8 Do Successful Invaders Exist? Pre-Adaptations to Novel Environments in Terrestrial Vertebrates

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8.1 Introduction

Central in invasion biology is to understand why alien species, whose initial populations are generally small and genetically depleted, can succeed to establish themselves in environments to which they have had no opportunity to adapt (Sax and Brown 2000). This paradox is usually resolved by invoking pre-adaptations of non-indigenous species to novel environments. The idea is that some species are successful invaders because they have attributes that pre-adapt them to survive and reproduce in novel environments (Mayr 1965). However, do we really have evidence that there exist properties of successful invaders?

The goal of this chapter is to evaluate to what extent establishment success of terrestrial vertebrates may be understood by the existence of pre-adaptations of species to novel environments. This implies answering two interrelated questions: (1) do species differ in their invasion potential? And if so, (2) what are the features of the species that identify some as successful invaders? Answering these questions is important not only to fully understand how animals respond to new environmental conditions, but also to help identify and prevent situations where the risk is high that a species becomes established and causes ecological impact when introduced in a novel region.

8.2 Framework

A population is considered to be established when it is able to develop a self-sustaining population, that is, a population that is maintained over time by reproduction without the need of additional introductions. To become estab-

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lished, the invader needs to find an appropriate niche to survive and reproduce in the novel environment, which should include environmental conditions (e.g., temperatures or precipitations) that the species may tolerate, resources (e.g., food or shelter) that are not monopolized by other species, and a pressure from enemies (e.g., parasites or predators) low enough to not compromise population growth. Consequently, any property of a species that increases the likelihood to find an appropriate niche in a variety of diverse environments will also make the species a potentially successful invader.

Yet, finding an appropriate niche in the novel region is not a guarantee of successful establishment. Introduced populations generally start in low numbers, which makes them vulnerable to extinction by demographic, environmental and genetic stochasticity (Legendre et al. 1999; Lockwood et al. 2005). Thus, the first stages in the invasion process are particularly critical in determining the chance that a species establishes a self-sustaining population. Not only is it necessary that the balance between births and deaths be positive, but also that the increase of population size is fast enough to reduce the period in which the population remains vulnerable to stochasticity.

The need to grow fast in numbers has four main implications for understanding the invasion process. First, the likelihood of establishment is likely to increase with the size of the founder population, an idea that is strongly supported by evidence in both birds and mammals (Lockwood et al. 2005). Second, a non-indigenous species that, due to the Allee effect, has a reduced per capita growth rate at low population densities will be particularly prone to extinction (Reed 1999). Third, a non-indigenous species with a life history that facilitates a higher intrinsic rate of population increase will be more likely to escape the critical founding stage, and hence have higher chances to develop a self-sustaining population. Finally, any property of the invader that reduces survival or reproduction in the novel environment will impair population growth, increasing the risk of population extinction.

Thus, the ideal invader should posses a combination of traits that allows it to pass three main barriers toward establishment (Fig. 8.1). Such a combination of traits is unlikely to be found in a same species, implying that for most species, establishing self-sustaining populations in novel environments should be inherently difficult. Indeed, Williamson and others have repeatedly noted that most past introductions of plants and animals have failed to establish self-sustaining populations (e.g., Williamson and Fitter 1996). Moreover, many species that establish successfully in new regions often do so only after having failed in multiple earlier introductions (Sax and Brown 2000).

Despite the inherent difficulty to invade a new region, some vertebrates appear to be extremely successful invaders, while others are not (Ehrlich 1989; Williamson and Fitter 1996). Such varying invasion success is often held to arise from differences in certain properties of species (Ehrlich 1989), yet a similar pattern could result from a variety of alternative processes. For example, differences in invasion success could be explained by simple neutral

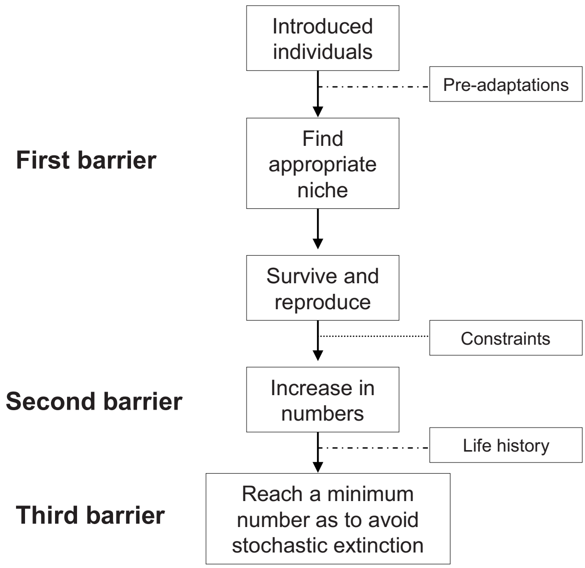

Fig. 8.1 Schematic representation of the three main barriers a species may pass to become established in a novel region. The species must first be able to find an appropriate niche to survive and reproduce, then have to reproduce at a rate high enough to counterbalance mortality, and finally must grow in number to reach a population size large enough to escape the effects of stochasticity. The success to pass each one of these barriers may mostly be affected by different attributes of the invaders

processes, such as differences in the number of individuals released, without the need to invoke differences in the properties of species. So, we must start asking whether differences between species really matter when it comes to determining invasion success.

8.3 Do Successful Invaders Exist?

The main difficulty in answering the above question is how to estimate the invasion potential for a given set of species. The invasion potential defines the ability of a species to establish itself in novel regions (Lonsdale 1999). The ideal approach to measure it would be to conduct experimental introductions under controlled conditions (e.g., releasing the same number of individuals of each species) in a variety of regions, and then use the rate of successes as an estimate of the invasion potential of each species. In terrestrial vertebrates, however, such large-scale experiments are not generally feasible for ethical and practical reasons.

As alternative, the invasion potential may be assessed using information of past historical introductions. The use of past introductions within a comparative framework has become the most widely used tool to study the success of vertebrate invasions, broadening our understanding of the invasion process, and providing general principles that are realistic enough to be used in risk assessments of future invaders (Duncan et al. 2003). Yet, past historical introductions are not randomized experiments, and hence their utility in understanding the invasion process is not exempt of problems.

One difficulty in using past introductions is the need to know not only those introductions that were successful, but also those that were unsuccessful. While the species that have succeeded at establishing themselves are relatively easy to determine, much more difficult is to know those that have failed, as they may have left no traces of their presence in the region. If the probability of detecting failures varies between species, then some species will appear to be very successful invaders simply because they have many unrecorded failures. Fortunately, very accurate records of both successes and failures are available for vertebrates. In birds, for example, many introductions in the 18th and 19th centuries were carried out by acclimatisation societies, which kept accurate records of the year of introduction, its outcome, and even the number of individuals released, providing high-quality data to estimate the invasion potential (Sol et al. 2005a).

Provided that reliable information on past introductions is available, a simple way to estimate the invasion potential would be to calculate the proportion of introductions that were successful. This method is nonetheless problematic when one uses historical introductions. It is well-known that introductions are non-randomly distributed across regions (Blackburn and Duncan 2001b), and that some species have been introduced in larger numbers than others (Cassey et al. 2004). In vertebrates, there is good evidence that success increases with the size of the founder population, so even successful invaders are expected to fail in some introductions if released in low numbers (Lockwood et al. 2005). Moreover, some regions may be easier to invade than others, as a result of their characteristics (e.g., species richness or degree of disturbance), as well as their ecological similitude with the native regions of the species introduced (Williamson 1996; Shea and Chesson 2002). In birds, for example, exotic species are more likely to fail on islands with species-rich mammalian predator assemblages (Cassey et al. 2005). Consequently, one species may seem to be a worse invader than another simply because it has been introduced in lower numbers, or in hard-to-invade regions. Clearly, differences in invasion potential between species must be evaluated under similar conditions of introduction.

One possibility suggested in the literature to obtain reliable measures of the invasion potential is the use of generalized linear mixed models (Blackburn and Duncan 2001a; Steele and Hogg 2003; Sol et al. 2005b). The idea is to estimate the magnitude of species (or higher taxonomic levels) differences in establishment success while accounting for the confounding effect of differences in the conditions of introduction. This is done by including species (or higher taxonomic levels) as random effect coefficients into a multivariate model that contains as co-variates the region of introduction, introduction effort, and other confounding variables. Thus, the random effect coefficient of each species provides a relative measure of the ability of the species to establish itself in a novel location, having controlled for region and introduction effort effects. The need for generalized linear mixed model is because the response variable is either success or failure of introductions, which has to be modeled with a binomial structure of errors.

The mixed model approach has provided evidence that, at least in birds, species differ in their invasion potential: once controlled for region and introduction effort, some species show a higher probability of establishment than others (Blackburn and Duncan 2001a; Sol et al. 2002). Interestingly, most variation in establishment success is evident at low, rather than at high taxonomic levels, indicating that even closely related species may differ substantially in their probability of establishment. Such a pattern may imply that the traits that affect establishment success primarily vary between closely related species. Nonetheless, the possibility that differences in invasion success also exist at higher taxonomic levels cannot be completely ruled out (Forsyth and Duncan 2001; Moulton et al. 2001; Sol et al. 2005b). For example, for a given number of individuals introduced, ungulates were more likely to succeed in New Zealand than were birds (Forsyth and Duncan 2001).

Mixed models have also revealed that species may not simply be separated as successful and unsuccessful invaders. The majority of species has intermediate levels of invasion potential, so they may either succeed or fail when introduced into novel regions (Fig. 8.2). This finding contradicts what Simberloff and Boecklen (1991) called an all-or-non pattern, where some species are particularly good invaders and so succeed everywhere they are introduced, whereas others are poor invaders and always fail, regardless of the characteristics of the recipient community (Moulton 1993; Duncan and Young 1999). Deviations from an all-or-non pattern have several possible interpretations (Duncan and Young 1999; Duncan et al. 2003). First, some species may

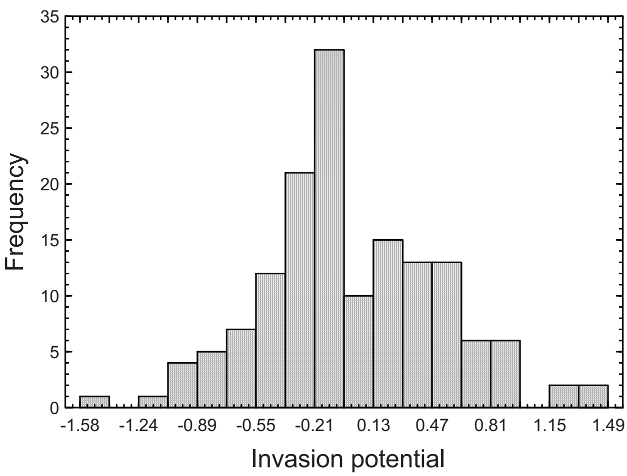

Fig. 8.2 Variation in invasion potential between avian species, when both introduction effort and region are accounted for by using generalized linear mixed models

have properties that make them good invaders when released in certain habitats, but not in others. Second, establishment success may be determined by a combination of properties that are unlikely to be all present in most introduced species. Finally, it is quite conceivable that even an exceptionally good invader might occasionally fail to establish itself due to a chance set of unfavorable circumstances, and that a poor invader may occasionally succeed under favorable circumstances. Thus, even though there exist differences in invasion potential at the species level, success still remains a very idiosyncratic event, limiting the utility of using past invasion success to assess the outcome of future introductions.

8.4 What Makes a Species a Successful Invader?

While in vertebrates there is evidence that species differ in their invasion potential, controversy still exists regarding the nature of the features best defining those species that are more successful. One important unresolved question is whether species are born as, or evolve to be successful invaders. Coming from distant regions, invaders are often confronted to sudden environmental changes to which they are unlikely to be fully adapted. Thus, evolutionary responses are likely to be important, at least in the long-term, to better fit the population into their new environment. Post-invasion evolutionary response has been suggested as one of the possible explanations for the time lag observed in many invasion events (Williamson 1996; Mooney and Cleland 2001), where the invader population remains at low numbers for a long time before starting an exponential population growth phase.

Post-invasion evolution has been shown in a number of studies (Mooney and Cleland 2001), but whether such evolutionary adjustments are important in determining differences between species in invasion potential remains unclear. This requires that successful invaders show a higher evolutionary potential over different ecological contexts (e.g., because of a higher genetic diversity) than less successful invaders, an aspect that still awaits empirical confirmation. Moreover, adaptive evolution is relatively slow in long-lived species such as vertebrates, and the evolutionary response of the population can be limited by insufficient genetic variation. This suggests that evolutionary adjustments should be more important in later transitions of the invasion process than during the process of establishment, at least in vertebrates.

The alternative to evolutionary responses is that successful invaders have some pre-adaptations that facilitate their establishment in novel environments. A large number of traits have been hypothesized to affect the invasion potential of terrestrial vertebrates (Table 8.1). Whether some of these features affect the invasion potential may be evaluated by measuring differences in

Table 8.1 Hypotheses proposed on the attributes that characterize successful invaders in terrestrial vertebrates[a]

Hypothesis	Description	Supporting evidence
Pre-adaptations to new environments		
Niche breadth	Generalist species should be better invaders than are specialists, because the former are more likely to find appropriate resources in a new environment[1,2]	Birds[3,4]
Behavioral flexibility	Species with larger brains and higher behavioral flexibility should be better invaders than less flexible ones, because they may behaviorally adapt to the new environment[1,5]	Birds[5–7]
Social behavior	Social species should be better invaders than solitary ones[1]. Social foraging may be advantageous for invaders because it can increase the probability of detecting a predator, locating food, and learning about new food sources. However, social species may also have difficulties to survive and/or reproduce when they are in low numbers due to the Allee effect, which may counterbalance the benefits	None
Pre-adaptations to specific environments		
Human commensalism	Human commensalists should be better invaders than non-commensalists[1,8], because introductions are generally carried out in human-modified habitats	Birds[7]
Traits that help avoid stochastic extinction		
Life histories and population growth	Species with life histories that increase intrinsic population growth rates are expected to have a better chance of surviving[9], because these species may attain large population size faster	Birds[10,11], but see[12]
Lifespan	Long-lived species should show a higher probability of establishing themselves in a new habitat[13,14], as they are less exposed to stochastic extinctions	None
Traits that constrain establishment		
Migratory behavior	Species that migrate within their native range are less likely to establish themselves than non-migratory species[15,16]. Long-distance migrants may be handicapped in invading novel regions by the incapacity to either develop novel migratory adaptations to reach suitable wintering habitats, or to adapt simultaneously to prevailing conditions in breeding and wintering areas	Birds[16]
Sexual selection	Compared to non-sexually selected species, sexually selected species should have lower introduction success[17]. Sexually selected species may be more vulnerable to extinction, because of production and maintenance costs of secondary sexual characters, and their reduced effective population size[3,17,18]	Birds[3,17,18], but see[4]

Table 8.1 (*Continued*)

Hypothesis	Description	Supporting evidence
Trophic level	Herbivores are predicted to invade new habitats more easily than are carnivores[19,20]. This is based on the idea that competition is the prime determinant of community structure, and that competition is less intense for herbivores than it is for carnivores	None
Nesting site	Ground nesters should have lower probabilities of establishing themselves in a new environment than would be the case for canopy, shrubs, or hole nesters[3,21]. This is because nest predation is generally higher in ground nesters, which may enhance the probability of extinction when the population is small	Birds[3], but see[7]

[a] Data sources: 1. Mayr (1965); 2. Ehrlich (1989); 3. Mclain et al. (1999); 4. Cassey et al. (2004); 5. Sol and Lefebvre (2000); 6. Sol et al. (2005b); 7. Sol et al. (2002); 8. Brown (1989); 9. Moulton and Pimm (1986); 10. Green (1997); 11. Cassey (2003); 12. Blackburn and Duncan (2001a); 13. Pimm (1989); 14. Legendre et al. (1999); 15. Thompson (1922); 16. Veltman et al. (1996); 17. Mclain et al. (1995); 18. Sorci et al. (1998); 19. Hairston et al. (1960); 20. Crawley (1986); 21. Reed (1999)

establishment success between species that differ in those traits (Newsome and Noble 1986). Although such a comparative approach has been extensively used in the last two decades, surprisingly, most of the traits found to be significantly associated with establishment success primarily explain why certain species repeatedly fail to invade a new environment, but say much less about why other species are successful invaders (Duncan et al. 2003; Sol et al. 2005a). For example, some studies have found that sexually dimorphic species are less likely to establish themselves in new regions than are sexually monomorphic species (Mclain et al. 1995, 1999; Sorci et al. 1998). This is consistent with sexual selection theory, which predicts a lower success in sexually selected species due to, among other reasons, the costs of producing and maintaining secondary sexual characters that promote male mating success at the expense of survival. However, while sexual selection theory may help understand why some species are bad invaders, it says nothing about why other species are so successful.

Life history has also been classically suggested to affect the ability of animals to establish themselves in new regions (Pimm 1991), although theoretical predictions are controversial. In general, "fast" life histories (i.e., small body size, fast body growth rate, early maturity, and short lifespan; Saether 1988) are thought to facilitate establishment success by promoting faster population growth, thereby reducing the period in which the population is small and highly vulnerable to extinction. However, small-bodied species also tend to be more vulnerable to environmental risks, and they tend to have more variable populations than do large-bodied ones (Pimm 1991). These contradictory theoretical predictions over how life history strategies affect the invasion potential have as yet not been resolved empirically (Duncan et al. 2003). While some studies have reported positive relationships between clutch size and establishment success (Green 1997; Cassey 2002), others have reported negative relationships, or no relationship at all (Veltman et al. 1996; Blackburn and Duncan 2001a). Despite the controversy, it is conceivable that life history affects establishment by shaping key demographic parameters. Nonetheless, life history does not explain why some species are better armed to find an appropriate niche in new regions, which is the first barrier in the invasion process.

Most ecologists would agree that the chances that a species find an appropriate niche in a new region should be higher if its environment is similar to that found in the native region of the invader, as then the invader will already be pre-adapted to it, an idea known as the "environmental matching" hypothesis. In vertebrates, the existence of pre-adaptations to specific habitats is suggested by several indirect lines of evidence. Establishment success in birds is significantly greater when the difference between a species' latitude of origin and its latitude of introduction is small (Blackburn and Duncan 2001a; Cassey 2002), when climatic conditions in the locations of origin and introduction are more similar (Duncan et al 2001), and when species are introduced to locations within their native biogeographical regions (Blackburn & Duncan 2001a). Direct evidence for the existence of pre-adaptations to specific habitats is less clear. In birds, species with a history of close association with humans tend to be successful invaders (Sol et al. 2002), which agrees with the fact that many avian introductions have taken places in human-modified habitats (Case 1996). By contrast, a comparison of avian introductions across convergent Mediterranean regions revealed that success was not higher for those originating from Mediterranean systems than for those from non-Mediterranean regions (Kark and Sol 2005).

Traits that pre-adapt species to specific habitats, however, cannot explain why some species are extremely successful at invading a variety of environments. Moreover, environments that may look very similar to us may actually show subtle differences in key aspects such as available food types or diversity of enemies, sometimes a matter of life and death. If successful invaders have in common some general attributes that help them to invade new regions, then these should be pre-adaptations to exploit novel niches under a wide diversity of environments. Yet, do we have evidence for such general attributes of successful invaders in vertebrates?

If features of successful invaders do exist, then they should not be multifaceted; the reason is that adaptations that are useful in some environments are often inappropriate for other environments. Thus, it would seem more likely to find pre-adaptations to invade specific habitats, rather than a wide variety of habitats. Yet, ecological theory suggests at least two classes of attributes of vertebrates that might predispose them to be successful invaders: niche breadth and behavioral flexibility.

The "niche breadth–invasion success" hypothesis represents the first attempt at generalization that species have attributes that make them successful invaders (Vasquez 2006). It suggests that species with broad niches ("generalists") are more likely to invade new regions than are species with narrower niches ("specialists"), because the former are more likely to find the necessary resources or conditions in the novel environment. Supporting evidence for the hypothesis is found in analyses showing that introduced birds that are either dietary or habitat generalists are more likely to establish successfully in new regions (Mclain et al. 1999; Cassey et al. 2004). Also consistent with the idea that niche breadth is important is the finding that, following introduction, bird species with larger geographic ranges are more likely to establish (Moulton and Pimm 1986; Blackburn and Duncan 2001a). Species may have large geographic ranges because they can exploit a broad range of conditions, although the alternative that they simply utilize conditions that are themselves widespread cannot be ruled out (Duncan et al. 2003).

Ecological generalism reflects the capacity of an animal to use a variety of resources, and is thus a static concept. However, coming from distant regions, invaders have to respond to dramatic changes in the environment, often facing what Schlaepfer et al. (2002) have termed "ecological traps". Ecological traps occur when invaders make wrong choices of resources, relative to conditions in their native environments. For example, the contrasting successes in North America of the common starling, *Sturnus vulgaris*, and the closely related Southeast Asian crested myna, *Acridotheres cristatellus*, have in part been attributed to the fact that mynas retained breeding habits appropriate to their homelands, but inappropriate in their new home (British Columbia; Ehrlich 1989).

Animals may in part compensate for such poor adaptive fit by means of behavioral changes (Klopfer 1962; Sol 2003). Behavioral flexibility may aid establishment through, for example, the ready adoption of new food resources (Lefebvre et al. 2004), the adjustment of breeding to the prevailing environmental conditions (Arcese et al. 1997), or rapid behavioral changes to avoid novel enemies (Berger et al. 2001). Because behaviorally flexible species are believed to be more exploratory (Greenberg and Mettke-Hofmann 2001) and ecologically generalist (Sol 2003), they may also have higher chances of discovering and adopting new habitats or new resources that may be important to survive and reproduce in the novel environment. The hypothesis that behavioral flexibility enhances establishment dates from Mayr (1965), but has only recently received empirical support for birds. This derives from observations that, compared to unsuccessful species, established birds tend to have a larger brain size, relative to their body mass, and to show more innovative behaviors in their region of origin (Sol and Lefebvre 2000; Sol et al. 2002, 2005b). The importance of behavioral adjustments to deal with novel ecological problems is also supported by experimental evidence. Martin II and Fitzgerald (2005) found that house sparrows from an invading population in North America tended to approach and consume novel foods more readily than those from a well-established population.

8.5 Conclusions and Future Directions

Progress in the last decades has provided firm evidence in vertebrates supporting that species differ in their invasion potential, and that such differences are associated with certain features that facilitate establishment in novel regions. A number of features appears to combine to affect the ability of species to cross the three barriers that lead to successful establishment, yet only two of these characteristics appear to provide general explanations in understanding why some vertebrates are so extremely successful invaders: a broad ecological niche, and a high degree of behavioral flexibility. These traits are presumed to facilitate that vertebrates find an appropriate niche in a variety of environments, even in those to which they have had no opportunity to adapt to.

The conclusion that species attributes influence invasion success is important for three main reasons. First, it informs us on the mechanisms that allow animals to invade novel environments, improving our understanding of the invasion process, and providing cues to identify and prevent situations where the risk is high that a species becomes established in a novel region. Second, it indicates that invasion success cannot simply be explained by neutral processes, such as the differences in introduction effort, but that properties of the species matter when it comes to understand invasion success. Finally, it suggests that animals differ in the way they respond to changes in their environment, which has obvious implications for the conservation of vertebrates in the face of environmental threats such as the destruction and fragmentation of habitats, and global climate change.

Despite our progress, we still have a long way to go to fully understand why some vertebrates are so successful invaders. Below, I highlight five issues that I envision as important avenues of future research.

First, the role of some traits in determining the invasion potential of vertebrates remains unclear. The reasons include that the theoretical basis is insufficiently developed, that the empirical evidence is contradictory, or simply that the effect of the trait has never been tested. Traits that remain insufficiently studied include life history strategies, human commensalisms, and social behaviour. Testing the importance of these and other factors requires large, representative samples of introduced species, adopting appropriate methodologies that take into account the non-random nature of past historical introductions (Duncan et al. 2003).

Second, previous work has largely ignored possible interactions between species attributes and the characteristics of the recipient community, even though this may contribute to better understanding the underlying mechanisms. For example, if behavioral flexibility affects establishment by enhancing the individual's response to novel environments, then we should expect this to play an even bigger role when the species is introduced into habitats that differ strongly from its original one – and hence demand greater behavioral adjustments – than would be the case for more similar habitats. Likewise, migratory behavior has been suggested to constrain establishment success in vertebrates on the grounds that, on isolated islands, species cannot develop migratory routes (Veltman et al. 1996). Such a mechanism should be tested – not simply assumed – for example, by assessing whether migratory species are particularly unsuccessful when introduced onto very isolated islands.

Third, although establishment success is undoubtedly central in the invasion process, the impact of the invader is determined mostly by the ability of the species to grow in numbers, and expand over large regions. Thus, it is critical that we understand what determines that a species is able to successfully spread and impact over ecosystems. A particularly intriguing question is whether those traits that have been found to affect establishment also influence spread, as then we would easily detect situations of high risk. Indeed, both niche breadth (Brooks 2001) and behavioral flexibility (Sol 2003) have been suggested to affect spread, although supporting evidence is still lacking.

Fourth, most past work on establishment success has been done in birds. We need to extend the results to other terrestrial vertebrates, particularly in mammals for which good data are available on many successful and failed introductions (Forsyth and Duncan 2001; Forsyth et al. 2004). Such studies will allow us to ascertain the generality of the hypothesis suggested to explain establishment success, and hence build a general framework that is common to all vertebrates.

Finally, if we wish to fully understand the mechanisms that allow some vertebrates to be so successful, then we should progress from the present focus on comparative approaches toward increasingly experimental approaches. While experimental introductions are not generally feasible in vertebrates, we can nevertheless study underlying mechanisms by using translocations of species, or by running experiments on both native and introduced populations. One good example of the type of work required is the study of Martin II and Fitzgerald (2005), who used common garden experiments to evaluate differences in behavioral flexibility between an invading and a well-established population of house sparrows (*Passer domesticus*). The use of experiments will serve to validate the evidence stemming from comparative analyses, and will help better understand the exact mechanisms that facilitate that a species can establish itself in an environment to which it is not well adapted.

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