Animal behavior: an essential component of invasion biology

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A major challenge of invasion biology lies in the development of a predictive understanding of invasion processes. Attempts to identify the proximate causes of invasion success or to predict rates of spread seldom emphasize behavioral characteristics. Recent experimental work, however, illustrates that insight into the proximate causes of animal invasions often hinges on a careful assessment of behavioral mechanisms. For this reason, behavioral analyses should be more fully integrated into research on biological invasions. In addition to enhancing a general understanding of invasion processes, such approaches provide potentially underused opportunities for basic research in animal behavior.

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While ecologists have focused on ecological, genetic and life-history characteristics of invasive organisms[1–3], behavioral traits have received less attention. The rudimentary state of knowledge concerning the role of behavior in animal invasions perhaps reflects a more general lack of information concerning invasion processes. Given the enormous ecological problems and economic costs associated with biological invasions[4], determining how behavioral mechanisms contribute to invasion success is now more relevant than ever. This information is particularly important because successful control efforts require a detailed understanding of the mechanisms underlying invasion success.

To understand how specific behavioral characteristics influence invasion success, it is necessary to distinguish factors influencing the separate probabilities of colonization, establishment and spread; attributes that influence one aspect of invasion success might not influence others. For example, high dispersal ability, omnivory, gregariousness and asexuality are commonly believed to enhance the probability of colonization and establishment[2,3], but it is less clear how these attributes influence the competitive ability of an invasive species or its rate of spread subsequent to establishment. Here, we focus on behavioral mechanisms responsible for the post-establishment phase of invasions. Specifically, we discuss the importance of behavioral mechanisms in determining the outcome of competitive interactions between invasive and native species and how variation in behavioral traits influences patterns of spread. We focus on a few well studied examples; however, our discussion likely pertains to animal invasions in general.

Competitive displacement of native species

One attribute commonly invoked to explain the success of invasive animals is interspecific aggression. This observation applies to a range of animal taxa invading a variety of habitats[5–9]. Although interspecific aggression might be key to the ability of certain invasive species to displace native species[8,9], its general importance remains unclear.

For example, recent work on gecko invasions illustrates how interspecific aggression plays only a minor role. On islands throughout the southern Pacific Ocean, the sexual house gecko (*Hemidactylus frenatus*) has been displacing the asexual mourning gecko (*Lepidodactylus lugubris*). Although preliminary work found evidence for increased levels of aggression and antagonism by *H. frenatus* against *L. lugubris*[6], further research revealed that direct behavioral interactions between these two geckos were rare in the field and that the competitive displacement of *L. lugubris* by *H. frenatus* was largely the result of the superior exploitative abilities of *H. frenatus* for clumped resources in structurally simple habitats[10,11]. These studies are unique in that they pinpoint the mechanisms responsible for the success of an invading species by testing specific hypotheses for the relative importance of exploitative versus interference competition in the context of a widespread competitive displacement.

Interspecific aggression is also commonly invoked to explain the superior competitive ability of invasive ants[7,12–14]. Also typical of these species, however, is a reduction in intraspecific aggression, perhaps resulting from a reduced ability to recognize nestmates[7,12]. As a consequence, invasive ants are often unicolonial, occupying expansive supercolonies that lack obvious behavioral borders[7,12,13].

A well studied example is the red imported fire ant (*Solenopsis invicta*), which has invaded much of the southeastern USA and has been the focus of intensive ecological, behavioral and genetic studies[15–17]. The extent to which *S. invicta* displaces native ants (such as *S. geminata* and various *Pheidole* spp.) partly depends on an interaction between variation in its social behavior and escape from natural enemies.

In its introduced range, *S. invicta* occurs in two distinct social forms: a single-queened (monogyne) form and a multiple-queened (polygyne) form[15]. Although both social forms also occur in Argentina[15,17], polygyne colonies in the USA have high numbers of unrelated queens, whereas polygyne colonies in Argentina have multiple, closely related queens[16]. Compared with native populations of fire ants, introduced populations maintain higher nest densities, partly resulting from a lack of host-specific pathogens and parasites[18]. The higher population densities decrease opportunities for independent colony founding and increase the prevalence of polygynous colonies as dependent colony founding (mated queens adopted into established colonies) becomes more common[15]. Nestmate discrimination in polygyne colonies of *S. invicta* is greatly reduced relative to monogyne colonies[19], perhaps as a consequence of increased queen number. The loss of pronounced intraspecific aggression then leads to a breakdown in territoriality and a further increase in population density: polygyne populations are, on average, twice as dense as monogyne populations[20]. The higher nest densities in turn influence the competitive asymmetry between red imported fire ants and native ants.

Although both forms of *S. invicta* displace native ants, polygyne populations displace more species than do monogyne populations[21]. The greater numerical abundance of the polygyne form is probably key to its stronger competitive ability; numerical advantages determine the outcome of competitive interactions in ants generally[13]. The apparent disparity in competitive ability between the two social forms of *S. invicta* illustrates both how variation in behavioral characteristics can influence invasion success and how shifts in behavioral characteristics following introduction can enhance competitive ability.

   PII: S0169-5347(99)01636-5

The Argentine ant (*Linepithema humile*) provides another example of a species that, following introduction, has undergone behavioral changes that have increased its competitive ability. For example, recent work in South America demonstrates that the extreme unicoloniality typical of introduced *L. humile* populations is not representative of native populations. In its native northern Argentina, *L. humile* commonly exhibits pronounced intraspecific aggression over small spatial scales (<100 m)[22].

In contrast, introduced populations in California and Chile rarely exhibit intraspecific aggression at any spatial scale[22,23]. This widespread loss of intraspecific aggression and the concomitant breakdown of territoriality appear to be important contributing factors to the high population densities typical of introduced populations[12,22–24], although escape from coevolved natural enemies[25] could also play a role. The Argentine ant's high population densities are central to its ability to excel at both interference and exploitative competition[26,27]. For example, individual Argentine ant workers are often unable to win fights against individual native ant workers, and must therefore rely on numerical advantages to prevail in direct confrontations with other species[26]. High population densities also contribute to its strong exploitative ability: Argentine ants discover and recruit to food more quickly[24,26,27], and in higher numbers[27,28], than many native ants.

The success of highly invasive ants, such as *L. humile* and the polygyne form of *S. invicta*, thus appears to be influenced to a large extent by the population-level consequences of reduced intraspecific aggression. Although detailed studies of other highly invasive ant species, such as the little fire ant (*Wasmannia auropunctata*) and the big-headed ant (*Pheidole megacephala*), have yet to be done, most species of ants that invade natural communities and displace native ants are highly unicolonial[7]. This pattern points to the general importance of unicoloniality as a determinant of competitive dominance in ants. Given that aspects of colony structure of both the red imported fire ant and the Argentine ant differ between the introduced and native ranges, it will be enlightening to determine if shifts in colony structure or social behavior subsequent to introduction are general features of other invasive ants. If so, it will be of great interest to determine whether the routes to unicoloniality differ among species.

Although invasive species commonly exhibit pronounced interspecific aggression, the studies mentioned in the previous paragraphs suggest that other behavioral factors are also commonly involved. In some cases, differential interspecific aggression is only one of several factors responsible for invasion success[5], or is of minor importance[10,29]. It is therefore crucial to test alternative hypotheses for how invasive species outcompete native species[8,10]. Nonetheless, the question remains as to why some invasive species appear more aggressive than the species they displace. Perhaps they come from environments in which heightened aggression is adaptive[30,31]. For example, the infamous aggression of the africanized honeybee (*Apis mellifera scutellata*) is thought to be a response to a more sophisticated suite of nest predators in Africa compared with those present in the native ranges of the more docile races of this species[5].

The studies also suggest that the ecological success of invasive species might result from behavioral changes that occur subsequent to introduction, raising the question of why behavioral shifts occur in species invading new environments. One answer is that a loss of genetic variation, resulting from a bottleneck after introduction, influences behavioral characteristics. Shifts in behavior could also be adaptive responses to new environments. Such introductions can be used to test the selective forces responsible for maintaining behavioral characteristics.

For example, Zuk *et al.*[32] took advantage of unplanned introductions of crickets and phonotactic dipteran parasitoids on islands in the Pacific Ocean to test whether crickets modify their calling behavior relative to the threat of parasitism. Compared with cricket populations lacking parasitoids, male crickets in Hawaii sang less often when parasitoids were active, and delivered songs composed of individual components that were shorter in duration, suggesting that risky behaviors were selected against in the presence of the parasitoids[32].

Similarly, the invasion of the brown-headed cowbird (*Molothrus ater*), an obligate brood parasite, along the west coast of North America[33] provides an opportunity to study the mechanisms involved in the exploitation of novel hosts that have not developed discriminatory or rejection behaviors resulting from an evolutionary history to brood parasites.

These two examples, although not pertaining to the competitive displacement of native species, illustrate how invasions can be used to address fundamental questions in animal behavior.

The role of behavior in determining patterns of spread

An important facet of invasion biology lies in the prediction of post-establishment patterns of spread. This body of research has an especially rich theoretical foundation and has generated successful predictions of rates of spread[34–36], particularly for patterns of spread that resemble diffusion processes. Variation in behavioral characteristics, however, can influence the extent to which patterns of invasion resemble diffusion; such variation can make predicting rates of spread a more challenging task. For example, instances of jump dispersal (either natural or human-mediated) violate assumptions of diffusion models and, if common, make predictions of invasion rate difficult to obtain[36].

Invasive ants provide insightful examples of how variation in behavioral traits can influence patterns of spatial spread. As discussed already, the monogyne and polygyne forms of the red imported fire ant differ in numerous respects, including modes of dispersal and colony reproduction. Queens from monogyne colonies take part in mating flights and found colonies independently, whereas queens from polygyne colonies are adopted into established nests after mating and, as a consequence, colony reproduction occurs by budding[15]. These contrasting modes of dispersal result in a complex pattern of invasion, with the monogyne populations spreading three orders of magnitude more quickly than polygyne populations[37]. Superimposed onto these dual modes of spread is human-mediated dispersal, which can introduce propagules (e.g. small colonies and inseminated queens) well ahead of main invasion fronts. The recent and unfortunate human-assisted arrival of the red imported fire ant into southern California, USA, could offer a unique opportunity to scrutinize the interplay between these different modes of dispersal in a new environment.

The Argentine ant provides an even more extreme example. This species, at least in its introduced range, appears to undergo colony reproduction solely by budding. However, the Argentine ant's opportunistic nesting behavior and general dietary requirements allow this species to commonly associate with humans, greatly increasing the frequency of accidental transport. Because the maximum rates of spread for budding reproduction in this species are a few hundred meters a year, large-scale patterns of spread in this invasion are dictated by human-mediated jump dispersal[38].

These examples illustrate that variation in behavioral characteristics can influence spatial patterns of invasion and that the resulting patterns can deviate from simple diffusion (see Refs 39,40 for additional examples). Such complex patterns of spread are probably common and present an important challenge to the theory on the spatial spread of invasions[35,36].

Conclusions

There has been a recent growth of interest in the importance of behavioral mechanisms to aspects of conservation biology[41–43]. Given the grave problems caused by biological invasions, an improved understanding of how behavior contributes to the competitive ability and spread of invasive animals is also needed. This information will not only aid control efforts for particular species, but the identification of behavioral attributes common to different invasive taxa could also provide a basis for predicting which species have the potential to become problematic invaders.

The behavior of invasive species might also be relevant to basic research in animal behavior. Although a compelling case has been made for using introduced species to study social evolution[15], behavioral comparisons between native and introduced populations can be used more generally to examine the plasticity of behavioral repertoires or to test the specific forces responsible for the maintenance of behavioral characteristics. In this light, invasions might contribute to the study of animal behavior in ways that are reminiscent of how they have been used in community ecology to study interspecific competition[10,30], apparent competition[44] and trophic relationships[3].

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