

Territoriality in ants (Hymenoptera: Formicidae): a review

Eldridge S. ADAMS



Abstract

Territory defense by ants is a social process with strong ecological effects. I review the mechanisms by which ants partition space, the behaviors governing individual and colony territorial responses, and the effects of territory defense on populations and communities. Partitioning of space is sometimes accomplished by massive battles, but well defined boundaries are also maintained by less violent means, including avoidance of competitors. Ants flexibly adjust individual and group territorial behavior according to location, scent marks, prior experience, and the local density of nestmates and competitors. An ongoing theoretical challenge is to incorporate these processes into models that accurately predict division of space. Many studies have documented strong effects of territorial interactions on the growth, movement, survival, reproduction, and spacing of competing colonies. Far fewer studies have measured the net effect of territoriality on population dynamics. Fighting can be costly, but there is little evidence that it appreciably reduces worker density or that loss of territoriality promotes the invasiveness of exotic ants. Territorial ants are said to be at the top of competitive hierarchies that structure ant communities. Because much of the evidence is based on correlations, some claims about the community effects of territoriality have met with skepticism. Nonetheless, there is strong evidence from diverse habitats that territory defense produces multi-species mosaics of exclusive foraging areas and that territorial dominants influence the occurrence of some other ant species.

Key words: Aggression, ant mosaic, community structure, dear enemy, invasive ants, Lanchester's square law, review, spatial pattern, territory.

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Eldridge S. Adams, University of Connecticut, Department of Ecology and Evolutionary Biology, Storrs, CT 06269-3043, USA. E-mail: eldridge.adams@uconn.edu

Introduction

Territory defense is one of the most remarkable collective actions performed by insect colonies and one with particularly strong ecological effects. Thousands of insects from a single colony can deploy themselves over large expanses, attacking or repelling intruders, and recruiting reinforcements as needed to keep the foraging area nearly free of competitors (HÖLLDOBLER & WILSON 1990). Territoriality is the strongest form of competition between colonies and a major force shaping the evolution of cooperation, communication, and caste. Struggles over the control of space shape colony demography and population dynamics, and impose restrictions on the co-occurrence of species.

Territoriality is monopolization of space achieved by aggression, signaling, and avoidance. The degree of monopolization and the amount of fighting needed to enforce it vary widely among species; territoriality grades smoothly into other forms of competition. Ant biologists typically consider territorial species to be only those that defend a spatial domain extending beyond the nest and food sources (LEVINGS & TRANIELLO 1981, HÖLLDOBLER & WILSON 1990). Here, I review foundational studies and recent advances in understanding both behavioral and ecological aspects of territoriality. First, I describe well studied examples that illustrate the role of fighting, vigilance, and avoidance in partitioning of space. Second, I outline the

major behavioral mechanisms by which territory defense is controlled. Several recent issues are emphasized, including whether colonies adjust aggressiveness towards familiar neighbors, how force ratios affect mortality during battles, and how aggressiveness depends on circumstances. Finally, I discuss the effects of territory defense on population and community ecology.

How interactions between colonies partition territory space

In an influential synthesis, HÖLLDOBLER & LUMSDEN (1980) distinguished three types of territories: (1) absolute territories, in which the entire foraging space is defended regardless of where food is currently present, (2) trunk trail territories, in which defense is concentrated around long-lasting trails, and (3) spatiotemporal territories, in which defended regions shift from day to day according to where ants are foraging. Boundaries are most clearly defined in species with absolute territories. An example is shown in Figure 1, which reproduces part of GREENSLADE's (1975a) map of a population of the meat ant *Iridomyrmex purpureus*. To determine the limits of each colony's foraging area, Greenslade traced foraging columns, observed movements of individual foragers, and – in regions with sparse activity – placed baits and followed ants back to their nests.

Confrontations broke out where adjacent territories met. Intense struggles may re-occur at the same locations for years (GREENSLADE 1975b) or gradually advance towards declining colonies (ETTERSHANK & ETTERSHANK 1982).

Space is partitioned in three main ways: by fighting, guarding, and avoidance. The importance of these mechanisms varies among species.

The role of fighting: Organized aggression is the most conspicuous mechanism by which ants partition space. Mass battles have attracted the attention of writers from Henry David THOREAU (1854) to Pope Pius II (RÉAUMUR 1926) and have inspired some of the most vivid prose of academic writers. The propensity of ants to kill each other during these struggles varies greatly. In *Iridomyrmex purpureus*, encounters are typically restricted to ritual display, but they can also erupt into fierce fighting (ETTERSHANK & ETTERSHANK 1982, VAN WILGENBURG & al. 2005). During battles among leaf-cutting ants in the genus *Atta*, hundreds of ants grapple but few die (ROCKWOOD 1973). In other species mortal fighting is common (e.g., BROWN 1959, THOMAS & al. 2006, PLOWES & al. 2014).

The causes of battles and their effects on boundaries have been studied in detail in populations of wood ants (genus *Formica*). The remarkable work of MABELIS and others on *Formica polyctena* established the seasonal cycle by which boundaries form and move (DE BRUYN 1978, MABELIS 1979, DRIESSEN & al. 1984, MABELIS 1984, CZECHOWSKI & al. 2013). As temperatures rise in the spring, ants begin to forage, extending their main trails until they encounter workers from neighboring colonies. Wars break out in which ants die by the tens of thousands (MABELIS 1979). Nestmates are attracted to conflicts by the "war scent" of chemicals sprayed onto opponents, by pheromone trails leading back to the nest, and by tactile and visual cues. Battles drive dramatic shifts in territory boundaries and can kill whole colonies (DE BRUYN 1978, MABELIS 1979, DRIESSEN & al. 1984).

In the aftermath of a battle, *Formica polyctena* produce a "no-ant's zone" where ant abundance is low and baits may remain unvisited. From time to time, opponents meet in this zone and fight in small numbers. By following movement and prey retrieval by marked ants, DE BRUYN (1978) and MABELIS (1979) showed that boundaries are fairly sharp, with little intermixing of non-nestmates, and are reinforced by spatial memory. Ants are more aggressive to intruders within their own territory and do not often enter the foraging space of neighbors. In the autumn, aggressiveness towards non-nestmates declines, allowing some overlap of foraging areas (DE BRUYN 1978, MABELIS 1979).

MABELIS (1979) proposed that territorial battles in *Formica polyctena* are intimately related to predation. Ants killed in battle are consumed and constitute the vast majority of the prey in early spring when other sources of protein are scarce (DRIESSEN & al. 1984). Later in the year, when other insect prey is plentiful, contacts between neighbors become less frequent and less aggressive (DE BRUYN 1978, MABELIS 1979, 1984). Thus, neighbors fight when the demand for food exceeds supply. DRIESSEN & al. (1984) concluded that "battles between colonies can be regarded as an exchange of food, stored in the form of individuals".

Border guards: Ants that are capable of massive battles may avoid them by establishing guards at key points of contact with neighbors. Several tropical arboreal spe-

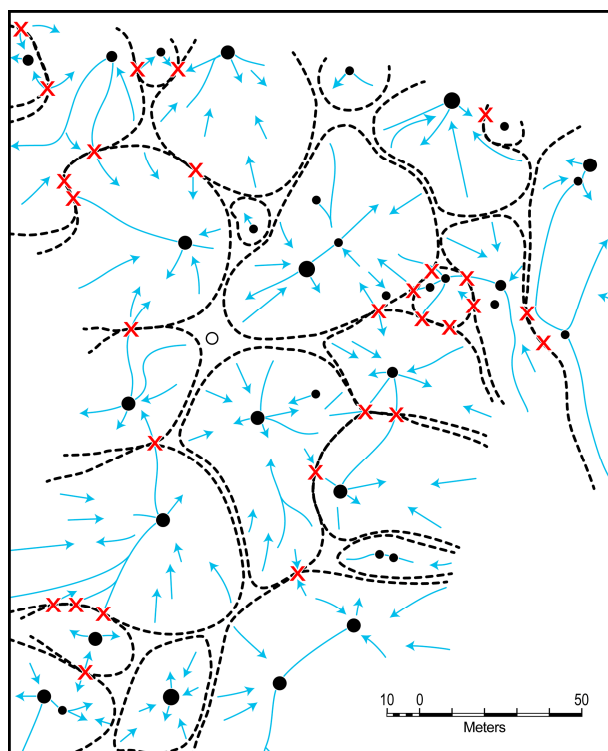


Fig. 1: Territories in a population of *Iridomyrmex purpureus* (see GREENSLADE 1975a). Boundaries (dotted lines) were determined by observing forager movement and the locations of confrontations (red crosses). Nest positions are shown by solid circles, an abandoned nest by an open circle, major trails by blue lines, and movement of foragers by arrows. Modified with permission from CSIRO Publishing (<http://www.publish.csiro.au/nid/90/paper/ZO9750495.htm>).

cies make use of guards, including the weaver ants *Oecophylla longinoda* and *O. smaragdina* (see HÖLLDOBLER 1979b, 1983), *Azteca trigona* (see ADAMS 1990a, ADAMS 1994), and the giant forest ant *Dinomyrmex gigas* (= *Camponotus gigas*; see PFEIFFER & LINSINMAIR 2001). Border guards are maintained at narrow constrictions provided by branches that connect trees, or at the bases of trunks where intruders approach from the ground. The guards remain on constant alert, often in defensive postures (Fig. 2), facing across a gap towards defenders on the other side. Ants occasionally advance towards the opposing group; upon contact they flee or fight or are caught and killed (ADAMS 1990a, PFEIFFER & LINSINMAIR 2001). A striking characteristic of these arboreal ants is that large battles are easily triggered by artificially forcing neighbors to intermix, yet such battles are absent or rare in natural circumstances. Guards deter intrusion by attacking enemy scouts, preventing them from discovering resources in the territory interior.

The role of avoidance: Borders can be produced and maintained with little or no fighting by any mechanism that strongly inhibits ants from entering a neighbor's territory, including avoidance of non-nestmates or foreign scent-marks. HAERING & FOX (1987) demonstrated the role of avoidance in mosaics of territories produced by two species of *Iridomyrmex*. Ants that were picked up and placed on their own side of a boundary wandered in the



Fig. 2: Border guards of *Azteca trigona* facing across the no-ant's land towards a competing group on the other side. Photograph by Eldridge Adams.

usual manner of foragers. Ants released 15 to 60 cm into the neighboring colony's territory were progressively more likely to run back to their own side, evading confrontations. These timid responses were sufficient to maintain division of space.

Avoidance underlies absolute territories in other ants as well. In more than a decade of work on territories of the fire ant *Solenopsis invicta*, I rarely saw naturally occurring battles. Battles developed only when large food items were fortuitously discovered by two colonies near their mutual boundary or when mature colonies attacked and killed much smaller nests (ADAMS 2003). On other occasions, the workers avoided neighbors or fought briefly in scattered pairs. Vacuum sampling of foragers reveals a zone of low worker density near the boundary (TSCHINKEL 2011). Yet populations of *S. invicta* and territorial *Iridomyrmex* produce well-defined territory mosaics that fill suitable habitat, and colonies quickly occupy space abandoned by their neighbors (WILSON & al. 1971, HAERING & FOX 1987, ADAMS 1998, 2003).

Trunk trails and foraging columns: Seed harvesting ants exemplify territory defense that is centered on foraging trails. In several species of *Pogonomyrmex*, *Messor*, and *Veromessor*, foraging and defense are clustered around major trails that channel the ants into particular sectors (e.g., HÖLLDOBLER 1976a, GORDON 1991, PLOWES & al. 2013). The territory can be depicted as a set of moveable arms radiating from a core area surrounding the nest (Fig. 3). Foraging columns are temporary, while trunk trails may persist for months.

The spatial configuration of major trails shapes competition among neighbors. Each day, the colony chooses among a pre-existing set of long-lasting trails (GORDON 1991, GREENE & GORDON 2007) or organizes new foraging columns leading in different directions (e.g., PLOWES & al. 2014). Workers leave the nest along these routes and then depart from them to search individually. Competitive encounters occur primarily where the tip of one colony's trail comes into contact with the trail of a neighboring colony (HÖLLDOBLER 1976a, GORDON & KULIG 1996, BROWN & GORDON 2000). Away from the nest and major trails, foraging areas may overlap and aggression is less intense (HÖLLDOBLER 1976a). When workers from different colonies meet, they may avoid one another or they may grapple and bite; a minority of encounters lead to in-

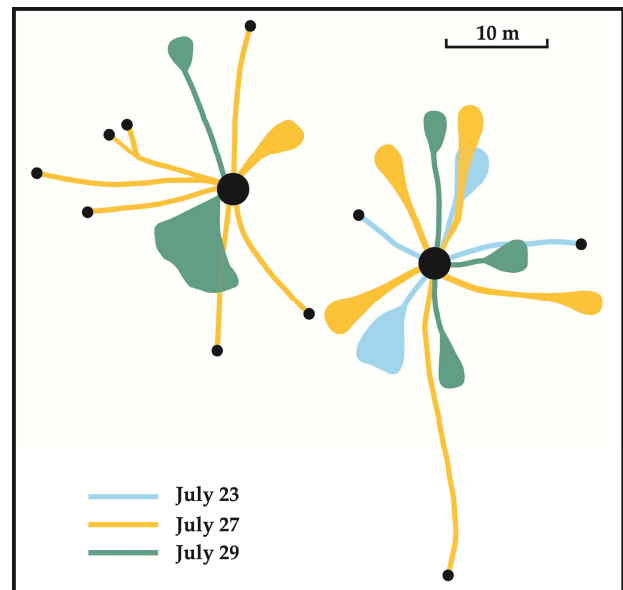


Fig. 3: Foraging trails of two neighboring colonies of *Pogonomyrmex barbatus*. Nest positions are shown by large solid circles; small circles represent shrubs. After trails of the two colonies met on July 27, both colonies selected trails leading in other directions. Redrawn from (GORDON 1991); copyright University of Chicago Press; reproduced with permission.

jury or death for one or both ants (HÖLLDOBLER 1976a, DE VITA 1979, GORDON & KULIG 1996, PLOWES & al. 2014). Larger conflict involving hundreds of skirmishes can last for hours or days (HÖLLDOBLER 1976a, BROWN & GORDON 2000, PLOWES & al. 2014).

HÖLLDOBLER (1976a) hypothesized that trunk trails function to divert foragers from neighboring colonies into different regions, reducing fighting. Trunk trails often point away from those of adjacent colonies, as if they were laterally repulsed (HÖLLDOBLER & LUMSDEN 1980, HARRISON & GENTRY 1981). Yet some trunk trails lead ants directly towards foraging paths or nests of neighbors, producing regions in which fighting is more common (HÖLLDOBLER 1976a), and colonies may continue to use trails that lead to fights for many days running (GORDON 1991). Is there a net tendency for major foraging trails to avoid areas foraged by competitors? Nearest neighbor pairs of *Veromessor pergandei* (= *Messor pergandei*) showed a marked tendency to forage away from each other and were slower to exploit seed baits placed in the direction of competing nests (RYTI & CASE 1986). Similarly, trunk trails of *Messor barbarus* were less likely to occur in radial sectors containing a nest entrance or trunk trail of an alien colony (ACOSTA & al. 1995).

In the short run, competitive encounters can either inhibit or promote foragers returning to the site of a conflict. On the one hand, aggressive confrontations may deter foraging. Workers of *Pogonomyrmex californicus* stayed in the nest longer after being forced to grapple with a competitor than if they were merely prodded with a pair of forceps (DE VITA 1979). When a foraging column of *Veromessor pergandei* impinges on another colony's column, fights ensue that result in injury or death to hundreds or thousands of workers; colonies are less likely to organize

foraging columns the day after a fight than on other days (PLOWES & al. 2014). Aggressive encounters can reconfigure trail use, causing colonies to withdraw or to reposition their trails (HÖLLDOBLER 1976a) or to select different trails on the next day (GORDON 1991). But the opposite trend has also been documented. Both observational and experimental methods showed that colonies of *Veromessor andrei* (= *M. andrei*) were more likely to return to a site the day following encounters with competitors (BROWN & GORDON 2000). Either way, competitive interactions constrain foraging areas. When colonies die, are removed, or are trapped within their nests by metal barriers, their neighbors soon advance into the vacated territory (HÖLLDOBLER 1976a, HARRISON & GENTRY 1981, GORDON 1992a). Studies on *Pogonomyrmex barbatus* have shown that colony age affects the outcome of these competitive interactions (GORDON 1991, 1992a, GORDON & KULIG 1996). When trails intersect, young colonies are particularly likely to fight while older colonies are more likely to respond by foraging in another direction the next day (GORDON 1991; Fig. 3). Colonies of intermediate age gained more territory than older colonies when neighbors were enclosed and kept more of it when the enclosures were removed.

Transient territories: HÖLLDOBLER & LUMSDEN (1980) distinguished "spatiotemporal territories" from territories that are more consistently demarcated. Spatiotemporal territories are transient, with limits that are identifiable only in places where two colonies temporarily come into conflict. This concept was developed to describe defense of space by the honey ant *Myrmecocystus mimicus*, a species that organizes bursts of recruitment to places where termite prey have been discovered (HÖLLDOBLER 1981). If ants from another colony are encountered in the vicinity of the prey, additional workers are recruited. Opponents engage in ritualized tournaments in which ants stand on stilt legs and antennate the abdomens of their opponents (HÖLLDOBLER 1976b, 1981). The positions of tournaments change from day to day, sketching partial outlines of changeable territories (Fig. 4). In addition, colonies of *M. mimicus* maintain small groups of guards from dawn to dusk at particular locations whose displays cause intruders to withdraw (HÖLLDOBLER 1981).

Behavioral control of territory defense

Ant territory defense is a social process. The main behaviors shaping the partitioning of space are recognition, communication, fighting, avoidance, and assessment. In both theoretical and empirical work, there has been a gradual shift from a focus on how individual colonies organize defense to a focus on interactions between colonies and how territory division emerges from individual and group behavior.

Recognition: Territory defense relies on an ability to distinguish colony members from outsiders. The mechanisms of nestmate recognition in ants have been studied in detail (reviewed by D'ETTORE & LENOIR 2009, HÖLLDOBLER & WILSON 2009, STURGIS & GORDON 2012). Identification of non-nestmates is based primarily on odors, which are affected by both environmental and genetic variation. Odors are well mixed within colonies, reducing errors in nestmate recognition, but individuals differ in their ability to detect non-nestmates and in their actions when

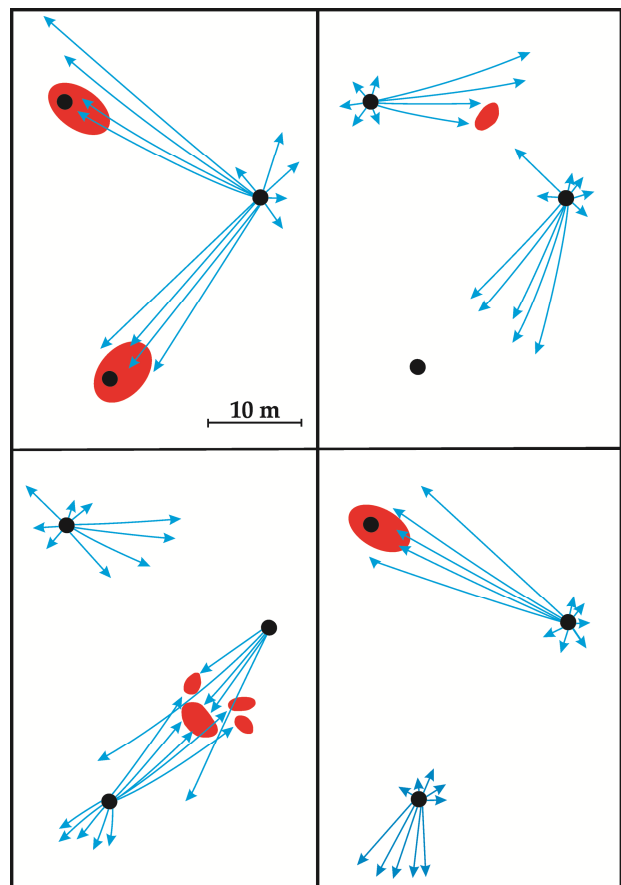


Fig. 4: Changes in the foraging routes (arrows) and tournament areas (shaded ovals) of three colonies of the honey ant *Myrmecocystus mimicus* over a period of three weeks. Nest positions are shown by solid circles. With kind permission from Springer Science + Business Media: HÖLLDOBLER, B. 1981. Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus* WHEELER (Hymenoptera: Formicidae). Behavioral Ecology and Sociobiology 9: 301-314, Fig. 8, modified with permission from the author. Copyright Springer-Verlag.

they do (NEWHEY & al. 2010a). The degree of antagonism shown towards particular alien colonies varies substantially both within and among species (e.g., HÖLLDOBLER 1979b).

The role of learning: neighbors and strangers: Do social insects colonies respond differently to neighbors and strangers? Every pattern has been reported: stronger reactions to neighbors (e.g., GORDON 1989, THOMAS & al. 2007, VAN WILGENBURG 2007, NEWHEY & al. 2010b, BENEDEK & KÓBARI 2014), stronger reactions to strangers (e.g., HEINZE & al. 1996, THOMAS & al. 1999, TANNER & ADLER 2009, DIMARCO & al. 2010), and lack of evidence for either trend (e.g., BOULAY & al. 2007).

Investigators frequently invoke evolutionary explanations based on presumed costs and benefits. Either neighbors or strangers could be the greater threat: neighbors because of their proximity (e.g., GORDON 1989, NEWHEY & al. 2010b, BENEDEK & KÓBARI 2014), strangers if they are the vanguard of a migrating colony (HEINZE & al. 1996, LANGEN & al. 2000). In some species, colonies that are closer together are more closely related (e.g., BEYE & al.

1998), which could favor lower aggression (LANGEN & al. 2000). Yet the status of these explanations is uncertain: It is difficult to test whether colonies that react more strongly to neighbors or strangers obtain fitness benefits from making those distinctions. Furthermore, there are plausible proximate reasons for these patterns that do not require strategic considerations (LANGEN & al. 2000). Recognition errors may be more likely among neighboring colonies because they are genetically similar (PIRK & al. 2001) or share more similar nest materials (HEINZE & al. 1996).

Experimental studies have convincingly demonstrated that learning shapes reactions to neighbors. Repeated exposure can sensitize ants to enemies, resulting in higher aggression (SANADA-MORIMURA & al. 2003, GILL & al. 2012). THOMAS & al. (2007) measured aggression between workers from adjacent colonies of the Argentine ant, *Linepithema humile*. Ants collected from nests very near the boundary were more aggressive to neighbors than ants collected from nests deep within the interiors of the same territories. In the lab, exposure to unfamiliar colonies led to an increase in aggression that faded when exposure ceased. Even a single encounter with a non-nestmate can elevate the aggressiveness of individual ants in subsequent encounters with conspecifics (VAN WILGENBURG & al. 2010). But other species show the opposite spatial and behavioral pattern: Aggression is higher among nests that are more widely separated, and ants become less hostile to non-nestmates after repeated contact (LANGEN & al. 2000, TANNER & KELLER 2012).

The low replicability of conclusions about neighbor-stranger discrimination raises concerns. At least four species of social insects have been studied by independent groups of investigators, yielding nearly opposite conclusions: *Iridomyrmex purpureus* (see THOMAS & al. 1999, VAN WILGENBURG 2007), *Formica pratensis* (see BEYE & al. 1998, PIRK & al. 2001, BENEDEK & KÓBARI 2014), *Oecophylla smaragdina* (see NEWEY & al. 2010b, GILL & al. 2012), and the territorial termite *Nasutitermes corniger* (see DUNN & MESSIER 1999, ADAMS & al. 2007). The methods used by different researchers differ and responses may vary with circumstances, but the low consistency suggests that chance differences in aggression can be mistaken for systematic patterns. For example, in a study on neighbor / stranger discrimination in a termite, DUNN & MESSIER (1999) used inappropriate criteria for determining which colonies were neighbors and violated assumptions of independence in their statistical analysis (ADAMS & al. 2007). Good practices help to distinguish signal from noise: using groups of workers rather than a single worker from each colony in assays of aggression (ROULSTON & al. 2003), blind tests (e.g., THOMAS & al. 2007, VAN WILGENBURG 2007), directly determining which territories abut in the field (e.g., DIMARCO & al. 2010), and using statistical models that account for multiple uses of the same colony (e.g., GILL & al. 2012).

Recruitment: Territoriality cannot be understood without understanding recruitment, the process by which ants bring their nestmates to the sites of conflicts (HÖLLDOBLER & WILSON 1990). The signature accomplishment of behavioral research on ant territoriality in the 1970s and 1980s was to establish the diverse mechanisms of recruitment used by species with contrasting ecological demands

(reviewed by HÖLLDOBLER 1979a, HÖLLDOBLER & LUMSDEN 1980, BRADSHAW & HOWSE 1984). Recruitment rapidly magnifies the local fighting ability of the colony in response to detection of competitors.

Two main kinds of chemical communication are used to organize recruitment during conflicts: alarm pheromones and trail systems. Both have evolved multiple times, co-opting various glands as the anatomical sources of pheromones (HÖLLDOBLER & WILSON 1990). Alarm pheromones are released into the air or streaked on the substrate, spread and fade quickly due to low molecular weight, and are used to alert and attract nestmates over distances of a few centimeters (HÖLLDOBLER & WILSON 1990). The constituent chemicals diffuse at different rates, producing an "active space" within which the concentration is high enough to trigger behavioral reactions. Responses include rapid movement, attraction, alarm postures, and biting; the choice depends on pheromone concentration (BRADSHAW & HOWSE 1984). Trail communication can attract even greater numbers of nestmates over longer distances. The same pheromones are used for trail-laying to enemies and food but, during conflicts, scouts may combine alarm pheromones with trail communication and may use additional tactile or motor displays (e.g., HÖLLDOBLER & WILSON 1978, ADAMS 1994). Victory in battle can depend on recruiting reinforcements faster than the opponent (ADAMS 1990a).

Mechanisms of fighting: Fighting behavior balances attack and defense: Workers try to inflict harm while protecting themselves. Ants kill by using their mandibles to crush or sever body parts, by stinging, and by inserting, applying, or spraying chemicals (HERMANN & BLUM 1981). Nestmates may join the attack, spread-eagling opponents (e.g., FLUKER & BEARDSLEY 1970, MERCIER & al. 1997) or forming clusters of interlocking ants (e.g., ROCKWOOD 1973, LANGEN & al. 2000). Especially in colonies with large worker forces, the low reproductive potential of workers makes them disposable (PORTER & JORGENSEN 1981). Worker ants are therefore more prone than solitary animals to risk injury. However, even in highly territorial species, fighting ants maneuver so as to reduce their own risks, circling, dodging, or appeasing opponents (e.g., HÖLLDOBLER & WILSON 1978, MERCIER 1999), fleeing or becoming immobile to escape attack (e.g., HAERING & FOX 1987, NOWBAHARI & al. 1999). Fighting behavior can become ritualized to serve as a signal between individuals or groups (LUMSDEN & HÖLLDOBLER 1983). For examples, rival ants may stand erect ("stilting") and box with the front legs (ETTERSHANK & ETTERSHANK 1982). The concept of ritualization is invoked when agonistic behavior is stereotyped and non-fatal (HÖLLDOBLER 1976b, LUMSDEN & HÖLLDOBLER 1983, MERCIER & al. 1997, MERCIER 1999, PFEIFFER & LINSENMAIR 2001, VAN WILGENBURG & al. 2005, SANADA-MORIMURA & al. 2006).

Caste: Territory defense is typically accomplished by a subset of the worker force. In polymorphic species, larger workers and majors are overrepresented at sites of conflict and are less likely to withdraw than smaller ants (e.g., HÖLLDOBLER 1981, 1983, ADAMS 1994, PFEIFFER & LINSENMAIR 2001). Majors and larger ants are often more aggressive (NOWBAHARI & al. 1999, BATCHELOR & BRIFFA 2011), have higher fighting abilities (FLUKER & BEARDSLEY 1970, BATCHELOR & BRIFFA 2010), are more likely to win control of resources (TANNER 2008), and are

themselves harder to kill (MORRISON 2000, BATCHELOR & al. 2012). In *Pogonomyrmex barbatus*, a species with monomorphic workers, task groups are defined behaviorally and can be distinguished by their hydrocarbon profiles. Only the patrollers and foragers are active away from the nest where competitors are encountered; patrollers are more aggressive than foragers and are the ants that determine which trails the colony uses each day (STURGIS & GORDON 2013).

Lanchester's laws and group fighting ability: What determines the killing power of the group? LANCHESTER's (1916) models of attrition and their extensions have provided the main theoretical basis for predicting mortality patterns in battles among social animals, but the lessons are widely misunderstood. Lanchester's key insight was that the capacity of a large group to concentrate its attacks on members of a smaller group can greatly magnify the importance of group size. Lanchester proposed two mathematical models of human warfare, both based on simple assumptions about death rates. Analysis of one model gave rise to the famous "square law", in which the fighting ability of the group is proportional to the square of its numbers but is only linearly proportional to individual fighting ability. Analysis of the other model yielded the "linear law", in which the fighting ability of the group is linearly proportional to both numbers and individual effectiveness.

FRANKS & PARTRIDGE (1994) proposed that Lanchester's models could describe fights among ants and other social animals and that either the linear law or the square law might apply, depending on how animals fight. The contrast between these two laws could have major implications for battle tactics and caste evolution (WHITEHOUSE & JAFFÉ 1996, MCGLYNN 2000). For example, battles conforming to the square law could favor allocation to numerous small workers rather than to fewer large workers.

FRANKS & PARTRIDGE (1994) also proposed a way to diagnose which law will hold for a particular species: When animals fight in the open so that multiple individuals can attack a single foe, mortality should follow the square law, but when combat consists of a series of one-on-one contests, mortality should follow the linear law. This turns out to be an insufficient basis for predicting mortality patterns, both theoretically and empirically. Knowing that ants from the larger group concentrate attacks on less numerous foes does not guarantee that the square law applies; indeed, that is an unlikely outcome (ADAMS & MESTERTON-GIBBONS 2003). One problem is that Lanchester's model of the square law assumes that a group's death rate is not directly affected by the number or effectiveness of its own soldiers. That may be an appropriate assumption for armies that fire guns or artillery, but ants fight at close quarters where superior size and weaponry are likely to affect both offense and defense. Furthermore, death rates in the smaller group may be limited by the time needed for ants in the larger group to find an opponent or because there are diminishing returns for increasing force ratios. When these effects are incorporated into Lanchester's models, the square law disappears even when animals from the larger group simultaneously attack less numerous opponents (ADAMS & MESTERTON-GIBBONS 2003). Mortality patterns need not conform to either the square law or the linear law and one cannot deduce the pattern simply by observing whether ant fight in groups or one-on-one.

What do the data show? There is no evidence supporting the square law for ants or other animals. PLOWES & ADAMS (2005) staged battles between workers from paired colonies of *Solenopsis invicta*, varying the ratios of initial numbers. Although the ants fought in the open and sometimes ganged up on opponents, mortality was mostly consistent with the linear law, and never consistent with the square law. The assumptions of the square law are also violated by fights among small groups of the wood ant *Formica rufa*; specifically, there is no evidence that concentration of attacks affects killing power (BATCHELOR & BRIFFA 2010).

Motivation and assessment: Territorial ants modulate the persistence and vigor of their aggression according to circumstances. The aggressiveness of individual ants depends on whether they are on their own territory (e.g., MABELIS 1979), whether they are on or near major foraging trails (HÖLLDOBLER 1976a, SAKATA & KATAYAMA 2001), the distance to the nest (HARRISON & GENTRY 1981, KNADEN & WEHNER 2003, VELÁSQUEZ & al. 2006), the size of the opponent (NOWBAHARI & al. 1999), the behavior of opponents (TANNER & ADLER 2009), the presence of scent marks (VILELA & HOWSE 1986), the ants' task group (STURGIS & GORDON 2013) and prior experience (VAN WILGENBURG & al. 2010), and the local density of nestmates and opponents (ADAMS 1994, TANNER 2006).

Spatial changes in the motivation to fight are crucial for boundary formation. Boundaries are stabilized by the tendency for ants to shift from aggression to timidity as they cross into a neighbor's territory. Sensitivity to scent marks can produce such changes. Colonies of the leaf-cutting ant *Atta laevigata* mark ground near the nest and proximal sections of foraging trails with colony-specific pheromones originating in the Dufour's gland (SALZEMANN & JAFFÉ 1990, SALZEMANN & al. 1992). In laboratory tests, workers placed on substrate marked by their own colony's scent were more likely to bite intruders, while those placed on substrate marked by another colony's scent showed alarm and submissive postures (VILELA & HOWSE 1986, SALZEMANN & JAFFÉ 1990). In the field, *A. laevigata* workers were more aggressive close to their own trails, presumably due to chemical marking (SALZEMANN & JAFFÉ 1990). Some other species of ants also alter their aggressiveness on marked substrate (e.g., HÖLLDOBLER & WILSON 1978, JAFFÉ & PUCHE 1984, MERCIER & al. 1997, CAMMAERTS & CAMMAERTS 1999, WENSELEERS & al. 2002) while others apparently do not (e.g., ADAMS 1994, DEVIGNE & DETRAIN 2002). Territorial pheromones may serve more than one function, being used for orientation as well as signaling prior occupancy (SALZEMANN & JAFFÉ 1990, DEJEAN & BEUGNON 1991).

Sensitivity to numbers is a second mechanism that can produce spatial changes in aggression. Fighting ants use assessment strategies (ARNOTT & ELWOOD 2009), adjusting behavior according to the local density of their own nestmates and of opponents. During ritualized tournaments, workers of *Myrmecocystus mimicus* respond to both the size and numbers of opponents. Small workers are likely to yield to larger ones, and outnumbered groups tend to withdraw (HÖLLDOBLER 1981). The tournaments function as a form of communication between colonies in which collective strength is compared (LUMSDEN & HÖLLDOBLER 1983). TANNER (2006) kept *Formica xerophila* in groups

of different sizes just prior to one-on-one or five-on-five contests with workers of another species. Workers that were in larger groups before the encounters were substantially more likely to lunge at or bite workers of *Formica integroides* and were, as a consequence, more likely to gain control of a food item. In controlled assays, *Lasius niger* workers were more likely to attack a dummy ant and less likely to flee if they were in the presence of 20 nestmates than if they were alone (SAKATA & KATAYAMA 2001). By contrast, in staged encounters of *F. rufa*, the average intensity of attack was higher for ants from small groups (5 individuals) than for ants from larger groups (10 or 20 individuals; BATCHELOR & BRIFFA 2011).

The impact of sensitivity to numbers is greatly magnified when it affects trail-laying. In fights staged between colonies of *Azteca trigona*, the rate of recruitment depended on the relative numbers of nestmates and opponents present during the early stages of the fight. Workers are more likely to lay trails and less likely to flee when members of their own colony locally outnumber ants from the neighboring colony, and assessment of numbers underlies the formation of boundaries (ADAMS 1990a).

Correlates of territoriality: Territoriality is associated with large colony size, a steady and predictable supply of food, colonies with multiple nests and queens, and – among arboreal species – the ability to construct nests that free the colony from dependence on existing plant cavities (ROOM 1971, LESTON 1973, LEVINGS & TRANIELLO 1981, BLÜTHGEN & al. 2000, DEJEAN & CORBARA 2003, DEJEAN & al. 2007, GIBB & CUNNINGHAM 2009). Arboreal territories may be easier to defend than terrestrial ones because entry is restricted to trunks and to branches that connect to other trees (JACKSON 1984, BLÜTHGEN & al. 2004). DAVIDSON (1997) proposed that territoriality is promoted by modifications of the proventriculus, the organ regulating passage of fluids from the crop to the midgut, to permit exploitation of liquid food that comes directly or indirectly from plants. Analysis of isotope ratios confirmed that most of the abundant territorial ants of tropical forest canopies obtain the majority of their nitrogen from plants, rather than from arthropod prey (DAVIDSON & al. 2003).

Control of territory size: Empirical and theoretical work on solitary animals has identified three primary influences controlling intraspecific variation in territory size: the fighting ability of the resident, the frequency and intensity of intrusion, and the abundance of food (rev. by ADAMS 2001). In ants, the fighting ability of the colony and competitive pressure applied by intruders are clearly important, as illustrated by research on the fire ant *Solenopsis invicta*. Territories tend to be larger for more populous colonies (TSCHINKEL 2011) and smaller when other large colonies are nearby (ADAMS 1998). When colonies were weakened by removing some of their worker force, they quickly lost territory to neighbors (ADAMS 2003). The balance of power among neighbors shifts on an annual cycle because small colonies emphasize production of workers while large colonies put more energy into rearing alates that depart during mating flights (TSCHINKEL 2011). Consequently, small colonies tend to gain ground from their older neighbors during the summer and are able to squeeze their way into the territory mosaic (ADAMS 2003). In some other ants too, bigger colonies tend to have larger territories (e.g., MABELIS 1979) and experimentally weakening a colony or

restricting its activity allows neighbors to expand (HAERING & FOX 1987, ADAMS 1990a, GORDON 1992a).

Numerous experimental studies on non-social animals have shown that residents adjust territory size as resource availability changes (ADAMS 2001). Social insect biologists have paid little attention to this possibility, although in theory resource renewal rates should affect partitioning of space (ADLER & GORDON 2003). In a population of *Solenopsis invicta*, experimentally enhancing the food supply for particular colonies did not cause significant changes in territory area relative to controls, regardless of whether the food was offered centrally or at the periphery of the territory (ADAMS 2003). I know of no similar studies on other territorial ants.

In theoretical studies of ant territory size, there has been a shift from models that focus on a single colony to models of interactions between competing neighbors. Early contributions were optimality models (HÖLLDOBLER & LUMSDEN 1980), which assume that the territory holder adjusts the region defended according to area-dependent costs and benefits. The main limitation of this type of model is that it represents the decisions of only a single entity – the focal colony. The actions of its competitors are incorporated into the cost function, which depends on the area or perimeter of the territory. This approach implicitly assumes that territories are not contiguous (ADAMS 2001).

When space is filled, the cost of expanding a territory depends on how neighbors react and models are needed that consider the simultaneous actions of two or more competitors. Several such models have been developed, but as yet none embodies the full complexity of decision-making. ADAMS (1998) considered how pressure applied by neighbors molds territory boundaries. Simple quantitative rules could account for much of the observed variation in territory size and shape in *Solenopsis invicta*. PLOWES & al. (2014) analyzed how competition affects optimal decisions about the length and direction of foraging columns used by the harvester ant *Veromessor pergandei*. ADLER & GORDON (2003) used game theory to calculate the expected spatial allocation of foragers in the face of exploitation and interference competition. All of these models were partially validated by application to mapped populations of competing colonies but they all greatly simplify the process of defense, as they do not allow colonies to vary their aggression in response to neighbors. There is clearly room for further development of mechanistic and game theoretical models of group behavior and its effects on partitioning of space.

Ecological consequences

Territorial competition can affect any aspect of colony demography.

Mature colonies kill queens and incipient colonies: Territorial ants kill queens and incipient colonies of their own species and often of other species as well. Although a nest-founding queen is not herself much of a threat to a mature colony, she is the seed from which a formidable competitor may grow. Workers from established colonies maul mated gynes as soon as they complete their nuptial flights, or dig below ground to execute them in their nest chambers (e.g., ROCKWOOD 1973, WHITCOMB & al. 1973, HÖLLDOBLER 1981, PFENNIG 1995, JEROME & al. 1998).

In some populations, new colonies are especially likely to appear where mature colonies are less abundant (e.g., FOWLER & al. 1984, CHEW 1987, GORDON & KULIG 1996). However, it is difficult to use correlative evidence to measure the effects of mature colonies on nest founding because of the confounding effects of habitat quality and dispersal. For example, in a study on *Pogonomyrmex occidentalis*, COLE & WIERNASZ (2002) found that the density of gynes attempting to found nests was positively correlated with the density of mature colonies due to limited dispersal, which could obscure effects of competition between old and new colonies. However, several controlled experiments, including one on *P. occidentalis* (see BILLICK & al. 2001), have shown that removing mature colonies increases new colony establishment (MAJER 1976c, FOWLER & al. 1984, ADAMS & TSCHINKEL 2001).

Competition among young colonies drives mortality: In several species, high-density clusters of incipient colonies are rapidly thinned by brood raids, struggles in which the surviving colonies acquire the workers and developing brood of other colonies (e.g., BARTZ & HÖLDOBLER 1982, RISSING & POLLOCK 1991, TSCHINKEL 1992). By experimentally planting young colonies at different densities, ADAMS & TSCHINKEL (1995a, b) showed that colony survivorship is density dependent. Similarly, young ant-plants are often discovered by multiple queens that establish competing nests, yet larger plants typically host a single colony, implying that one colony eliminates its rivals over time (e.g., LONGINO 1989, YUMOTO & MARUHASHI 1999).

Territorial competition reduces colony growth: Colonies with bigger territories tend to have larger worker populations, estimated from nest volumes or mark-recapture methods (e.g., MABELIS 1979, NIELSEN 1986, TSCHINKEL 2011). The causation can work either way: (1) Greater numbers of workers may allow colonies to acquire larger territories or (2) larger territories may promote growth of the worker population. Experiments discussed above confirm the first of these hypotheses: Weakening colonies by removing some of their worker population causes territory loss (HAERING & FOX 1987, ADAMS 1990a, 2003). The second hypothesis was confirmed by an experiment in which colonies of *Solenopsis invicta* were killed within several plots. For surviving colonies just outside the removal zones, territories expanded and worker populations grew at an accelerated rate compared to control colonies of the same initial size (ADAMS & TSCHINKEL 2001). Conversely, the size of the forager population of *Veromessor pergandei* or *Pogonomyrmex californicus* colonies was not significantly affected within three years by removal of possible competitors (RYTI & CASE 1988a).

Territorial competition can lower survivorship of established colonies: Territorial struggles can wipe out entire colonies, especially if one colony is considerably larger than the other (e.g., MABELIS 1979, HÖLDOBLER 1981). Experimentally joining trees occupied by different territorial species can trigger fights that exterminate nests of weaker colonies (e.g., DAVIDSON & al. 1989, PALMER & al. 2000, FLANDERS & al. 2013). Even when fighting costs are low, territorial competition is likely to affect mortality by curtailing colony growth, because annual survival is lower for small colonies (e.g., GREAVES & HUGHES 1974, GREENSLADE 1975b, MABELIS 1979).

Crowding may or may not lower colony survivorship. Surveys of 1000 nests of *Pogonomyrmex occidentalis* revealed that size-specific survival rates were lower where nearest neighbor distances were short (WIERNASZ & COLE 1995). By contrast, crowding had little effect on mortality of established colonies in *Pogonomyrmex barbatus* (GORDON & KULIG 1998) and a controlled experiment on *Solenopsis invicta* found no effect of neighbor removal on size-specific mortality rates (ADAMS & TSCHINKEL 2001).

Territorial competition lowers reproduction: Observational studies suggest that colonies with more workers and larger territories are more likely to reproduce and, when they do, tend to produce greater numbers of alate reproductives (e.g., BRIAN & ELMES 1974, COLE & WIERNASZ 2000, SANADA-MORIMURA & al. 2006). Crowded colonies of *Lasius flavus* and *Pogonomyrmex barbatus* have lower reproductive output (PONTIN 1961, GORDON & WAGNER 1997). Impacts of competition on reproduction have been confirmed experimentally: Removing neighbors of the harvester ants *Veromessor pergandei* and *Pogonomyrmex californicus* led to increased production of alate reproductives (RYTI & CASE 1988a). Ant colonies also reproduce by budding, and the death of an older colony may allow neighbors to expand their territories and to produce daughter nests (e.g., GREAVES & HUGHES 1974).

Territorial competition shapes spatial patterns: The spatial distribution of ant nests often tends towards regularity: Nests are farther from their nearest neighbors than one would expect if they were randomly placed (reviewed by LEVINGS & TRANIELLO 1981, RYTI & CASE 1992). Regular spatial patterns are usually interpreted as evidence of competition; indeed, there is little support for any other possible cause (RYTI & CASE 1986).

However, the degree of regularity should not be used as an index of the strength of competition (RYTI & CASE 1992). Just as in plants (PIELOU 1960), competition among ants can produce clumped, random, or regular spatial patterns. Suppose that mature colonies occupy much of the available space and that new colonies can establish only in the gaps between existing territories or where older colonies die. Clustering of young colonies in these gaps can produce a spatial pattern that is clumped at the population level. In addition, uneven colony densities at large scales, driven by variation in habitat quality, can obscure regular spacing at small scales (CUSHMAN & al. 1988, SCHOOLEY & WIENS 2003). It is therefore not surprising to find clumped or random spacing in competitive populations (e.g., GORDON 1991). Greater regularity of colony spacing at higher densities has also been suggested to be an indicator of competition (CUSHMAN & al. 1988, RYTI 1990, SCHOOLEY & WIENS 2003) but strong competition can produce either positive or negative associations between density and dispersion (RYTI & CASE 1992, ADAMS & TSCHINKEL 1995b).

Strong evidence of the effects of territoriality on spatial pattern comes from experiments and from repeated censuses that reveal the mechanisms underlying non-random spacing. In several species, the positions of nest sites excavated by queens after the mating flights are clumped, but the positions of older colonies tend towards regularity (BARTZ & HÖLDOBLER 1982, CHEW 1987, RYTI & CASE 1988b, ADAMS & TSCHINKEL 1995b, WIERNASZ & COLE 1995, COLE & al. 2001). What processes drive this shift towards uniform nest dispersion? Possible answers

can be categorized by the age of the colonies (founding queens, incipient colonies, or mature colonies) and by the mechanism that breaks up clusters (avoidance, migration, or death).

Consider the spatial consequences of nest founding. Following mating flights, the arrangement of newly founded nests is shaped by the gynes' avoidance of mature colonies (e.g., KAWECKI 1992), by preferences for particular habitats or topographical features (e.g., TSCHINKEL & HOWARD 1983), and by limited dispersal from source colonies or mating sites (e.g., WIERNASZ & COLE 1995). Competition from existing colonies can result in newly founded colonies being closer to one another (RYTI & CASE 1988b, GORDON & KULIG 1996) and farther from mature colonies than expected by chance (CHEW 1987, SCHOOLEY & WIENS 2003). Yet PFENNIG (1995) found that new colonies of *Veromessor pergandei* were more likely to survive if they were closer to mature colonies. He hypothesized that habitat quality was higher near mature colonies and that gynes select these regions despite the high risk of attack. Here too the confounding effects of unmeasured variables complicate interpretation of observational studies.

Among mature colonies, spatial patterns are shaped by death and migration. Large colonies typically have low annual death rates that do not depend much on crowding (e.g., GORDON & KULIG 1998, ADAMS & TSCHINKEL 2001), but in some populations, small colonies that are close to neighbors are more likely to die (WIERNASZ & COLE 1995). Territory defense is connected to colony migration in two ways. First, persistent attack by neighbors may stimulate colonies to relocate (e.g., HÖLLDOBLER 1976a). Second, when neighbors die or are removed, colonies may expand their territories into the vacated space and subsequently relocate their nests in that direction (ADAMS & TSCHINKEL 2001). Repeated surveys of harvester ant nests have produced mixed results: Colony migration tends to increase nearest neighbor distances in some populations (e.g., DE VITA 1979, BROWN 1999), but not in others (e.g., HARRISON & GENTRY 1981, GORDON 1992b).

Population regulation and worker density: One of the main ecological goals of studies on territoriality is to understand its effects on population dynamics. In vertebrates, territory defense regulates populations by limiting the density of animals that can settle in a crowded habitat or by reducing per capita reproduction (LÓPEZ-SEPULCRE & KOKKO 2005). Struggles between established residents and potential settlers are key interactions controlling local density. In social insects, the role of territoriality is fundamentally different. Resident-settler interactions in ants consist primarily of workers from large colonies preying upon newly mated queens, rather than contests among mobile adults. Furthermore, colonies of the same species vary enormously in size, spanning orders of magnitude in territory area and worker population (e.g., SANADAMORIMURA & al. 2006). Because available space may be filled by a few large colonies, many small colonies, or by a mix of colonies of different sizes, the limit to population growth cannot be described by colony density alone. Instead, it may be meaningful to describe population limits by the number or biomass of individual insects supported per unit area (ADAMS & LEVINGS 1987).

Does territorial competition regulate ant density? Given the importance of this issue, remarkably few studies have

evaluated the strength of population regulation in ants. Some investigators have suggested that constancy of colony numbers as some die and new ones appear reflects the stabilizing effects of territoriality (e.g., YASUNO 1965a, MABELIS 1979), but their observations were shorter than the maximum life-span of a colony. Many generations of data are needed to detect population regulation from time series analyses (ZIEBARTH & al. 2010).

Ant populations are not necessarily limited by competition. Long-term studies on *Pogonomyrmex occidentalis* suggest that colony density is restricted by the rate of arrival of foundress queens, rather than by competitive interactions, across much of the study site. Experimentally adding mated gynes led to increased numbers of surviving colonies; this relationship did not saturate until around 80 gynes were added per 0.25 ha plot (COLE & WIERNASZ 2002). Furthermore, removal of established colonies led to higher establishment of new colonies only within some regions (BILLICK & al. 2001). Thus, competition between foundresses and mature colonies exerts density-dependent effects only locally.

Strong evidence of population regulation comes from a convergence experiment (sensu MURDOCH 1970) on the fire ant *Solenopsis invicta*. ADAMS & TSCHINKEL (2001) eliminated all mature colonies from six plots while monitoring six control plots of the same size. Within two years, the average biomass of ants on the removal plots returned to the same level as that of control plots; mean biomass on the two types of plots showed nearly identical fluctuations over the next three years. The rapid convergence of biomass on experimental and control plots shows that the population is tightly regulated, tending to return to equilibrium levels following perturbation. Territorial interactions produced the regulatory force; colony establishment, growth, and migration were all density dependent (ADAMS & TSCHINKEL 2001).

Studies on invasive ants have led to an additional hypothesis about the population-level effects of territoriality; namely, that territoriality reduces worker density due to the costs of fighting (HOLWAY & al. 1998, TSUTSUI & SUAREZ 2003). The principal support for this idea comes from studies on the Argentine ant, *Linepithema humile*, a species that has been inadvertently transported from its native range in South America to other continents. Within Argentina, workers collected from nests separated by a few hundred meters typically fight, but within invaded areas workers taken from nests separated by those distances often intermix without aggression (SUAREZ & al. 1999, TSUTSUI & al. 2000). Vast supercolonies, spanning 100s or 1000s of kilometers, across which ants show little or no hostility to each other, occur in several invaded regions (GIRAUD & al. 2002, CORIN & al. 2007, SUAREZ & al. 2008). Several researchers have posited that this shift in population structure arose because of loss of territorial behavior occurring during the invasion of new regions, which in turn caused the density of ants to rise. Under this hypothesis, genetic bottlenecks (TSUTSUI & SUAREZ 2003) or selection against unusual colony odors (GIRAUD & al. 2002) reduced the variability of recognition alleles that allow ants to distinguish members of their own colony from competitors. If a breakdown in nestmate recognition leads to reduced territorial fighting, that could allow ant densities to reach higher levels in invaded regions than in na-

tive populations (HOLWAY & al. 1998, GIRAUD & al. 2002, HOLWAY & al. 2002, KRUSHELNYCKY & al. 2009).

However, the causes of the considerable difference in colony sizes between invaded and native populations of Argentine ants are a controversial matter and the contrast may not be due to changes in territoriality. Territoriality has not been lost in introduced populations. In both native and invaded areas, workers are antagonistic to conspecifics from other colonies but not to workers from other nests of the same colony (TSUTSUI & al. 2000, GIRAUD & al. 2002, BUCZKOWSKI & al. 2004, HELLER 2004, PEDERSEN & al. 2006, VOGEL & al. 2009). Where supercolonies come into contact in California, they engage in massive battles (THOMAS & al. 2006). Furthermore, genetic evidence does not confirm that supercolonies were formed by fusion of unrelated nests, as might be expected if territorial reactions were weakened (HELANTERÄ & al. 2009). Colonies can be orders of magnitude larger in introduced populations (SUAREZ & al. 2008) but there is no need to postulate loss of territoriality to account for this; colonies may simply spread without opposition in newly invaded areas until they eventually run into competitors or the limits of suitable habitat (PEDERSEN & al. 2006, HELANTERÄ & al. 2009, VOGEL & al. 2009, VOGEL & al. 2010, MOFFETT 2012). Thus, when ants collected from distant nests do not fight, that may be because they are members of the same enlarged colony, rather than because nest-mate recognition is impaired.

Regardless of how the vast invasive supercolonies of Argentine ants arose, they lack intraspecific territorial boundaries across large expanses. Yet there is no field evidence that release from the costs of intraspecific fighting has elevated worker densities. A lab experiment suggested the potential for such an effect. HOLWAY & al. (1998) connected pairs of nests to the same central foraging arena and monitored aggression and colony growth rates. If the two nests were from different supercolonies, they fought more and grew less than if they were from the same supercolony. Two aspects of the design are likely to exaggerate the apparent importance of aggression: the colonies were confined to small containers, and food was offered only in a central arena, where the two groups came into contact. In the field, territorial ants have protected access to food within their own territories and a much greater opportunity to avoid conflicts during foraging.

Although some authors imply that densities are higher in invaded areas than in the native range (e.g., HOLWAY & al. 1998, TSUTSUI & al. 2003), they cite no supporting data. Comparative estimates are available from only a few areas and they vary considerably. HELLER (2004) examined *Linepithema humile* in multiple habitats in central California and in northeastern Argentina. Neither nest nor ant density differed significantly between these two areas; indeed, the highest ant densities were observed in Argentina (see also VOGEL & al. 2009). Densities in invaded areas of Hawaii and Argentina (INGRAM 2002a) were also within the range observed by HELLER (2004) in native populations. Moreover, there are many reasons besides fighting why nest or worker density might vary among sites (INGRAM 2002b, VOGEL & al. 2009).

What about other species? HOLWAY & SUAREZ (1999) suggested that lack of territoriality in the polygyne form of *Solenopsis invicta* leads to higher worker density com-

pared to the territorial, monogyne form. Yet, as summarized above, there is little fighting where territories of the monogyne form meet. The difference in worker density between the two social forms is likely because colonies of the monogyne form allocate much more energy to production of alates, which depart on mating flights; the polygyne form produces far fewer alates and puts energy into worker production instead (TSCHINKEL 2006). Moreover, as many of the studies discussed in this review show, highly territorial ants typically have mechanisms that reduce the costs of fighting at boundaries. Even in species with massive battles, such as *Formica polyctena*, the net effect is apparently to bring populations in line with resource supply. In one of the few studies to estimate total losses due to fighting, GORDON & KULIG (1996) concluded that deaths suffered by *Pogonomyrmex barbatus* colonies could be easily replaced within the same season. While it seems possible that territorial aggression could affect worker density, especially in ants that engage in large battles, documenting such an effect is a daunting challenge that has not yet been met.

Effects on ant community structure: With large colonies of active and aggressive workers, territorial ants can have particularly strong effects on community structure. Syntheses of ant ecology in habitats as diverse as boreal forest, arid regions of Australia, and tropical forest canopies put territorial ants at the top of a competitive hierarchy that organizes interspecific interactions and community assembly (MAJER 1972, VEPSÄLÄINEN & PISARSKI 1982, SAVOLAINEN & VEPSÄLÄINEN 1988, ANDERSEN & PATEL 1994, PARR & GIBB 2009). The territorial dominants are hypothesized to have complementary distributions and to suppress the density and activity of species lower in the hierarchy.

Within some habitats, there is clear evidence that interspecific territoriality produces a mosaic of patches occupied by different species of ants. Examples are seen in temperate and boreal forests where various species of *Formica* are dominant (e.g., YASUNO 1965c, TANNER 2009, CZECHOWSKI & al. 2013), among *Iridomyrmex* species in Australian heathland (HAERING & FOX 1987), where exotic ants have invaded islands (e.g., FLUKER & BEARDSLEY 1970, LIEBERBURG & al. 1975), and in the canopies of lowland tropical forest (reviewed below). Within these mosaics, experimentally weakening or removing colonies of one species leads to territory expansion or increased reproduction by colonies of competing species, while adding territorial colonies has the reverse effect (PONTIN 1961, YASUNO 1965b, PONTIN 1969, MAJER 1976c, HAERING & FOX 1987, ADAMS 1990a). Particularly strong examples of interspecific exclusion achieved by vigorous fighting are seen on specialized ant-plants (e.g., DAVIDSON & al. 1989, PALMER & al. 2000, PALMER 2004).

Both observational and experimental methods are used to study the effects of territorial ants on other species. Controlled field experiments are difficult and tend to confirm fewer competitive relationships than observational studies suggest (e.g., KING & TSCHINKEL 2006). For example, in Scandinavian forests, several patterns imply that territorial wood ants suppress the abundance of species that are lower in the competitive hierarchy. Where territorial species of *Formica* occur, the diversity of non-territorial species is lower, and they tend to switch food types or foraging times

(SAVOLAINEN & VEPSÄLÄINEN 1988, 1989). VEPSÄLÄINEN & PISARSKI (1982) observed workers of *Formica polyctena* entering the nests of other species and preying on their workers and brood. Yet experimental support for effects of dominant *Formica* on other species is limited. When colonies of territorial *Formica* were transported to small islands, they attacked colonies of *Lasius* and reduced their numbers (ROSENGREN 1986, CZECHOWSKI & VEPSÄLÄINEN 2009). However, reducing the density of *F. aquilonia* produced no detectable responses by other species after a year (GIBB & JOHANSSON 2011). In another study, when *F. aquilonia* nests were removed, the subordinate ant species *Camponotus herculeanus* and *Myrmica ruginodis* increased in abundance, but only in some forest types (GIBB 2011).

In arid regions of Australia, experimental evidence that territorial *Iridomyrmex* affect community structure is also mixed. When colonies of *Iridomyrmex sanguineus*, a dominant species, were confined by fences for several weeks, foraging success by other ants nearly doubled relative to controls (ANDERSEN & PATEL 1994); the effect disappeared when the fenced colonies were released. GIBB & HOCHULI (2004) caged colonies of *I. purpureus* for a year on four rock outcrops, comparing the abundance of foragers of other species of ants to that on outcrops with uncaged *I. purpureus* colonies and on outcrops that naturally lacked the dominant ant. Caging of the territorial dominant increased foraging success of several other ants at baits, but the only ants whose abundance increased significantly were other species of *Iridomyrmex* (GIBB & HOCHULI 2003, GIBB 2005).

Tropical ant mosaics: The effects of territory defense on community structure have been intensively studied in tropical arboreal ants. Early studies in coconut plantations revealed that the most abundant ant species occupied distinct blocks of neighboring palms and that severe fighting accompanied replacement of one species by another (WAY 1953, VANDERPLANK 1960, GREENSLADE 1971). By the 1970s, discoveries from tropical plantations coalesced into the "ant mosaic concept" (ROOM 1971, MAJER 1972, LESTON 1973, ROOM 1975, MAJER 1976a, b, c, TAYLOR 1977), encompassing the following claims (reviewed by MERCIER 1999, DEJEAN & CORBARA 2003, BLÜTHGEN & STORK 2007, DEJEAN & al. 2007). Among the ants foraging in the canopy, the numerically dominant species defend territories that form a three-dimensional mosaic filling much of the forest canopy (LESTON 1973, TAYLOR 1977, DEJEAN & al. 2007, RIBEIRO & al. 2013). Habitat variation contributes to the mosaic pattern (e.g., JACKSON 1984, DEJEAN & al. 2007) but the dominant species are mutually intolerant and do not share space, with the exception of pairs of species called co-dominants (MAJER 1972). The remaining non-territorial species can co-occur with dominant ants but are much less numerous and rely on niche partitioning, armor, or other means to persist within the territories of the dominants (MAJER 1972). A more controversial hypothesis is that each dominant territorial species is associated with particular suite of non-dominant ants (e.g., ROOM 1975, TAYLOR 1977). Besides structuring the ant community, dominant ants can influence other insects through predation and tending of Hemipterans, indirectly affecting plant fitness (RICO-GRAY & OLIVEIRA 2007). The prospect of controlling herbivorous insect pests by mani-

pulating the ant mosaic is one of the chief motivations for studying arboreal ant ecology (WAY & KHOO 1992).

The existence of arboreal territory mosaics in tropical habitats is supported by all types of evidence used to demonstrate ant territoriality generally. Detailed maps, made where boundaries can be readily observed, show that the foraging areas of multiple species abut but do not overlap (e.g., WAY 1953, ADAMS 1994). Ants from adjacent colonies fight where they come into contact (e.g., MAJER 1976c) and transfers of ants from one tree to another stimulate highly aggressive social responses as the intruders are pursued and killed (e.g., HÖLLDOBLER 1979b, ADAMS 1994). The spread of one species drives losses by others (WAY 1953, GREENSLADE 1971) and removing or weakening colonies leads to expansion by neighbors and increased survival of founding queens (MAJER 1976a, ADAMS 1990a).

Two aspects of the ant mosaic concept are debated. The first is whether some or all of the co-occurrence patterns suggested by sampling ants on trees are produced by chance. Some early studies on ant mosaics were based on chi-square tests of association for each pair of species, excluding those that occur on only a few trees (ROOM 1971, 1975, TAYLOR 1977, MAJER & al. 1994). Tests that were significant at the 0.05 or the 0.1 level were displayed in web diagrams appearing to show highly structured communities. This method has serious flaws (BLÜTHGEN & STORK 2007). The large number of pair-wise tests is likely to produce multiple type I errors, exaggerating the degree of community structure. Furthermore, data from adjacent trees do not provide independent estimates of the probability of species co-occurrences because large colonies occupy many trees. Because of these problems, many of the reported associations among territorial ants and co-dominant or non-dominant species may not be real.

An alternative approach is to evaluate the significance of ensemble measures of community structure such as C scores (checkerboard indexes). Some of these tests provide evidence of non-random community structure (PFEIFFER & al. 2008) but others do not (e.g., FLOREN & LINSEMAIR 2000, DEJEAN & al. 2010). RIBAS & SCHOEREDER (2002) re-evaluated data on multi-species assemblages and found that the co-occurrence of dominant ants was significantly below random expectation in only two of eight cases. Some other community-level analyses have failed to find non-random community patterns expected under the ant mosaic hypothesis (FLOREN & LINSEMAIR 2000, FLOREN & al. 2001, SANDERS & al. 2007, DEJEAN & al. 2010, FAYLE & al. 2013). But these analyses are also problematic. The sampling units are often too coarse to reveal whether territories overlap, too close together for statistical independence, and too few to provide much statistical power, especially if Bonferroni corrections are used (BLÜTHGEN & STORK 2007). In short, when an analysis fails to reject the null hypothesis of random co-occurrence, it is not always clear whether there is no ant mosaic or whether the method used to detect it is weak.

By focusing on the biology of particular ants, ecologists have confirmed community patterns that might not be revealed by testing null hypotheses applied to a larger set of species. Strong relationships may be obscured by ensemble tests that lump them with numerous weak relationships (BLÜTHGEN & STORK 2007). For example, statistical analyses by RIBAS & SCHOEREDER (2002) and SAN-

DERS & al. (2007) did not detect non-random community patterns involving highly territorial *Oecophylla* and *Azteca*, but other work, based on mapping, experimental removals and behavioral studies, demonstrates that ants in these genera exclude some other abundant ants, producing mosaics (MAJER 1972, HÖLLDOBLER 1979b, ADAMS 1990a, 1994, ARMBRECHT & al. 2001, RIBEIRO & al. 2013). *Oecophylla* and *Azteca* selectively recruit to particular species of intruders, creating selectively permeable boundaries (HÖLLDOBLER 1979b, 1983, RIBEIRO & al. 2013). Positive associations between territorial ants and other ant species have also been confirmed. *Crematogaster castanea* co-occurs with the territorial dominant *Oecophylla longinoda* (see ROOM 1971, LESTON 1975, MAJER 1976c) and the two species tend to spread or disappear concurrently following manipulation of the dominant ants (MAJER 1976c). Some non-dominant ants live preferentially or exclusively within the territories of particular aggressive species whose trails they follow to food sources (ADAMS 1990b, POWELL & al. 2014). DAVIDSON & al. (2007) found that colonies of *Polyrachis bihamata* and *P. ypsilon* were strongly associated and co-dominant with several territorial species of *Colobopsis* (formerly placed in *Camponotus*), the most abundant ants in a Brunei rainforest. Workers of the *Polyrachis* species parasitize the *Colobopsis* colonies by following their trails to food but also cooperate with them to defend resources from *Oecophylla*.

A second controversial issue is whether tropical arboreal territory mosaics exist in natural forests, as opposed to plantations (FLOREN & LINSÉNMAIR 2000, BLÜTHGEN & STORK 2007). The height and structural complexity of forests inhibit detailed mapping and observations of behavior at boundaries in the canopy. Nonetheless, territory mosaics have been documented in many natural tropical forests. The evidence from mangroves is particularly strong because they are structurally simple and amenable to experiments (ADAMS 1990a, FLANDERS & al. 2013). Mosaics of exclusive territories occur in primary rain forest in Colombia (ARMBRECHT & al. 2001) and Brunei (DAVIDSON & al. 2007), in Australian rain forest (BLÜTHGEN & al. 2004, BLÜTHGEN & STORK 2007), and in secondary forests in Panama (RIBEIRO & al. 2013), Brazil (LESTON 1978), and Cameroon (DEJEAN & al. 1994, DEJEAN & GIBERNAU 2000). In a rainforest in Borneo, TANAKA & al. (2012) inferred that the aggressive ant *Crematogaster difformis* excluded other species of ants from the trees it occupies. On the other hand, sharing of foraging space among abundant ants was more common in French Guiana (DEJEAN & al. 1999) and up to 44% of trees in inland forests of Madagascar lacked dominant ants (DEJEAN & al. 2010). Negative associations among numerically dominant ants have been documented in Australian rainforest (BLÜTHGEN & STORK 2007), but no evidence of non-random ant community structure was found by several studies in Malaysian rain forests (FLOREN & LINSÉNMAIR 2000, FLOREN & al. 2001, FAYLE & al. 2013).

To summarize, while competition is only one of several forces structuring communities, both experimental and mechanistic studies demonstrate strong effects of territoriality on the co-occurrence of some ant species.

Conclusions and prospects

As a particularly strong form of competition, defense of space links individual and colony behavior to population and community dynamics. Only some aspects of this linkage are well understood.

On the behavioral side, there is a rich literature on the variety of ways that ant colonies organize territory defense and interact with neighbors to partition space (HÖLLDOBLER & WILSON 1990). Two open questions require a synthesis of theory and experimentation. (1) How do territorial interactions self-organize? Competitive struggles at boundaries involve distributed decisions by numerous workers – sometimes tens of thousands – none of which has global information on the status of its colony's territory (PLOWES 2008). Experimental work has revealed positive and negative feedbacks that are likely to shape the self-organization of territory defense, but these have not yet been put together into a unified framework. (2) What processes control intraspecific variation in territory size? A major goal of studies on territoriality in solitary animals has been to understand how residents adjust territory size in response to changes in food supply; territory defense is seen as a crucial intermediate between fluctuations in resource distribution and changes in animal density (ADAMS 2001). Myrmecologists have tended to neglect these issues. We know little about how colonies respond behaviorally or demographically to changes in the abundance of food and the theory of ant territory size is only partially developed. Models of sets of interacting colonies, incorporating game theory and realistic mechanisms, are needed to understand territorial strategies and their ecological effects (ADLER & GORDON 2003).

On the ecological side, there is strong evidence that territorial competition affects colony fates as well as some aspects of ant community structure. Much less is known about population and community dynamics, partly because it is difficult to measure population growth rates in social insects. Most studies lack information on at least one important component of population change: colony establishment, growth, movement, survival, or reproduction. Purely observational studies on ant ecology are subject to confounding effects of habitat heterogeneity. Large-scale and long-term experiments are badly needed, despite the logistic difficulties, so that the full demographic and community effects of density manipulations can be measured.

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