

CHAPTER 14

The role of behavioural variation in the invasion of new areas

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Overview

Behaviour determines the rate at which invasive species spread, as well as the impact they have on natives. When behaviour varies between individuals (as it almost always does), then the mean behaviour is often less important than the extremes of behaviour. The rate at which a species spreads, for example, is governed primarily by the most extreme dispersers. Similarly, individuals of native species that are extreme in their behaviour may be more, or less, likely to suffer impact from a given invasive species. Thus, we argue, an understanding of behavioural variation is critical if we are to understand the long-term impacts of invasive species in a changing world.

14.1 Introduction

Biological invasions are now widely considered to be a form of global change (Vitousek et al. 1996). In addition to severe economic consequences (Pimental et al. 2000), the introduction of species into new environments can have devastating ecological impacts (Mack et al. 2000; Parker et al. 1999). It is something of a relief then that we don't have a lot more invasive species, particularly given that every year probably hundreds to thousands of species are introduced outside their natural range. Luckily, very few of these go on to establish, spread, and have large ecological impacts. Why is this so? It turns out that the different stages of the invasion process—transportation across dispersal barriers, establishment of a population at the new location, and post-establishment spread—act as strong phenotypic filters, winnowing out the majority of species. Thus, a non-random subset of all taxa are transported, a non-random subset of these are then capable of establishment, and then a non-random subset of these become spreading invaders

(Blackburn and Duncan 2001; Simons 2003; Tingley et al. 2010). Very few species pass easily through all three filters.

Importantly, the same filtering process that applies to taxa also applies to individuals within an invasive taxon (in fact, it applies to the individuals first, and the taxon only as an after-effect). The individuals that are transported, that form established populations, and that become invasive are all potentially non-random subsets of the population from which they originated (Phillips et al. 2010a). Thus, population-level variation in traits associated with invasion success is a key determinant of the success, or otherwise, of a particular invasion.

Invasive species do not, however, occur in a vacuum. As an invader spreads, its interactions with resident species become more widespread and the success of the invader, as well as that of the invaded, may well depend on these interactions. Variation is important here too. Introduced species often interact negatively with native species (either directly, as predators, competitors, and parasites; or indirectly, through habitat modification). So the variation in

traits mediating these interactions will determine which native individuals survive and which do not: natural selection in action.

Many of the traits associated with invasion and interspecific interaction are behavioural. In this chapter, we focus primarily on behaviour during the post-establishment stage of invasion: spread. We discuss the processes that lead to population spread, and some of the behaviours that facilitate those processes. We also discuss the role of behaviour in determining the outcomes of interspecific interactions between introduced and resident species. In both cases we focus not just on behaviours, but on the effect of behavioural variation. We will see that behavioural variation not only matters, but that it is central to understanding both the process of invasion, and the impact of invaders on natives.

14.2 Behaviours influencing the process of spread

14.2.1 The mechanics of spread

Populations spread through space as a function of two fundamental processes: dispersal and population growth (Skellam 1951). Dispersal moves

individuals through space (and into new space), and population growth fills space (including newly colonized space) with individuals. The rate at which a population spreads, then, is determined almost entirely by these two fundamental processes. This said, however, a surprising array of spread dynamics are possible (including lags, accelerating, pulsed, and constant spread rates) depending upon how these fundamental processes are executed (Hastings et al. 2005; Johnson et al. 2006).

If there is variation in a population for traits affecting dispersal or population growth rate, things get more complex. In addition to the two fundamental processes of spread (dispersal and population growth), two unavoidable consequences of spread allow trait variation to come into play (Phillips et al. 2010a). The first unavoidable consequence is that, on the invasion front, individuals are spatially assorted by dispersal ability. This is known as the Olympic village effect, or spatial sorting (Phillips et al. 2008a; Shine et al. 2011), and leads to assortative mating by dispersal ability and runaway selection for increased dispersal on the invasion front (Travis and Dytham 2002; Hughes et al. 2007; Fig. 14.1). The second unavoidable consequence of range advance is that individuals on the expanding

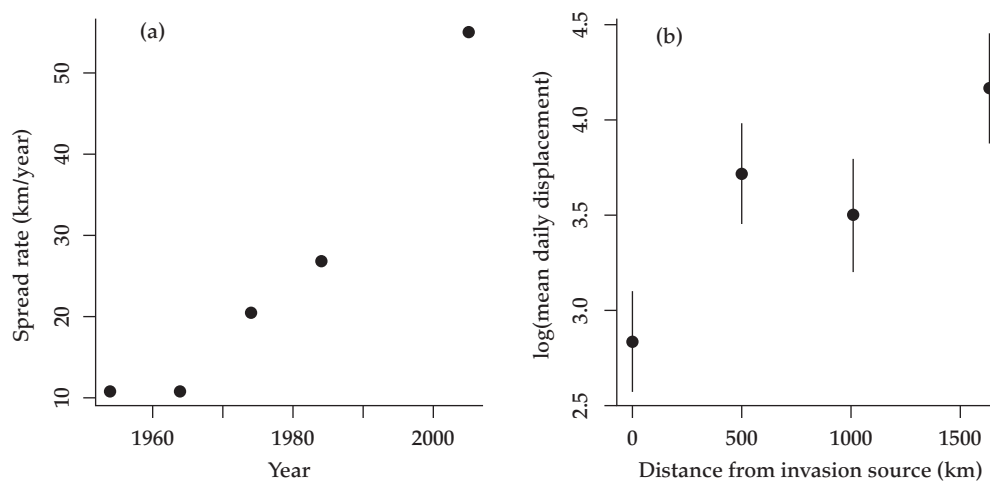


Figure 14.1 The accelerating rate of invasion of cane toads *Rhinella marina* across northern Australia (a), is associated with evolutionarily increased dispersal rates (b) shown here as an increase in mean daily displacement of animals collected from populations spanning the earliest introduction point (zero on the x-axis) through to the still-expanding invasion front. This is a pattern increasingly seen in the rate of spread of many invasive species. Error bars are one standard error. Data redrawn from Phillips et al. 2006, 2008a.

edge are in an environment with a very low density of conspecifics relative to established populations. In such an environment, traits that increase reproductive rate or decrease Allee effects are favoured (Burton et al. 2010).

With these two fundamental processes and two unavoidable consequences, we now have a framework with which to examine the influence of behaviour, and behavioural variation, on spread.

14.2.2 Dispersal behaviour during spread

Dispersal, the permanent movement of an animal from its birth place to its place of first reproduction (*sensu* Howard, 1960), carries strong costs, but despite this, is almost ubiquitous across all living organisms (Clobert et al. 2001). Dispersal, therefore, must also carry strong rewards, and these include the avoidance of inbreeding and kin competition, escape from parasites and pathogens, as well as the subtler advantages of colonizing newly available patches in an extinction prone landscape (e.g. Hamilton and May 1977; Van Valen 1971; Gandon and Michalakis 2001; Weisser et al. 2001). Thus, most organisms disperse, but getting from A to B can be done in an astonishing number of ways. It can be done passively, such as a windborne seed, actively, such as a kangaroo hopping, or in an amalgam of the two.

The most successful invaders are those that spread over large areas very quickly. Invasive species will therefore tend to have behaviours that generate long-distance dispersal relatively cheaply (Bartoń et al. 2009). Typically, such dispersal strategies involve some form of passive or active/passive combination. In terrestrial realms, flight is perhaps the most obvious amalgam of active and passive dispersal: although getting airborne might be energetically expensive, the ability to harness the movement of air once aloft can disperse airborne animals over vast distances. Thus, many of the most rapid and famous invasions have involved flying species, such as the house finch *Carpodacus mexicanus*, house sparrow *Passer domesticus*, the European starling *Sturnus vulgaris*, the Eurasian collared dove *Streptopelia decaocto*, and the gypsy moth *Lymantria dispar* (Elton 1958; Veit and Lewis 1996).

Another cheap technique is to hitch a lift. Small species that allow other, typically much larger, species to effect their movement may get around very cheaply indeed. Some of the best examples of such facilitated dispersal come from epidemiology, where diseases are spread rapidly across an area by their animal vectors (e.g. spread of West Nile virus, Loss et al. 2009; Seidowski et al. 2010). Of course humans also make excellent targets for facilitated dispersal. Human-mediated jump dispersal is not only responsible for creating new foci of invasion well away from established populations, but may also be the primary means by which some species spread at the landscape level (e.g. Argentine ants *Linepithema humile*, Suarez et al. 2001; snails *Xeropicta derbentina*, Aubry et al., 2006).

Finally, in cases where dispersal is active, increased efficiency can be gained by straightening the movement path (Bartoń et al. 2009): individuals that disperse in a relatively straight line will, ultimately, displace much further than individuals following a more tortuous path. Indeed, a tendency to follow straight paths is a clear attribute of the most rapidly spreading populations of invasive cane toads *Rhinella marina* in northern Australia (Alford et al. 2009; Phillips et al., 2008a).

14.2.3 Behaviour and population growth during spread

In broad terms, population growth is the net result of the number of births in a population minus the number of deaths. The number of births and deaths, however, is a gross summary of the myriad behaviours, morphologies, and physiologies that allow individuals in a population to survive, grow, and reproduce. In this light, then, almost any behaviour has some influence on population growth. For logistical reasons then, we focus here on behaviours that have an obvious bearing on the colonization of new areas: behaviours that allow individuals to survive and quickly capture resources for growth and reproduction in a new environment. Although there has been no definitive 'laundry list' of behavioural characteristics that convey invasion success, it has been suggested that some degree of sociality along with high levels of aggression, activity (foraging/search-

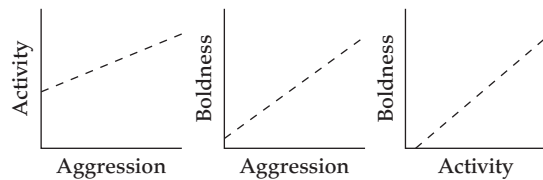


Figure 14.2 Relationship between foraging activity, intraspecific aggression, and boldness in the invasive signal crayfish *Pacifastacus leniusculus*. All correlations are significant ($p < 0.05$) and are based upon comparisons of population means. Data redrawn from Pintor et al. 2008.

ing behaviour), and vigilance (boldness/antipredator behaviour) may be important (Cote et al. 2010; Holway and Suarez 1999; Kolar and Lodge 2001).

Over the past decade, there has been a growing literature on consistent individual differences in behaviour, frequently termed behavioural syndromes or animal personality (Sih et al. 2004a). Some common behavioural traits, such as exploratory behaviour, aggression towards conspecifics, and boldness in risky situations, may be both consistent and positively correlated within individuals (Reale et al. 2007) and could provide an advantage to colonizing species (Sih et al. 2004a; Fogarty et al. 2011). For example, using the framework of behavioural syndromes, Pintor and colleagues (2008) found that foraging activity, intraspecific aggression and boldness were highly correlated across populations of signal crayfish *Pacifastacus leniusculus* (Fig. 14.2). Crayfish were most aggressive, active and bold in introduced areas with low prey biomass and an absence of interspecific competitors, suggesting this correlated suite of behaviours may be beneficial for establishing new populations where resources are scarce (Pintor et al. 2008).

14.3 The effect of behavioural variation on spread

The unavoidable consequences of invasion—reduced conspecific density and assortative mating by dispersal ability on the invasion front—can potentially drive phenotypic changes. These shifts might be simple plastic responses to the new environment, or might reflect evolved shifts in response to directional selection during spread. Irrespective, these phenotypic changes can, in turn, feed back

into the spread process. Importantly, plastic responses will have an almost instantaneous effect on spread rate (as they occur as a direct response to the environment), whereas evolved responses will take longer (several to many generations) to play out. Plastic responses may or may not increase spread rate, whereas evolved responses will likely always increase spread rate.

14.3.1 Plastic responses

Behavioural flexibility, particularly in relation to novel stimuli and introduction into novel environments, has been suggested as a possible explanation for why some species become successful invaders (Sol et al. 2002; Wright et al. 2010). For example, some individuals might quickly notice a new prey type and alter their foraging tactics, whereas others might adopt less plastic strategies (Sih et al. 2010). The more behaviourally flexible individuals would be more likely to prosper in newly-invaded areas; they would be more likely to have positive population growth and less likely to suffer Allee effects. Using brain size as a surrogate for behavioural flexibility, Sol and colleagues found that relative brain size was a strong predictor of invasion success for birds and mammals (Sol and Lefebvre 2000; Sol et al. 2008). A similar pattern has since been observed for invasive amphibians (Amiel et al. 2011), so brain size is shaping up to be a strong predictor of invasion success generally. Although bigger brains might provide greater behavioural flexibility, it is important to note that brain size (or behavioural flexibility) itself may be under selection during the course of an invasion: invasion may be selecting for behavioural flexibility. Whether brain size changes during the course of invasion, or influences spread rate has, however, yet to be adequately tested.

Other brain-size related plastic responses might include learning or social cues. In a world where conspecifics are rare (such as an invasion front), individuals may need to invest greater effort into locating those conspecifics. For example starlings from newly invaded areas are more responsive to the calls of conspecifics than are starlings from long-established areas (Rodriguez et al. 2010). Again, whether this results purely from growing up lonely,

or as a consequence of longer term selection for individuals that are better at finding mates in situations of low conspecific density, is unknown.

Plastic responses might also occur as accidents of a changed environment during invasion. For example, many frog species alter both their behaviour and developmental rate as tadpoles in response to the presence of aquatic predators (Kiesecker and Blaustein 1997; Relyea 2001). One of the consequences of low conspecific density and assortment by dispersal on the edge of an invading population is that coevolved predators often get left behind (Phillips et al. 2010d). If this happens, then the cues driving the typical predator response may be absent, and a morphologically and behaviourally ‘predator free’ phenotype will emerge (even if predators, albeit unfamiliar ones, are still present). Typically, tadpoles in the absence of predators spend more time active, and have higher growth rates than conspecifics in the presence of predators (e.g. Thiemann and Wassersug 2000; Relyea 2001). Higher individual growth rates resulting from tadpoles behaving in a predator free manner could, conceivably, lead to higher population growth rates and faster spread, although this net effect would be an accidental byproduct of an animal in an unfamiliar environment. Alternatively, of course, increased predation rates driven by inappropriate responses to unfamiliar predators could depress population growth and slow spread. The effects of plasticity could, conceivably, either accelerate or decelerate an invasion.

14.3.2 Evolved responses

Traditionally, we have thought about evolution in invasive species as being about adaptation to their new environment (Mack et al. 2000). While this standard adaptive process must indeed be happening after an invasive population has become established, it is increasingly apparent that evolutionary processes on the invasion front itself are driven by additional forces (Phillips et al. 2010a). Invasion fronts can capture rare, and even deleterious, mutations, drive them to high frequency, and then spread them across large areas as the invasion front moves through space (Travis et al. 2007). Coupled with this are the processes of assortative mating by dispersal

ability, and *r*-selection (driven by low conspecific density), which drive selection for increased dispersal and reproductive rates (Burton et al. 2010). Thus, during invasion, behaviours will evolve to increase dispersal and, if possible given trade-offs with dispersal, increase reproductive rates. Our brief survey of behavioural traits that facilitate invasion (above) gives us an idea as to the potential suite of traits that might evolve in this way during invasion.

Empirical evidence for changed dispersal behaviour during invasion is rapidly accumulating. Insects on expanding range edges have been shown to invest more in dispersal than their conspecifics in older, established populations (Hughes et al. 2007; Simmons and Thomas 2004; Léotard et al. 2009), and invasive cane toads in northern Australia have evolved increased dispersal rates on the invasion front relative to their conspecifics from older, established populations (Phillips et al. 2010b; Phillips et al. 2008a).

Empirical evidence for the evolution of behaviours facilitating population growth is, however, weaker. Higher growth rates have been found in invasion front populations of cane toads (Phillips 2009), but the behavioural correlates of this higher growth rate, if any, remain to be elucidated. The increased sensitivity of invasion front starlings to the calls of their conspecifics (Rodriguez et al. 2010) might be plastic or evolved (or both), we simply do not know yet. But as an adaptation to reducing Allee effects and increasing population growth rate on an invasion front, we might expect it to be an evolved shift. Generally, the importance of comparing newly colonized and older established populations inside the invasive range is only recently being appreciated. So the field is open for behavioural ecologists to start investigating behavioural shift in response to range shift.

Another intriguing aspect of evolution during invasive spread is that it may bring together multiple behavioural traits into sets. Being such a strong directed selective pressure, and being directed at dispersal and reproductive rates (complex traits typically driven by multiple behaviours), we would expect range shift to start accumulating individuals with multiple behaviours that increase dispersal and reproductive rates, whilst minimizing Allee

effects (Travis et al. 2010; Shine et al. 2011). In Australian cane toads, individuals from the invasion front grow faster, move more often, move further when they do move, and follow straighter paths than their trailing conspecifics, all of which conspires to increase their net dispersal and reproductive rates (Phillips et al. 2008a; Alford et al. 2009; Phillips 2009). Similarly, we might expect all traits that influence dispersal and reproductive rates to become associated in invasion front populations. Given that many of the traits associated with animal personality (e.g. aggression and boldness: Duckworth 2008; Duckworth and Badyaev 2007; Sih et al. 2004b) may also be associated with dispersal and/or reproduction, range shifts can, over time, assemble populations with distinct personalities (e.g. aggressive, risk taking, and highly active). Why animals exhibit distinct ‘personalities’ is a current focus amongst behavioural ecologists (Dingemanse et al. 2010; Sih et al. 2004b). It may be that selection for dispersal (Cote et al. 2010) during invasion is a currently under-appreciated way for animal personalities to be assembled. Future work exploring this possibility would likely be rewarding. Such work would focus strongly on behavioural variation, and how it varies through invasion history.

14.4 Behavioural variation and the impacts of invasive species on natives

Invasive species are typically of broad interest because of their perceived impacts on native species. Almost all the impacts of invasive species on natives are likely mediated by behaviour. Both the behaviour of the invader, and that of the native, determine the outcome. Where the outcome of an interaction is negative (either for the native or the invader, or both), we might expect to see rapid evolution of behaviour. Thus, species invasions offer immense opportunities for behavioural ecologists interested in the evolution (and coevolution) of behaviour. Invasive species often represent a novel selective force in the environment that native species need to respond to through behavioural means (Ashley et al. 2003).

Many of the biggest impacts from invasive animals occur when the invader is a predator. More

than 22 species of native mammal were lost from the Australian continent following the arrival of the invasive cat and fox (McKenzie et al. 2007). Similarly, in Lake Victoria, the introduction of the Nile perch *Lates niloticus* led to the extinction of around 200 species of native cichlid fish (Ogutu-Ohwayo 1999). In New Zealand, the introduction of Pacific rats *Rattus exulans* led to the extinction from the mainland of many species of birds and lizards (Townsend et al. 2007). These examples of extinction point to situations where native species simply didn’t have appropriate behavioural variation (in both evolved and plastic senses) to cope with the arrival of a new predator. Potentially, however, there may be many more (unreported) instances where natives can modify behaviours in response to predation, and so persist. For example, Hoare et al. (2007) show that, on New Zealand islands colonized by Pacific rats, native geckoes *Hoplodactylus duvaucelii* rapidly shift their habitat preferences to avoid interactions with the predatory rats. Unfortunately, these subtler examples (where native species are not extirpated, but survive through behavioural shifts) are understudied.

The impacts of introduced species are also likely to be density dependent (Yokomizo et al. 2009). Therefore, behaviours that influence the density of species in introduced populations may disproportionately influence their impact. For example, intraspecific competition is often cited as a primary mechanism that regulates relative abundance (e.g. Ryti and Case 1988; Comita et al. 2010), so highly territorial species that exclude conspecifics from large areas are not likely to become ‘high-impact’ invasives. In contrast, social species that do not exhibit discrete or exclusive territories may attain higher densities and may also avoid Allee effects that inhibit population spread. While an association between intraspecific aggression and impact has not been explored across many taxa, it has been suggested as a mechanism for the success of invasive ants (Holway and Suarez 1999). Many introduced populations of highly invasive ants are ‘unicolonial’—spatially separate nests behave as ‘one colony’ across the entire population (Holway et al. 2002); a situation that is not always the case in their native range. In unicolonial populations where

intraspecific territorial behaviour is absent or reduced, colonies often exhibit higher resource retrieval rates, and greater brood and worker production relative to native species that exhibit territorial behaviour (Holway et al. 1998). The origin and maintenance of unicoloniality in ants may provide insight into the role of behavioural variation in the success and impact of invasive species more generally, and is currently the subject of intense debate and study (Helantera et al. 2009).

Behavioural variation across environmental contexts may also be important in influencing the outcomes of competition with invasive species. For example, by hanging lights in abandoned Second World War aircraft hangers in Hawaii, Petren and colleagues (1993) were able to experimentally demonstrate how increasing the local abundance of insects influenced competitive interactions between two species of gecko: the invasive *Hemidactylus frenatus* and the resident *Lepidodactylus lugubris*. The larger, more aggressive *H. frenatus* was able to forage more effectively and monopolize clumped resources in open areas relative to the less aggressive *L. lugubris*. However, the effects of competition between the species disappeared if resources were not clumped or if complex topography was added around the light sources to provide safe refuges for the less aggressive species to hide in (Petren and Case 1998; Fig. 14.3).

Another well-studied example of behavioural mediation of impacts concerns the arrival, in Australia, of the toxic cane toad. In Australia, toads occur in very high densities, and show no territoriality. They are a predator, but their major impact appears to be on native predators that mistake toads as palatable prey. Numerous native predators, which were naïve to the toxins in the toads' skin, have been fatally poisoned following the arrival of toads. Despite the simplicity of the impact mode—poisoning—impacts have varied tremendously, both within populations as well as between closely related species (Shine 2010). Much of this variation in impact is driven by subtle differences in the natives' prey handling behaviour. For example, death adders *Acanthophis praelongus* in northern Australia handle different prey species (all of which are frogs) differently, depending upon the prey spe-

cies' toxicity (Phillips and Shine 2007). Non-toxic frogs are simply grabbed and swallowed, whereas frogs which secrete a sticky glue or which are neurotoxic are envenomated and released to die, after which the snake then tracks the meal down and ingests it. Snakes wait around ten minutes between bite and consumption for the gluey frogs but wait much longer (typically around 40 minutes) before tasting and, ultimately, consuming the neurotoxic species. When these snakes first encounter a toad, the response of individuals varied: some snakes treat the toad as if it was non-toxic, while others treat them as if they were gluey, neurotoxic, or something that is ultimately inedible (Hagman et al. 2009). Almost all death adders that consume a toad die, thus, a snake's classification of this new prey item (and the subsequent behaviours that flow from that classification), strongly defines the impact that the arrival of toads will have on that individual. This correlation between behaviour and impact suggests strong selection operating on prey preference in this species (Phillips et al. 2010c), and indeed at least one Australian snake species appears to have evolved behavioural avoidance of toads as prey due to this strong selection pressure (Phillips and Shine 2006).

These examples show the critical importance of the behaviour of both native and invasive species in mediating the invasive's impact. Importantly, however, they also demonstrate the critical importance of behavioural variability (both plastic and evolved) in determining the long-term outcome of that impact. Behavioural plasticity or rapid evolved responses may be integral for native species to persist in invaded landscapes.

14.5 Conclusion and future directions

Through both theory and example, we have demonstrated the importance of behaviour to both the spread and impact of invasive species. Spread rate (governed by dispersal and population growth) is, ultimately, an outcome of the behaviour of the invader. Similarly, the impact of the invader depends on the interaction between its behaviour and that of nearby native species. The central importance of behaviour in these cases is not particularly surpris-

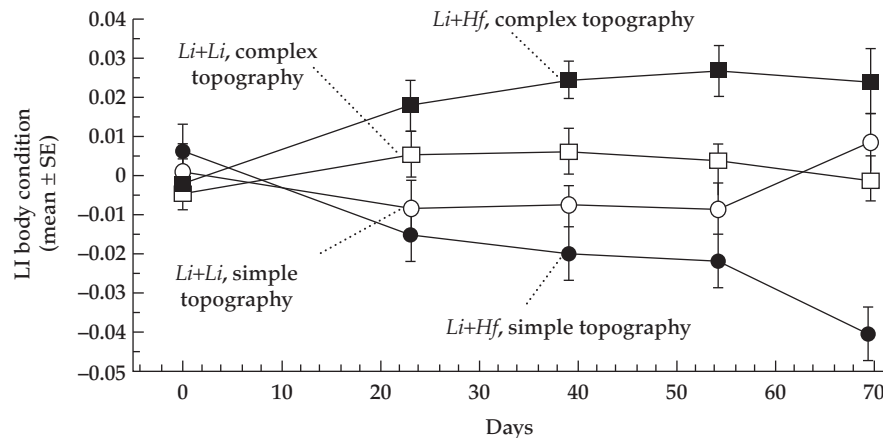


Figure 14.3 The distribution of resources (clumped versus dispersed) and the degree of habitat complexity influences the outcome of interspecific competition between invasive *Hemidactylus frenatus* Hf, and resident *Lepidodactylus lugubris* Li, geckos. When insect resources are clumped at light sources, and the space around the lights is open, the larger more aggressive *Hemidactylus* can monopolize access to insects. However, if resources are not clumped and/or baffles are placed around the lights creating refuges for the geckos, *Lepidodactylus* are able to forage more effectively, evidenced by an increase in body condition. Figure reprinted from Petren and Case 1998, with permission. Copyright (1998) National Academy of Sciences, U.S.A.

ing, but consideration of behavioural variation (either plastic or evolved) can lead to surprising results. For example, early predictions of the spread rate of cane toads across northern Australia were rendered wildly inaccurate by the rapid evolution of increased dispersal behaviour in this species (Phillips et al. 2008b). Similarly, many predictions of deleterious impacts of invasive species on natives may prove to be fleeting as native species exhibit behavioural flexibility in response to the invader (e.g. Langkilde 2009).

The future, thus, should be about variation. When an invader arrives, the average behaviour often turns out to be much less important than extremes of behaviour. Extreme dispersers come to dominate the vanguard of an invasive population, and extreme behaviours may be associated with individuals most or least at risk from the presence of an invader. The challenge for behavioural ecologists is thus clear. We need to understand behavioural variability; within and between individuals and, within and between populations. We need to understand both the genesis of such variation as well as its environmental correlates. Only by understanding this variation can we hope to predict behavioural responses into the future, in a changing world.

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