during the dry season, from February to April 1997. All baits were placed in the Arboretum at La Selva, which has little understory vegetation and abundant leaf litter for the nesting of resource-defending ants. Ant nest densities ranged from 2–8 per square meter (McGlynn, unpublished data). Baits were placed along 45 m arbitrarily selected non-overlapping transects, with 10 baits per transect. Large holed and small-holed bait platforms were placed in alternating order 5 m apart on the transects, greater

Table 1
The occurrence of monopoly at platforms with small and large entry holes

Ant size	Small holed platform	Large holed platform	<i>p</i>
Small	6	7	ns
Medium	3	2	ns
Large	11	4	<.05

I compared the occurrence of monopoly between platform type within each group, by a chi-square test against an equal distribution of monopoly. $N = 40$ for each platform type.

than the foraging distance of the ants in this study (Kaspari, 1996a). A maximum of one transect was sampled per day. A total of 80 baits were used, with 40 of each platform type. All of the baits were placed between 9:30 and 11:30 am, and were collected two h after placement. This time period coincides with high levels of ant foraging activity (Kaspari, 1993). I collected baits by quietly approaching the platforms and rapidly covering with parafilm, keeping the ants inside. Many of the platforms contained ants on the exterior of the platform, often different species from those foraging on the bait inside. The field placement of the baits prevented complete collection of ants on the exterior, but many of those on the outside of the dish were trapped under a layer of parafilm wax. No ants entered the platform during collection, because the entrance to the platform was quickly covered. The platforms were frozen to kill the ants, and the number and species of the individuals inside the petri dish recorded. All ants were identified to species or morphospecies by the author (according to Bolton, 1994, 1995; Longino and Hanson, 1995, and the Ants of Costa Rica web pages by Longino at www.evergreen.edu/ants).

I used two measures of behavioral dominance at baits. The first measure of dominance was the number of foragers inside the bait platform. The number of ants at a food resource is associated with the amount of food that is returned to the colony (Bourke and Franks, 1995; Hölldobler and Wilson, 1990). I used standard abundance ranks for foraging ants (Alonso, 1998; Andersen and Patel, 1994). The second measure of behavioral dominance was the bait monopoly, the presence of only one species within the bait platform. The frequency of monopoly does not indicate the amount of food gathered, but does indicate that a species is successful at preventing its competitors from utilizing the bait item. The frequency of monopoly at baits (see Table 1) was tested using a chi-square test against a null hypothesis of equal occurrence of monopoly among baits. The relative abundance of ants was compared using logistic regression. Using only the small ants, I compared the distribution of abundance ranks of ants at the large holed baits with the distribution of abundance ranks at the small holed baits. I repeated the logistic regression separately for the medium-sized ants and the large-sized ants (see Figure 2).

RESULTS

The resource-defending ground-foraging ant community at this site was diverse and contained ants in three distinct size classes. Small-sized ants, less than 4 mm in length, nested primarily within the leaf litter. These myrmicine ants were generalized in food preference, and were most commonly *Pheidole* spp., *Wasmannia auropunctata*, and *Solenopsis (fugax group)* spp. The medium-sized ants were primarily ground-nesting *Pheidole* spp., which are greater than 5 mm in length.

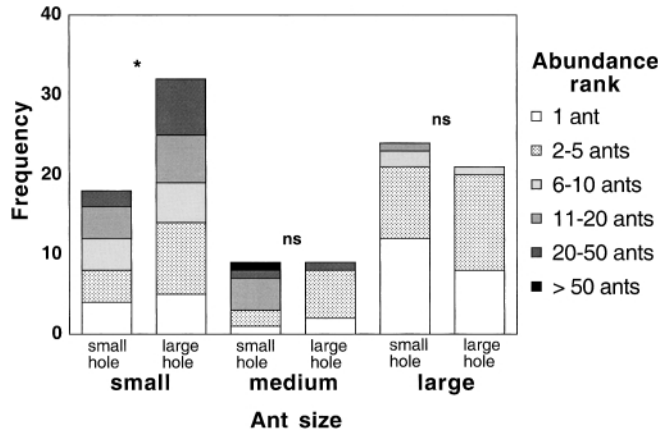


Figure 2
Abundance of ants at food platforms with small and large entry holes; *indicates $p < .05$ by logistic regression.

Occasionally, medium-sized arboreal ants (*Crematogaster* spp. and *Azteca* spp.) came down the trunks of canopy trees to forage at baits placed on the ground. The opportunist, *Paratrechina steinheili*, belonged in the medium-sized guild but rarely persisted at baits after competitors arrived. The large-sized guild contained ants over 1 cm in length. In another study, the large-sized extremely common ponerine *Ectatomma ruidum*, recruited to over 90% of the baits placed on the ground at this site (McGlynn, unpublished data). Less frequently occurring members of the large-sized guild include *Aphaenogaster araneoides*, *Pachycondyla* spp., and *Odontomachus* spp. A common opportunistic species, *Paratrechina steinheili*, was occasionally found dead at the baits, suggesting competitive exclusion.

The ants present at the baits after 2 h ranged over an order of magnitude in size. Minute ants less than 2 mm long often arrived at the same food items as the large ants, which were greater than 1 cm in length. Even though these ants are very different in size, they compete for the same resources found on the forest floor. In a previous study at this location, ants of all size classes were found interacting with one another at naturally occurring food items as well as artificial baits (Alonso, 1998).

Large-sized ants monopolized more small holed platforms than large holed platforms (see Table 1). In many instances of monopoly by large ants, a relatively small number of large ants occupied the small holed platform, while many other smaller sized ants were moving directly outside the platform. Occasionally, I found workers of the small species *Pheidole* and *Solenopsis* near the openings of the platforms monopolized by *E. ruidum*. There was no significant difference in the frequency of monopoly by smaller-sized ants, though small ants did monopolize the large holed platforms at a higher rate than the small holed platforms.

The significant difference in bait abundance was among the small-sized ants (see Figure 2). Small-sized ants were significantly more abundant at the large holed baits, though this was not observed for the large-sized ants. In most cases when a small ant was highly abundant in a platform, fewer than five heterospecific individuals shared the platform. Even though these small ant species rarely monopolized platforms, the small ants were not openly sharing the food items with neighboring colonies. The design of the large-hole platform with a 180 degree opening permitted recruiting species to interact with one another more frequently than found at open baits with full 360 degree availability.

Many of the monopolized platforms contained different

species in and outside. The frequent proximity of some species to food while only one species acquired food suggests that the exterior ants were aware of the food, but either lost or had not attempted a confrontation.

DISCUSSION

The results qualitatively supported the application of Lanchester's laws to the biology of ants. Small ants were more successful in the large holed platforms, and large ants were more successful in the small holed platforms. The results did not show that small ants were the only ants feeding in the large holed platforms, nor did large ants exclusively feed within the small holed platforms. Even though ants of any size had the capability of feeding upon the bait regardless of platform, the significant differences in behavioral dominance at the bait platforms are consistent with predictions of Lanchester's laws. The prediction for dominance of large ants at small holed baits was observed in monopoly but not abundance, while the dominance of small ants at large holed baits was observed in abundance but not monopoly. The two ways ants achieved behavioral dominance reflects differences in the foraging biology of the large ants and the small ants.

It makes sense that large-sized ants were behaviorally dominant by means of monopoly but not by abundance. The most common large species was *Ectatomma ruidum*, which has a well-studied foraging biology (e.g., Breed et al., 1990, 1992; Lachaud, 1995; Perfecto, 1993; Schatz et al., 1994). *E. ruidum* colonies rarely recruit more than a dozen workers to high quality carbohydrate or protein baits, regardless of distance from the nest (Breed et al., 1999; personal observations). I recorded (see Figure 2) only a single instance of large ants recruiting more than 10 workers to bait, which was 11 *E. ruidum* workers completely filling a small holed platform. Thus large ants like *E. ruidum*, *A. araneoides*, and *Odontomachus* spp. rarely demonstrate numerical superiority. Yet their large size permits them to monopolize platforms, by excluding other ants and occasionally destroying intruders. *E. ruidum* nests in the ground and forages within litter, but I often have observed this species foraging on understory plants and feeding at extrafloral nectaries, interacting with other ants: such linear arenas facilitate one-on-one interactions.

Small-sized ants can show numerical superiority at large holed baits, but frequently fail to monopolize these baits. This finding is sensible in light of our knowledge of the foraging biology of these species. Unlike *E. ruidum*, the litter-nesting colonies of *Pheidole* spp., *Solenopsis* spp., and *Wasmannia auropunctata* often send out the majority of a colony's workers to obtain food from high quality baits (Byrne, 1994; personal observations). In many cases, two or more species cohabited bait platforms, though the vast majority of workers belonged to a single species. In these cases a colony would not be monopolizing a bait item, but still would take most of the food at the bait back to its nest. The colonies always inhabited separate portions of the platform, with clear separation among foraging areas, even though individuals did interact with one another frequently. Fighting with other colonies is energetically expensive and the presence of many workers is often enough to prevent another colony from removing much food from the area. Other studies have shown that the initiator of an interspecific confrontation usually wins without a fight (Brian, 1955; Human and Gordon, 1999).

Factors other than Lanchester's laws to explain why certain ants are successful at bait items have been studied extensively (reviewed by Carrol and Janzen, 1973; Hölldobler and Wilson, 1990). These factors include the territoriality and aggressiveness of the species, nutritional needs of the colony, time of year, time of day, distance between the food and nest, and

intensity of competition. In previous studies in similar sites, such factors have affected foraging behavior significantly (Kaspari, 1993; Levings and Windsor, 1984). I suggest that when all of these other factors are equal, Lanchester's laws impact the outcome of ant competition. An important caveat is that although Lanchester's laws reflect competition in this diverse and densely populated Costa Rican leaf litter community, areas with fewer species or lower nest densities may present different results.

The fact that non-native ant species are significantly smaller than the mean size of congeneric species (McGlynn, 1999) is fascinating in light of Lanchester's laws. Behavioral dominance at food items is an important mechanism in the success of non-native ants (e.g., Clark et al., 1982; Crowell, 1968; Haskins and Haskins, 1965; Holway et al., 1998; Human and Gordon, 1996; Lieberburg et al., 1975; Porter and Savignano, 1990). Non-native ants are small in size, particularly successful at rapidly recruiting workers to food items, and often monopolize foods from native species (Holway, 1999; Williams, 1994). Likewise, non-native ants are smaller in size than the native ants in the locations where invasions have occurred (Holway et al., 1998). The application of Lanchester's laws may be important in understanding the ability of non-native species to overcome their native competitors. As a practical recommendation for insect control, I recommend that platforms delivering toxic bait to non-native ants be designed with large openings for interspecific competition, which will favor food delivery to large colonies of small-sized non-native species.

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