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Supercolonies of billions in an invasive ant: What is a society?

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All societies are characterized by the capacity of their members to distinguish one another from outsiders. Ants are among the species that form "anonymous societies": members are not required to tell each other apart as individuals for the group to remain unified. Rather, each society depends on shared cues recognized by all its members. These cues permit societies to reach populations in the low millions in certain ant and termite species, and to grow indefinitely populous, expansive, and possibly long lasting in a few other ant species, which are described as having supercolonies. Anonymous societies are contrasted with "individual recognition societies" such as those of most vertebrates, which are limited to a few individuals by the necessity that the members individually recognize each other. The shared recognition cues of ants provide clear criteria for defining colonies and are what enables a supercolony to remain a single society no matter how large it becomes. I examine the often conflicting ideas about the best studied ant with supercolonies, the Argentine ant (*Linepithema humile*). Its invasive supercolonies, containing in some cases billions of workers and queens spread over hundreds of square kilometers, can be most parsimoniously understood as single colonies that have had an opportunity to expand across regions of suitable habitat because of a lack of well-matched competitors. This capacity for unrestricted growth is the defining characteristic of supercolonies. There is no evidence that the local patchiness of nests and patterns of worker and food traffic within these wide-ranging populations are so invariant that supercolonies do not exist but instead are collections of numerous independent nest clusters that should be called "colonies." Nor is there evidence for the hypothesis that invasive supercolonies have been able to grow large and successful overseas only as a result of evolving through genetic drift or selection to become fundamentally different from the smaller colonies typical of the species' region of origin around northern Argentina. The most unique feature of the Argentine ant, however, is not that its colonies are anonymous or that they can grow indefinitely large—though the last trait is found only in a few ant species and humans. Rather, it is that Argentine ant colonies do not interbreed. Indeed, the only fighting among Argentine ants occurs along colony borders, which even reproductives seldom, if ever, cross and survive. For this reason, each Argentine ant supercolony acts as virtually a sibling species. *Key words:* Argentine ant, polydomy, recognition system, reproductive isolation, society, speciation, supercolony, unicolonial. *[Behav Ecol]*

INTRODUCTION

Argentine ants form exceptionally massive colonies—supercolonies. This occurs because the queens stay in their natal colony, so all their progeny add to the colony's population. By budding—when the workers and queens move together to new sites, making colonies extremely polydomous (having multiple nests: Debout et al. 2007)—each colony can expand its territory as far as environmental conditions allow. Examples of limiting conditions include the availability of suitable nest sites and the presence of competing colonies that could hem the colony in. *Linepithema humile* is native to the region around northern Argentina (Wild 2004), where colonies span just hundreds of meters. But where the Argentine ant has invaded elsewhere by jump dispersal (movements over a distance, invariably piggybacking on human transport), its generalist diet and flexible nest habitats, coupled with a lack of effective competitors, has contributed to its status as one of the most damaging invasive species (Lowe et al. 2004), by permitting single colonies to leapfrog continents and grow across hundreds of square kilometers (Vogel et al. 2010; van Wilgenburg et al. 2010).

Indeed, the invasive colonies of Argentine ants are the largest recorded societies of multicellular organisms. Among the supercolonies of this species spreading globally, Large Supercolony (as it is known in California, where it might contain a trillion individuals: Moffett 2010) is the champion, spanning 1000 km from San Francisco to the Mexican border in California, 6000 km in Europe, 2800 km in Australia, 900 km on the North Island of New Zealand, and ever-widening regions of Hawaii and Japan (Giraud et al. 2002; Vogel et al. 2010; van Wilgenburg et al. 2010). Carry an Argentine ant worker, queen, or male within or between any of these regions and it merges with the ants living there with at most a subtle initial pause to inspect them (Björkman-Chiswell et al. 2008). It joins the local labor force without a hitch because it is still home, in a sense—Large Supercolony controls the entire expanse.

Three other Argentine ant colonies vie with the Large Supercolony for the land near San Diego, however. They collide along centimeters-wide borders that extend for kilometers: each month, more than a million ants die in battles between 2 of the colonies alone (Thomas et al. 2007). It is a death sentence for an ant to move just beyond its colony's territory onto ground controlled by one of these competitors (Figure 1). The same would be true if that ant came upon a fledgling Argentine ant colony offloaded from a ship from

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Figure 1
Top: Workers of different Argentine ant colonies pulling each other apart in the native range in Argentina. Bottom: Dead ants pile up along the battleline between Large Colony and Lake Hodges Colony near San Diego, CA.

Argentina. In short, at no stage in colony growth is there ambiguity as to the limits of the colony unit. The ants show a universal lack of social strain or dysfunction toward other colony members, and a clear attack response to outsiders, even after their colony range has expanded across continents.

This is astonishing, given that *Atta laevigata* ants, for example, are sometimes briefly hostile toward colony mates from far parts of the same enormous nest (Whitehouse and Jaffe 1996; Jaffe K, personal communication). One might therefore have predicted something similar for the Argentine ant. We might even predict the social equivalence of a ring species, in which all the individuals of a geographically variable population interact peacefully, except when individuals from extreme parts of the range have accumulated enough differences in how they identify each other to fight to the death if brought together: even this could still be considered one colony (Moffett 2010, p. 261). Instead, colony distinctions in the Argentine ant seem just as clear as in most ant species, where responses to conspecifics serve as a litmus test to distinguish colonies in the field. Only after colony boundaries are understood is it possible to study in a straightforward way how colonies form and perpetuate—the often intricate issues of kinship and chemical identity cues included.

Some researchers, however, claim that the invasive supercolonies are fundamentally different from the smaller native colonies. Others have pointedly denied their existence entirely: "In fact there is no functional super-colony of Argentine ants, no single giant colony stretching for miles, much less across the globe" (Gordon 2010b).

Regardless of their professed opinions, many experts on Argentine ants have been inconsistent in how they write about supercolonies. For example, one part of an article may portray an entire population occupying a region as one colony, much as I did above, but then elsewhere in the same text the authors either explicitly or implicitly interpret local groups of nests within the supercolony as different colonies, typically when puzzling over how so many ants can live together harmoniously at a specific site.

The current article explores such alternative interpretations of Argentine ant social order. These interpretations are so varied that this paper serves to correct and unite them into a cohesive model and framework for future research. First, however, let me address some broad ideas about animal societies relevant to the discussion.

SOCIETIES, SOCIAL IDENTITY, AND SUPERCOLONIES

At issue is what we should consider a colony (or society). The literature on sociobiology provides surprisingly little guidance. A society has been defined as "a group of individuals belonging to the same species and organized in a cooperative manner" (Wilson 1975; Hölldobler and Wilson 2008), but this description is incomplete: While such individuals can be described as "social," they must perceive each other as uniquely similar and all outsiders as different for a specific group of them to represent a "society." The recognition system that ants use for identification with a colony and rejection of aliens is based on shared cues, typically a colony-specific odor blend generated by queens or workers (though environment has its influences: Crozier and Dix 1979; d'Ettorre and Lenoir 2010). As a result, ant colonies remain tightly knit without each individual necessarily having been in direct contact with every one of its nestmates.

Compare these "anonymous societies," as I call them, with the societies of nonhuman vertebrates such as dolphins, elephants, cooperative breeding birds, and primates like the chimpanzee, where societies are defined by members recalling each other individually to know who is in their group and who is not (Wrangham R, Reiss D, Orians G, personal communication). I suggest calling these "individual recognition societies." As a general rule such societies have at most 100 members. This mode of delimiting social groups, which requires prior association (sensu d'Ettorre and Lenoir 2010) between every pair of individuals, is little studied. Group membership is not mentioned, for example, in a review of the roles of individual recognition (i.e., in territoriality, aggressive competition, and parental care: Tibbets and Dale 2007). It therefore is possible, but I think unlikely, that unstudied traits (such as kin-specific nuances in vocalizations) could be useful in forming the societies of some species.

Preliminary examination of the literature suggests most species fit unambiguously into either the individual recognition or the anonymous category. A possible exception is the naked mole-rats, which have not just individual recognition but a colony-specific odor (Burda 1995; O'Riain and Jarvis 1997; Jacobs and Kulper 2000) and probably not coincidentally also have the largest societies of any vertebrate (up to at least 295: Lacey and Sherman 1997). This dual ability is probably widespread in cooperatively breeding mammals (Sherman PW, personal communication) and exists as well in certain invertebrate kin groups (e.g., the isopod *Hemilepistus reaumuri*: Linsenmair 1985, see also Wyatt 2010). In these species, it will be important to investigate whether the animals must recognize as individuals all the other members in their group to fully demarcate a society. If they do not, I would still consider their societies to be anonymous (as is the case for human societies today). Anonymity is believed to be complete among ants, where workers do not identify each other individually, even in small societies, albeit they may distinguish among classes of individual such as caste members like a queen or soldier (e.g., Hölldobler and Carlin 1987; d'Ettorre 2008). Although a few ant species form dominance hierarchies, for example, these do not employ individual recognition (Peeters and Liebig 2009).

GLOSSARY

Terms coined or substantially redefined by the author are denoted by an asterisk. For terms relating to recognition systems, see Tsutsui (2004). Under the definition for supercolony, my note about population size was modified in response to commentator concerns.

**Society.* A cooperative group of conspecific individuals that are able to distinguish group members from outsiders and reject outsiders on that basis. As pointed out by Wilson (1975), cooperation must extend beyond mere sexual activity. If there is no clear group membership, other terms, such as "herd," should be applied. Societies can be either permeable or closed (see below).

**Anonymous society.* A society in which group members are distinguished from outsiders based on shared cues, such as odors in ants.

**Individual recognition society.* A society defined by every member recalling every other member individually. Note that recognition per se does not confer membership, in that members may also be able to recognize some outsiders as individuals.

Colony. The term for a society of ants, other social insects, and some other organisms (see Wilson 1975).

**Supercolony.* A colony with the capacity to grow without bounds when conditions are suitable. (Of course, beyond a certain size this condition requires polygyny and polydomy.) Note that this term has always been applied only after such colonies grow exceptionally large—I suggest with populations well in excess of 1 million.

Unicolonial. A species (or population within a species) in which the ants can form supercolonies (Pedersen et al. 2006). (No examples are known for an alternative use of this word, to describe a species for which colony distinctions do not exist.)

**Superorganism.* A society in which the members are permanently bonded together such that there are no social mechanisms allowing for permanent departure from the society, including transfer to another society (Moffett 2010). The only exception is when well-defined reproductive individuals leave to form a separate society with a distinct identity. Such "closed societies" are especially prone to develop the additional characteristics of many organisms addressed by Hölldobler and Wilson (2008). By this definition, the colonies of all ant species are likely to be superorganisms.

Closed Society. A society where intergroup transfers are impossible (Wilson 1975, p. 17).

Permeable society. A society that has social mechanisms allowing in outsiders, often under stringent conditions, after which they are identified as society members.

Polydomy. A single colony residing in multiple nests.

Monodomy. A colony residing entirely within one nest.

Nest. A physical structure inhabited by members of a society, typically including brood, and cleanly separated in space from any other such structures.

Colony mates. Individuals identifying with the same colony.

Nestmates. Colony mates coinhabiting the same nest over time. The term should be avoided in polydomous species that exchange individuals between nests.

The size attained by anonymous societies need not be limited by the capacity of its members to recognize each other as individuals (again, consider modern human civilizations). In fact, no ant worker in a society with a population in the tens or hundreds of thousands is likely to encounter every one of its nestmates during its brief lifetime. This is most obvious in polydomous species, and necessarily true in supercolonies (where nestmates are more accurately called "colony mates": Thomas et al. 2007), even where workers and queens move readily and often between nests as they do in the Argentine ant (Heller, Ingram, et al. 2008). No problems arise as long as colony mates are distinguished by shared cues from outsiders. Moreover, in most healthy ant societies, identification once learned is permanent and nontransferable (though at the same time remarkably adaptable, e.g., Moffett 2010, p. 215). Unlike chimpanzees or elephants, which have social mechanisms for group transfers, adult queens and workers are not able to move between colonies, except as parasites (e.g., chapter 12 of Hölldobler and Wilson 1990). Their unbreakable group identity makes ants in colonies powerful analogs of cells in bodies. This is the superorganism idea sensu Moffett (2010): Ants identify each other using chemical cues on their body surfaces, and in a healthy society, they invariably avoid or kill alien ants with different cues; cells identify each other by means of chemical cues on their surfaces, with the immune system attacking any cells with different cues (thought to originally have been hydrocarbons [Fernàndez-Busquets and Burger 2003], as they are in the social insects).

In the case of certain ant species with supercolonies, spatially separated but compatible populations that are offshoots of each other can retain the same identity and therefore remain part of one superorganism (a strain of fungus can be viewed as a single organism that may similarly be patchily distributed: Money NP, personal communication). There are no hostilities between Argentine ants from sharply different environments within this range. The massive yet precisely defined battlefronts that arise where colonies meet are not situated with respect to environmental conditions; and ants from different supercolonies continue to kill each other even after months of eating the identical foods (Giraud et al. 2002; Suarez et al. 2002; Thomas et al. 2006). Some publications nonetheless attribute fighting in Argentine ants to diet because the mere contact between Argentine ants and African brownbanded cockroaches (*Supella longipalpa*), provided as an artificial diet, can induce colony mates to kill each other (Liang and Silverman 2000). From this, it was concluded that "whether Argentine ants fight depends on the similarity of the food they eat and the impact of their food on their hydrocarbons" (Gordon 2010a). Yet environmental influences on behavior have to be assessed under the conditions in which a species actually lives (West-Eberhard MJ, Futuyma DJ, personal communication). On this basis, local environment, including food, is of trivial importance to how Argentine ants form their identities. In nature, Argentine ants treat the presence of their genetically determined colony-recognition odor (Brandt et al. 2009) as a life-and-death matter. In terms of how we recognize their social affiliations, no matter how large these may be, we should, too.

While most researchers have used the word supercolony simply to describe the largest in a continuum of colony sizes, Pedersen et al. (2006) attempt a more precise usage: "a colony that contains such a large number of nests that direct cooperative interactions are impossible between individuals in distant nests." Because their societies are anonymous unions, however, the potential for direct interactions has no clear significance for these or any other ant. As I noted, proficiency at identifying a colony mate is not based on the frequency or likelihood of prior contact. As long as the individuals produce appropriate identity cues (or "labels": Tsutsui 2004) and recognize them on one another, they will accept the other as a colony mate even if they have not been in contact before, regardless of whether they happen to live far apart or to be from the same locality. Nor is it clear at what distance "direct cooperative interactions are impossible." Rather than moving indiscriminately, ants of many species specialize in parts of the home range (Hölldobler 1983; Fresneau 1985; Rosengren and

Fortelius 1986; Traniello et al. 1991; Kohler and Wehner 2005; Buczkowski and Bennett 2006), limiting their interactions with the majority of their colony mates. The surprise, then, is how far Argentine ants wander: Heller, Ingram, et al. (2008) were able to detect workers marked with food dye up to 50 meters from the initial food source after 2 weeks, whereas Markin (1968), using a radioactive tracer, found ants commonly traveled even further and faster. In fact, many went as far as he could measure, 40 meters, in just 3 days.

Most ant species have a narrow range of mature colony sizes (Hölldobler and Wilson 1990). Only in a few species like the Argentine ant do colonies grow without bounds under favorable conditions. I propose that the word supercolony be employed only for colonies that show such indeterminate growth, which is the most distinctive attribute of these species. Such ants are of course by necessity polydomous. “Supercolony” has furthermore been applied only to colonies of such species that have reached an exceptional size (which is why I will use colony and supercolony interchangeably to describe any large Argentine ant society: see the GLOSSARY). I therefore propose that a particular colony be referred to as a supercolony when its population is at least a million ants. Why? Among multicellular animals other than humans, only a few ants and termites have colonies reaching a population of about a million, with colonies of much greater size being restricted to supercolonial species (except certain army ant colonies, which exceed this number somewhat, e.g., Leroux 1982).

I agree with Pedersen et al. (2006) who suggest another inconsistently employed term, unicolonial, be used to describe any species that can form supercolonies rather than to connote the obligatory absence of colony distinctions. Where no distinct colonies have been found, there is always the chance that supercolonies exist but have not yet been distinguished—as was true for Argentine ants generally until Suarez et al. (1999) alluded to the presence of multiple colonies in California (see Moffett 2010)—or that one supercolony has taken over completely by dominating the area before other colonies arrive or by driving its competitors to extinction.

Supercolonies might turn out to differ in organization and ontogeny among the unrelated ant species to which this word has been applied (e.g., Helanterä et al. 2009). For this reason, I focus this report entirely on Argentine ants—certainly it is hard enough to disentangle what some authors mean by nest or colony (society) for this relatively well-studied species. My arguments are in part semantic, and yet these words refer to fundamental sociobiological concepts that have been largely ignored, especially when compared with the numerous expositions published about such terms as “altruism” and “group selection.”

SUPERCOLONIES ARE NOT AGGREGATIONS OF MANY SMALLER COLONIES

Argentine ants in a supercolony recognize each other as part of one society even though they can be distributed in a complex patchwork over a wide area. Any sufficiently populous society is likely to develop a complicated spatial organization, in part as adaptations to occupying a broad and varied environment. Some of this population structure will represent responses to variation in such basic factors as temperature and humidity; some of it might be the outcome of socially driven rules for the ontogeny of nests and trails, as when weaver ants build barrack nests at strategic defense locations around a colony perimeter (Hölldobler 1983). The spatial organization of polydomous colonies is unfortunately little studied. To date, few patterns are clear (such as a the minimum nest population size of Pharaoh ants: Buczkowski and Bennett 2009), and there is no indication of a general “polydomy syndrome” (Debout et al. 2007; Steiner et al. 2010). The need for further research is especially compelling for supercolonies because they dominate entire landscapes.

Deborah Gordon and coauthors focus more than anyone else on the levels of organization within Argentine ant supercolonies, through their research at Jasper Ridge Biological Reserve, in the foothills of the Santa Cruz Mountains (most relevant here: Ingram and Gordon 2003; Heller and Gordon 2006; Heller et al. 2006; Heller, Ingram, et al. 2008; Heller, Sanders, et al. 2008). As defined by genetics (van Wilgenburg et al. 2010) and the extreme aggressive response of its workers to conspecifics (Holway et al. 1998), the Jasper Ridge ants belong to the Large Supercolony, at the northern limit of its California range (Suarez et al. 2001).

Ingram and Gordon (2003) found evidence for population structuring, that is, “a lot of genetic diversity, which indicates that there were probably many introductions [to Jasper Ridge] in the past” (Gordon, quoted in Schwartz 2004). Although introductions through jump dispersal would homogenize a population in the long term, recent dispersal events may indeed contribute to this genetic patchwork in a kind of transient effect, particularly behind a growing colony border where the ants advance onto unoccupied terrain primarily by nest budding (Ingram and Gordon 2003).

The genetic differentiation recorded by Ingram and Gordon (2003) has been brought to bear to support the view that what others call supercolonies should be treated as “genetically related groups of colonies” (Gordon 2010a), that is, collections of many small colonies. But experiments in which ants are translocated have shown that such introductions succeed only when the arriving population not only has the same pedigree but the same identity as those Argentine ants already occupying the site. The transplanted ants, being vastly outnumbered, will be killed unless they come either from another place in the same contiguous supercolony population or one of its offshoots or from its mother population in Argentina or one of its offshoots. Regardless of any geographic variations among them, all these ants were, and remain, part and parcel of the same society.

What then are the “groups of colonies” mentioned by Gordon (2010a)? Prior to Gordon (2010b) writing “there is no functional super-colony of Argentine ants,” Gordon and coauthors (Heller et al. 2006) described supercolonies as being “sub-divided into many smaller colony units” that are “clusters of interacting nests”:

> Nests may be considered to belong to the same supercolony if, when ants from those nests are placed together by an experimenter, the ants do not fight. By contrast, nests belong to the same colony only if they are connected by trails.

Broadening this definition to consider the interchange of ants and resources generally, not just those moving along pheromone trails, Heller, Ingram, et al. (2008) define an Argentine ant colony as “a group of nests among which ants travel and share food.”

Putting aside for the moment the question of what might cause the nests to cluster, how significant are these movement patterns? We should not be surprised by this species showing some level of population viscosity and intense local interactions based on our knowledge of other polydomous ants (e.g., Hölldobler and Lumsden 1980; Traniello and Levings 1986; Debout et al. 2007). More specifically, we would expect most of the flow of queens and workers to occur between the nearby nests, with the workers laying down trails to food from the closest possible nest sites and successively smaller portions (if any) of this food reaching more distant locations through a series of secondary trails that largely connect neighboring nests, as Heller, Ingram, et al. (2008) describe. Equating nest clusters with colonies is therefore a premature and probably unrealistic conclusion, not only because of the absolute and unmistakable borders between (super)colonies but because the data in Heller, Ingram, et al. (2008) cannot exclude some transfer of ants and food between the clusters that contain up to 5 million ants; indeed, by stating that "the ants tend to share resources within a spatially bounded group of nests," the abstract of this article allows that such exchange can occur between the clusters.

Even assuming that no ants and food move between nest clusters, a few questions need to be addressed to adequately show that the clusters are permanent "distinct" populations—certainly before granting them the status of colonies. Most critically, how is the separation of clusters maintained, given the lack of antagonism among all the ants throughout Jasper Ridge—do they have different identity cues? (Heller, Ingram, et al. 2008 cite Rosengren and Pamilo 1983 for other instances in which ants and food are not exchanged between nests and yet "relations may be neutral or agnostic," but I was unable to find any such cases in this paper, and Pamilo P, [personal communication] considers the question still open.) Are there persistently unoccupied regions between clusters that all ants avoid even when the habitat is favorable; or is there a line between clusters that the ants never cross? In either case how do the territorial demarcations arise? Alternatively, do the home ranges of the ants from the different clusters overlap, with each worker always returning to her "home" cluster? Is intermixing between nest clusters impossible—for example, do ants transferred experimentally to another cluster avoid the local population and never enter its nests, and how do workers keep from building trails that connect clusters when food baits are placed between those clusters? Finally, is the separation of nest clusters truly so stable the groups of nests can be said to "reproduce independently" (Gordon 2010b)? Though what is meant by "reproduce" and "independently" is unclear given the queens do not disperse on mating flights: Does one cluster bud a new autonomous cluster?

Heller, Ingram, et al. (2008) conclude that "what was thought to be an enormous phalanx of ants, blanketing huge regions, is instead a mosaic of small, distinct, and very effective legions." Yet no one describes an Argentine ant (super)-colony as a single "phalanx," in that the distribution of ants within each colony is known to be far from either continuous or homogeneous. Researchers since Newell and Barber (1913) have found Argentine ants to be "nest site opportunists" (Hölldobler and Wilson 1977), taking over protected sites that offer suitable temperatures and moisture levels and changing nests as conditions change, for example, with inclemency or season (Markin 1970; Holway and Case 2000; Menke and Holway 2006). As a result, the nests can be a patchily distributed, though under these circumstances even the word nest is problematic, as Rosengren and Pamilo (1983) describe: "It is sometimes a matter of semantics whether we prefer to characterize a *Formica* colony as an aggregate of cooperative nests or as a single but highly decentralized supernest." This is true for Argentine ants, where some of the queen and brood traffic between nest chambers happens to occur across the ground surface rather than along below ground passages. Each site (or nest) therefore contains a constantly changing assemblage of workers and queens rather than a static group of its original founders (as should not be assumed for species with nest budding, e.g., Gardner and West 2006).

One result of this fluid organization is that across the vast range of any Argentine ant (super)colony are countless instances in which nests containing workers and queens have become separated from those of their colony mates by the absence of connecting trails. Most researchers report that such nests can remain apart briefly or indefinitely, depending on its degree of isolation, such that portions of a colony merge or separate as conditions and opportunities permit. In contrast, Heller, Ingram, et al. (2008) and Gordon (2010b) consider their nest clusters to be independent and apparently permanent (albeit seasonally expanding and contracting) social structures.

I will not argue between these points of view, except to say that whether nest clusters are ephemeral or permanent, the distribution and connectedness of a population cannot be used as the basis for defining a colony: proof of identity cues remains paramount. Regardless, if Argentine ants are not the nest site opportunists that most researchers suppose but rather form nest clusters of functional importance, these clusters deserve to be given a suitable name and studied in depth.

How do the clusters at Jasper Ridge arise? Could their existence be explained, for example, by purely environmental factors? Many of the Jasper Ridge nests have been occupied for years (Heller et al. 2006). Given that Argentine ants generally do little excavation from scratch (Newell and Barber 1913), this suggests that the colony may take over persistent patchily distributed cavities such as abandoned burrows. In addition, it is reasonable to infer from the seasonal shifts in nest clusters that the ants are avoiding areas of oversaturated soil: "these aggregations break apart and disperse" (Heller, Sanders, et al. 2008) and nests become "more randomly distributed" (Heller, Ingram, et al. 2008) when more sites become suited for Argentine ants in the dry season (Heller, Sanders, et al. 2008). (During the wet season, the colonies often retreat to nests "at the base of shrubs in which the ants tend scale insects," so food may also be an issue: Gordon 2010a.) Soil saturation at Jasper Ridge varies widely at the spatial scale of tens of meters at which the patches of nests occur, even across areas that appear otherwise similar (Jackson RB, personal communication). The dry conditions prevalent around San Diego lead to the opposite problem, often relegating Argentine ants to riparian zones and watered lawns (Menke and Holway 2006). Impassably wet or dry stretches would put limits on occupancy and exchange that are very different from the boundaries between colonies.

The genetic differentiation recorded by Ingram and Gordon (2003) between sites at Jasper Ridge is at the same low level as within the smaller supercolonies of Argentina (Tsutsui et al. 2000; Pedersen et al. 2006; Vogel et al. 2009) and therefore appears insufficient to disrupt the unity of this supercolony or to justify the hypothesis of separate colonies within it. Nevertheless, every supercolony has the opportunity, unavailable to a more locally confined society, of having parts of its population diverge by genetic drift or natural selection (in the latter case, acting mostly on queens [Helanterä et al. 2009], though the population viscosity seen in this species, especially by Heller, Ingram, et al. 2008, may allow selection to act on the worker caste as well). The ants stay bound together as long as the colony identifying cuticular hydrocarbon signature is not adversely affected. Whenever it is, however, the mutation will be weeded out because, with queens never dispersing from their mother colony, affected queens and their offspring will be quickly killed by colony mates. Although the genetic uniformity of the largest supercolonies (Tsutsui et al. 2000; Pedersen et al. 2006, van Wilgenburg et al. 2010) suggests behavioral plasticity is more important than local adaptation in explaining the survival of this broad generalist across diverse landscapes, the possibility therefore remains that evolutionary changes can arise from place to place within wide-ranging Argentine ant colonies. This could explain the subtle genetic variations recorded by Ingram and

Gordon (2003). Yet these changes do not signify that separate colonies exist.

SUPERCOLONIES ARE NOT "EVOLVED" COLONIES

The evidence indicates that all Argentine ant colonies share a capacity to grow to any size, which can seem implausible: To make use of the perspective famously suggested in the final chapter of "Sociobiology" (Wilson 1975), imagine the confusion of a zoologist from another planet who first visits Earth when all people live in hunter-gatherer groups and then returns to find us inhabiting nations with populations exceeding a billion. Many studies have therefore pursued the alternative proposition, that, to form the supercolonies found elsewhere in the world, Argentine ants have had to be altered fundamentally from their source populations in Argentina, by evolving through either natural selection or genetic drift caused by population bottlenecks (Holway et al. 2002; Giraud et al. 2002; Tsutsui et al. 2003; Suarez et al. 2008).

As described below, however, none of the 5 features normally mentioned as unique to invasive colonies of *L. humile* require evolutionary changes in the ancestral (native Argentinian) repertoire of the species:

1) Introduced populations show "no apparent antagonism" (Suarez et al. 2008) and have "poorly defined boundaries" (Buczkowski et al. 2004). Incredulity is often professed (e.g., Tsuji 2010) at what can appear to be a complete absence of aggression among invasive Argentine ants at sites far from the distinct territorial borders of a colony (where any and all conspecific fights occur in this species, as we expect for any polydomous ant with absolute territories: Hölldobler and Lumsden 1980). Yet because ants form anonymous societies, it is unlikely any difference in discrimination behavior is required to integrate either a 100-m-wide colony in Argentina or a 100-km-wide introduced colony. Certainly, both are enormous from the point of view of the ants, and, indeed, aggression between colonies could reach similar intensities in native and introduced populations (Vogel et al. 2009). To summarize, then: Within any spatially uninterrupted population of Argentine ants, distinct boundaries marked by fighting indicate the presence of multiple colonies, whereas the absence of such boundaries shows there is a single colony.

2) Native populations coexist with other ants in species-rich communities, whereas introduced Argentine ants are competitively dominant, wiping out other ant species (LeBrun et al. 2007; Suarez et al. 2008). This difference arises because "interactions with other dominant ant species clearly compromise the competitive ability of *L. humile* in northern Argentina," whereas invasive colonies are released from interspecific and intraspecific competition (LeBrun et al. 2007; Suarez et al. 2008). Competition may explain another recently discovered attribute of the native Argentine ant colonies: their high turnover. While no introduced colony is known to have died out even after many decades at a site, about one-third of the colonies in Argentina are replaced at a given location by others each year (Vogel et al. 2009).

3) Introduced colonies achieve higher ant densities (e.g., Tsutsui et al. 2003). This distinction is believed to arise because colonies come to monopolize areas in which they no longer face population-growth limits incurred elsewhere by inter- and intraspecific competition (though Heller 2004 found the densities of the ants in Argentina is actually no lower than overseas).

4) Native populations are composed of relatively small colonies, typically tens or hundreds of meters wide (though 1-km-wide colonies are known). Relatively small colonies are actually also the norm in nonnative habitats such as the southeastern United States that experience a high frequency of introduction of different colonies of Argentine ant and also of its formidable competitor in Argentina, *Solenopsis invicta* (Suarez et al. 2001; Buczkowski et al. 2004; Vogel et al. 2010). Rather than proposing any intrinsic regional differences in colony ontogeny, it is sensible to view the limits of growth for Argentine ant colonies as universally reflecting the abundance and density of distinct colonies of conspecifics and other competitively matched species.

5) Introduced populations exhibit lower levels of genetic variation and genetic differentiation at local scales (over hundreds of meters: Tsutsui et al. 2000). Tsutsui et al. (2000) attribute this to the founder effect—for example, the founding population of the colony occupying western Europe contained 6–13 queens (Giraud et al. 2002). Such genetic bottlenecks should be ubiquitous among Argentine ants, however, including native populations, because a new colony appearing at a site in Argentina likewise will have arrived by jump dispersal of a group of ants (Helanterä et al. 2009), prior to the arrival of humans probably carried mostly on river-borne detritus in the floodplains where the ants live. Indeed, some native colonies are now known to be less diverse than some of the "supercolonies" in other parts of the world (Vogel et al. 2010). Founder effects may nonetheless be more severe overseas, and so may lower the diversity in invasive colonies, due to the small size of founding groups likely to survive a long voyage; the rarity of multiple inoculations of ants from the original mother colony when its source population is so distant; and the fact that many invasive colonies originate from other invasive populations that themselves underwent severe bottlenecks (Buczkowski et al. 2004; Corin et al. 2007; Vogel et al. 2010).

The fifth difference, loss of genetic diversity in "tramp" colonies, has been the subject of considerable theorizing based on a supposition that "increased similarity in introduced populations appears to promote widespread cooperative behavior" and "stabilize the unicolonial colony structure" (Tsutsui et al. 2003). As an explanation for this lowered diversity, an alternative to the "genetic bottleneck" hypothesis mentioned above is that there has been "genetic cleansing"—selection against rare genes influencing colony identity (Giraud et al. 2002). Both hypotheses are based on the supposition that evolutionary events simplify the genetics of colony identification, making workers more likely to treat one another as colony mates and alleviating the possibility of aggression between nests that would lead to social breakdowns. Although the low diversity caused by either founder effects or genetic cleansing might result in a fitness advantage of one colony relative to another (e.g., by causing a swifter offensive combat style: Tsutsui et al. 2003), there is nothing to show that this "similarity tolerance" (Queller 2000) is essential to the formation or functioning of large colonies per se (as later recognized by Giraud and coauthors, who retracted the genetic cleansing hypothesis in Pedersen et al. 2006). In fact, neither large colony size nor polygyny (the presence of multiple egg-laying queens) has been proven to cause society-level breakdowns among the workers of any ant species, and even Argentine ant supercolonies harboring the highest levels of diversity operate efficiently and without any sign of aggression among their many nests (Tsutsui et al. 2003; I exclude the periodic culling of queens that occurs in colonies of all sizes without social disruption: Keller et al. 1989). This means it is unlikely that these invasive colonies can be destroyed by increasing their internal genetic diversity to the levels found in their source colonies in Argentina (as proposed by Queller 2000; Tsutsui et al. 2000). The alternative of introducing competing colonies should, however, reduce the density of the ants (point 3 above) and thereby alleviate their environmental effects, though even this strategy is unlikely to succeed against a well-established supercolony.

The fact that “all nests function in an apparently cooperative, unicolonial fashion” within a supercolony (Holway et al. 2002) should not puzzle us if, rather than postulating that each invasive population convergently evolves all the characteristics described above, we propose that supercolonies everywhere, large or small, are simply following the dictates of the ancestral behavior of the Argentine ant (Chapman and Bourke 2001; Pedersen et al. 2006; Helanterä et al. 2009, Moffett 2010). In this view, any colony in Argentina could grow to the dimensions of a supercolony abroad and similarly dominate its environment with a high worker density if enough of its competitively matched neighbors were removed. Even if some tramp colonies evolve in response to the habitats they colonize, then, the evidence suggests that such local adaptations are not essential in generating the typical characteristics of overseas supercolonies.

In summary, a focus on how social animals distinguish group members from outsiders can clarify many issues about sociality, including in ants. Argentine ant colonies—or supercolonies, given their capacity for growth without limits—turn out to be like those of other ants: they are single entities that maintain a separation from each other by means of a reliable and enduring self-identity. Looking at Argentine ants this way is not only accurate but allows the most latitude for talking cogently about their colonies and the colonies of ants generally.

The root of much of the confusion about Argentine ants is that the “supercolonies confound our notions about societies, populations, and species like nothing else” (Moffett 2010). Consider how Argentine ants establish independent colonies. With no mating flight to allow a queen to start a nest with an identity separate from that of her natal colony, an intriguing possibility is that no truly new Argentine ant colonies ever arise, except as follows: Geographically isolated populations of the same colony might evolve to shift the genetic basis of their identity to the extent that the groups would start to kill each other if they came into contact again (Moffett 2010, p. 218; as may be occurring on the island of Corsica, which is occupied by what appears to be a long isolated part of the continental Europe portion of the Large Supercolony: Blight et al. 2010). Each Argentine ant colony, both in Argentina and abroad, potentially lasts indefinitely (by spreading locally through budding, or long distance through jump dispersal) as a “closed breeding unit” (Vogel et al. 2009), rejecting both queens and males from outside colonies (Jaquiéry et al. 2005; Thomas et al. 2006; Vogel et al. 2010; Sunamura et al. 2011) and possessing its own diagnostic genetically based characteristics (Torres et al. 2007). Therefore, the colonies appear to take independent evolutionary paths, virtually as sibling species (Helanterä et al. 2009; Drescher et al. 2010; Moffett 2010).

Despite the massive, seemly relentless, and possibly accelerating success of Argentine ants overseas during last century, the ultimate demise of their largest invasive supercolonies has been predicted based on the expectation that the worker caste in them will be altruistic toward unrelated individuals within a colony and so will no longer evolve adaptively and will degrade with time (Queller and Strassmann 1998). The nest clumping described by Heller et al. (2006) could potentially alleviate this difficulty for them (Helanterä et al. 2009). Regarding the Argentine ant’s competitive abilities, the degradation may be slow to manifest because, with their dense populations, Argentine ants are extreme examples of Lanchester’s square law, which shows that the poor fighting ability of the workers is trumped by their huge numbers (Franks and Partridge 1993; McGlynn 1999). Even viewed very long term, however, the eventual dissolution of large supercolonies should be no consolation to conservationists: it is not clear that modest-sized supercolonies are any less successful than large ones in exterminating native species. Moreover, large supercolonies may continue to arise as long as there are source populations of smaller Argentine ant supercolonies, such as those that have invaded the American southeast.

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