

THE ECOLOGY OF BIRD INTRODUCTIONS

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■ **Abstract** A growing number of species have been transported and introduced by humans to new locations and have established self-sustaining wild populations beyond their natural range limits. Many of these species go on to have significant environmental or economic impacts. However, not all species transported and introduced to new locations succeed in establishing wild populations, and of the established species only some become widespread and abundant. What factors underlie this variation in invasion success? Here, we review progress that has been made in identifying factors underpinning invasion success from studies of bird introductions. We review what is known about the introduction, establishment, and spread of introduced bird species, focusing on comparative studies that use historical records to test hypotheses about what factors determine success at different stages in the invasion process. We close with suggestions for future research.

INTRODUCTION

As humans have spread around the globe, they have deliberately or accidentally transported a huge variety of plant and animal species to locations beyond their natural ranges (Elton 1958; Lodge 1993; Williamson 1996, 1999). By design or accident many of these introduced species have established self-sustaining wild populations, which have subsequently increased and spread to varying degrees. Many of these species have profoundly affected the ecosystems they have invaded, and some have imposed substantial economic and health costs on human societies (Elton 1958, Ebenhard 1988, Lever 1994, Simberloff 1995, Williamson 1996, Vitousek et al. 1997, Parker et al. 1999, Dalmazzone 2000, Mack et al. 2000, Perrings et al. 2000, McNeely 2001). Thus, the establishment and spread of introduced species is currently recognized as a major risk worldwide. This risk is likely to increase as greater volumes of transport and trade increase the rate at which novel species are introduced to new locations (Ricciardi et al. 2000).

Nevertheless, only a small proportion of the species introduced to a new location establish wild populations, and of these only a small proportion become abundant or widespread and have significant impact (Lodge 1993, Williamson 1996, Williamson & Fitter 1996). Given that once established the eradication or control of introduced species is costly, the most effective way to minimize their impact is to prevent establishment or spread in the first place (Ricciardi & Rasmussen 1998, Mack et al. 2000). This approach requires that we understand the factors underlying success at different stages in the invasion process (Figure 1) so that we can identify situations where invasion risk is high. Specifically, what are the factors that allow certain species to establish and spread when introduced to locations outside their natural range?

Despite concerted effort, the field of invasion ecology has been criticized for its lack of success in answering this question (Ehrlich 1989, Vermeij 1996, Mack et al. 2000). In this review we hope to show that considerable progress has been made in identifying the factors underpinning invasion success using historical data on bird introductions. We discuss what is known about the introduction, establishment, and spread of introduced birds, focusing on comparative studies that use the historical record of bird introductions to test hypotheses about the factors determining invasion success.

Why Study Bird Introductions?

Data on historical bird introductions provide a rare opportunity to test hypotheses about invasion success for at least three reasons. First, there is an excellent record of the bird species introduced to locations around the world (Long 1981, Lever 1987). Most bird introductions occurred in the eighteenth and nineteenth centuries during the major period of European expansion and settlement. Introductions were often associated with the formation of acclimatization societies that aimed to establish beneficial or desirable species in the new settlements (see especially Thomson 1922) or with private individuals who sometimes attempted to naturalize a variety of species (e.g., Eastham Guild on Tahiti; Guild 1938, 1940). Birds were prominent among the species introduced by settlers, especially for hunting, biocontrol, and aesthetic reasons. Many societies or individuals kept records of the birds they introduced, sometimes including details such as the numbers of individuals released, the exact location of release, and the origin of the birds introduced (Thomson 1922, Long 1981, Lever 1987). Because most of these introductions occurred decades to centuries ago, and because birds are conspicuous and well studied, introduction outcomes can be determined with reasonable certainty. We can therefore compile comprehensive lists of the bird species introduced to new locations, whether or not those introduced species established wild populations, and the extent to which the established species have spread.

Second, because many attempts were made to introduce birds, there are data on a large and taxonomically diverse set of species introduced to a wide range of locations with which to test hypotheses about invasion success. Worldwide, there have been recorded more than 1400 attempts to introduce about 400 species

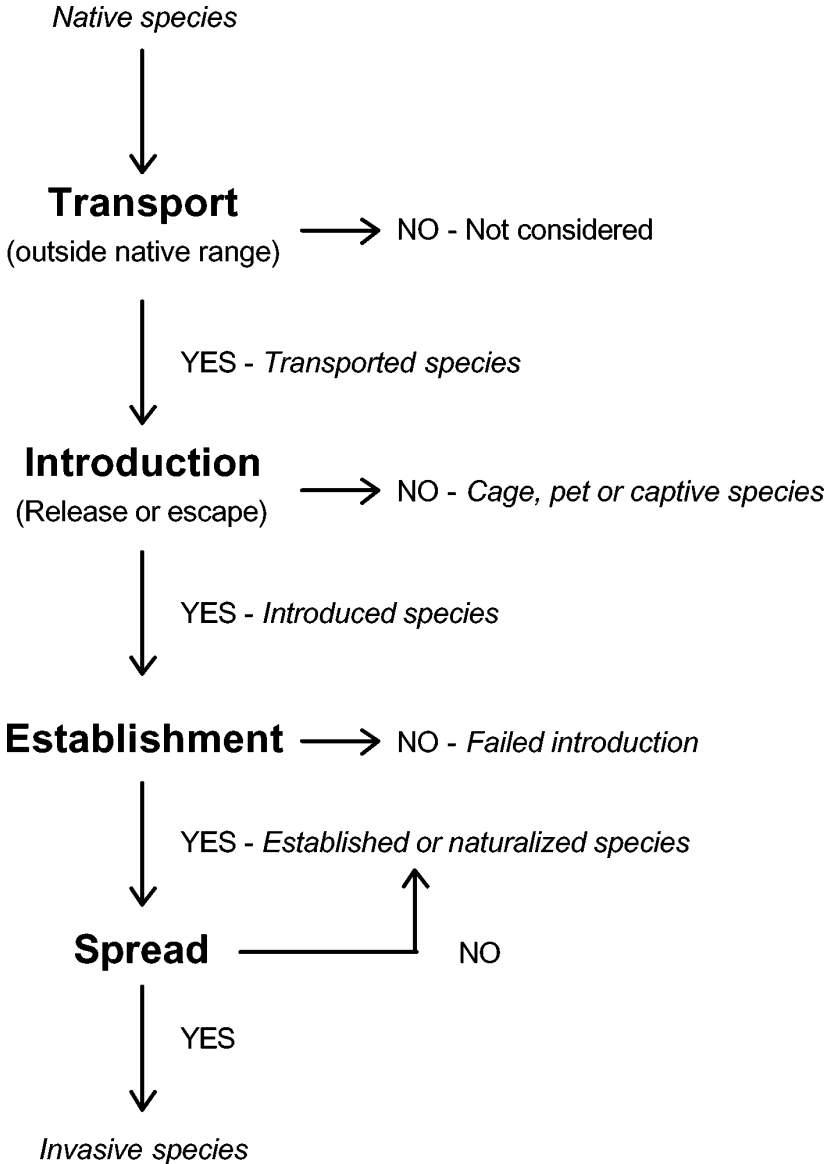


Figure 1 Schematic representation of stages in the process of a human-caused invasion that we recognize in this review. The stages through which a species must pass are shown in bold. The names of species that do or do not pass through each stage are shown in italics.

of birds (Long 1981, Lever 1987, Lockwood 1999, Blackburn & Duncan 2001b, Cassey 2002).

Third, birds in general are a well-studied group. Thus, we can supplement data on bird introductions with published information on the phylogeny, life history, ecology, and natural distribution of these species (e.g., Sibley & Ahlquist 1990; Sibley & Monroe 1990, 1993; Dunning 1993; Bennett & Owens 2002). The availability of these data is central to testing some key hypotheses about factors underlying invasion success.

Despite these advantages, there are two difficulties associated with using the historical record of bird introductions in quantitative studies. First, the historical record is incomplete, and the quality of the data varies from location to location. In New Zealand, which has perhaps the most complete and detailed historical record, at least seven birds were introduced that cannot be identified to species (Thomson 1922) and have therefore been excluded from analyses of introduction outcomes. The record of failed introductions will invariably be less complete than the record of successful introductions because species that failed to establish leave no further trace of their presence. We do not know the extent of this bias in historical data. Second, the choice of which birds to introduce to which locations was not made at random but was the result of historical circumstances. The resulting pattern of introductions is itself informative but raises important issues for statistical analysis and interpretation. We consider these issues and ways to deal with them in this review.

Definitions and Framework

Terms such as invasive and introduction have been used in different ways in the literature (e.g., Williamson 1996, Davis & Thomson 2000, Richardson et al. 2000, Daehler 2001, Kolar & Lodge 2001). In this section, we clarify our terminology and define stages that we recognize in the invasion process (Figure 1), which serves as a framework for our review.

We consider only introductions of alien, exotic, or nonindigenous bird species, all terms used to describe species transported and introduced to a new location by humans (see also Davis & Thomson 2000, Richardson et al. 2000, Daehler 2001, Kolar & Lodge 2001). We do not consider natural invasions or range expansions nor, for the most part, re-introductions of locally extinct species for conservation purposes. The term invasion here refers specifically to exotic species that have been deliberately or accidentally transported by humans to a new location beyond their normal geographic range limits.

We recognize four transitions in the process of invasion by an exotic species (Figure 1) (see Williamson 1996, Richardson et al. 2000, Davis & Thomson 2000, Daehler 2001, Kolar & Lodge 2001). First, the exotic species must be transported from its native geographic range to a new location. Second, the species must be released or escape into the environment. Third, the species must succeed in establishing a self-sustaining wild population following release. Finally, species that establish successfully may increase in abundance and spread beyond the release point; the extent of this spread defines their geographic range in the new environment. We

term these stages transport, introduction, establishment, and spread (see also Lockwood 1999, Kolar & Lodge 2001, Sakai et al. 2001). For a species to have reached a given stage in the invasion process, it must have passed through all prior stages.

An introduced species is one that passes through the first two stages and is released (or escapes) into a new environment. An established species is one that establishes a self-sustaining wild population following introduction (also termed naturalized). An established species that succeeds in spreading beyond the site of introduction is termed invasive. The introduction of a species to a location is termed an introduction event. When we use the term introduction, we refer to a species that has been transported to, and released or escaped into, an alien environment, regardless of whether it establishes or spreads.

Not all stages in the invasion process have been equally well studied, a fact reflected in the attention we give them in this review. Most effort has gone into identifying factors that influence the successful transition from introduction to establishment. No studies have attempted to quantify the first stage in the process: which species of birds have been selected for transport to new locations, regardless of whether they have been introduced or not (but see Guix et al. 1997 for an analysis of the pet trade of Neotropical parrots in Barcelona). We start, therefore, by addressing two questions associated with the introduction stage: (a) Which species were selected for transport followed by introduction to new locations; and (b) to which locations were birds introduced? We then examine factors associated with success in establishment and spread.

TRANSPORT WITH INTRODUCTION

Which Species Were Selected for Introduction?

Fewer than 5% of all bird species have been transported and introduced to a new location (Blackburn & Duncan 2001b). It is important to understand why some species and not others were chosen for introduction because biases in the type of species chosen, termed selectivity, may limit the generality of conclusions we draw regarding the factors affecting success in later stages of the invasion process. If only certain types of birds were chosen for introduction, then the factors that determine invasion success in this group may not necessarily apply to other groups of birds. Selectivity also has important implications for the statistical analysis of success at later stages in the invasion process (see below). Selectivity in the birds chosen for introduction has been examined with regard to the taxonomic affiliations of species, the geographic origin of species, and specific characteristics of the taxa chosen.

TAXONOMIC SELECTIVITY Taxonomic selectivity in global bird introductions has been examined for all introduced species (Blackburn & Duncan 2001b) and for the subset of species that were both introduced and established (Lockwood 1999, Lockwood et al. 2000). The results of both analyses are similar in that families over-represented at the introduction stage are also the families over-represented among

established species. This fact implies that a major cause of taxonomic selectivity among established species is taxonomic selectivity in the species chosen for introduction. Two thirds of all species chosen for introduction belong to just 6 of the 145 bird families: Anatidae, Columbidae, Fringillidae, Passeridae, Phasianidae, and Psittacidae (Blackburn & Duncan 2001b). The over-representation of species in these families almost certainly reflects two of the major motivations behind introducing birds. Species in the families Anatidae and Phasianidae were primarily introduced for hunting, while species in the families Fringillidae, Passeridae, and Psittacidae are frequently kept as cage birds, and many were introduced for aesthetic reasons (see Long 1981, Lever 1987). Nevertheless, between 69% and 94% of the species in these families have never been the subject of an introduction event (Blackburn & Duncan 2001b).

GEOGRAPHICAL SELECTIVITY As for many other taxa, bird species richness is higher nearer the Equator. Nevertheless, most birds chosen for introduction have their native geographic ranges centered in temperate regions, between 30° and 50° in both hemispheres (Blackburn & Duncan 2001b). Only around 8% of introduction events involve species from the Neotropics, although the Neotropics are home to around 30% of all bird species (Rahbek 1997). Conversely, about 16% of introduction events involve species from the Palaearctic, despite the fact that only about 10% of bird species have geographic ranges that include this region (Evans 1997; Sibley & Monroe 1990, 1993). Although there has been no formal test, species from tropical regions appear to be greatly under-represented in lists of introduced species.

Much of this geographical selectivity can be attributed to introductions carried out by European settlers, who mostly colonized other temperate parts of the world. Thus, opportunities for the transport and trade of birds during the eighteenth and nineteenth centuries would have been greatest between Western Europe and the predominantly temperate locations where Europeans settled, including North America, South Africa, Australia, and New Zealand. Around 60% of the bird species introduced to New Zealand originate from the Palaearctic and Australasian regions (Duncan et al. 2003), the two places with which trade and transport were most frequent during early European settlement of New Zealand.

CHARACTER SELECTIVITY These taxonomic and geographical patterns of selectivity imply that the birds chosen for introduction will be nonrandom with respect to their life history and ecological traits, because these traits are not randomly distributed across taxa or regions (see, e.g., Bergmann 1847; Lack 1947, 1948; Owens & Bennett 1995; Gaston & Blackburn 2000; Cardillo 2002). Thus, we would expect introduced birds predominantly to possess the characteristics of temperate game birds (Anatidae and Phasianidae) or cage birds (Psittacidae, Fringillidae, and Passeridae). There have been few tests of character selectivity for introduced birds, although for those introduced to Australia, a high proportion of species are ground nesters that use grassland, cultivated, or suburban habitats and have largely vegetarian diets (seeds, fruit, vegetation) (Newsome & Noble 1986). Introduced

species are also larger-bodied, on average, than would be expected if they were a random sample of bird species (116.6 g versus 50.5 g for introduced and all bird species, respectively; Blackburn & Gaston 1994, Cassey 2001a).

Character selectivity also occurs independently of taxonomic and geographical selectivity. For both a geographic (species in the British avifauna) and a taxonomic (order Anseriformes; wildfowl) subset of the world's birds, species with larger population sizes were significantly more likely to have been chosen for introduction (Blackburn & Duncan 2001b). In addition, larger-bodied wildfowl and resident British birds that were widely distributed had a higher probability of selection. Species with large population size, wide distribution, and resident status would have been the most readily available for capture and transport to new locations. While most species were released at very few locations, a few species, typically widely distributed and abundant in their native ranges, were widely introduced (Long 1981, Lever 1987, Cassey 2002).

Together, these results suggest a general hierarchy of causes that have contributed to the selective introduction of certain birds. First, the species chosen for introduction were concentrated in geographic regions that in large part reflect the origin of European settlers and their subsequent patterns of settlement and trade. Second, from within geographic regions, people chose certain kinds of bird for introduction for a variety of reasons. An emphasis on birds for hunting and aesthetic purposes has resulted in birds from five families being significantly over-represented among those chosen. Finally, given that birds were chosen for particular purposes and from certain regions, the species that were finally caught, transported, and introduced tend to be those that were common in the source locations. People preferentially selected abundant, widely distributed species, either because they were most readily available for capture or because they were species with which they were most familiar, and therefore most desired to introduce.

To Which Locations Were Birds Introduced?

People mostly introduced birds to islands. Although islands make up about 3% of ice-free land area (Mielke 1989), around 70% of introduction events have been to islands (Blackburn & Duncan 2001b). Slightly over one half of all introductions were to Pacific islands (especially the Hawaiian islands) and Australasia. The greatest number of mainland introductions was to the Nearctic, followed by the Palearctic, and continental Australia. Birds have been introduced to all major regions of the world and to most latitudes with ice-free land. However, relatively few introductions have been to equatorial regions; most were to latitudes between 10° and 40° on both sides of the equator (Blackburn & Duncan 2001b).

ESTABLISHMENT

A species introduced to a new location will either succeed or fail to establish a self-sustaining population. There are numerous reasons why introductions could fail, making it unlikely that we will ever be able to predict with certainty the outcome

of any one introduction event (Ehrlich 1989, Gilpin 1990). Nevertheless, a major goal of invasion ecology is to identify factors that have some ability to explain the outcome of introduction events, to rank factors in terms of their importance, and to determine whether different factors are important under different circumstances, and why (Williamson 1999).

Factors hypothesized to influence establishment can be grouped into three categories: (a) characteristics of the species introduced, such as their population growth rate or migratory strategy; (b) features of the introduction location, such as its environment or insularity; and (c) factors associated with, and often unique to, each introduction event, such as the number of individuals released. We term these species-, location-, and event-level factors, respectively (Blackburn & Duncan 2001a; see Williamson 1999, 2001).

Two crucial consequences of the selectivity in historical introductions (see above) are that factors at different levels are likely to be confounded, and that introduction events are unlikely to represent statistically independent data points when analyses include introduction data from more than one location. We first consider these issues because they are central to how we analyze and interpret comparative data on establishment success in any taxonomic group.

Statistical Analysis of Historical Introduction Outcomes

Species-, location-, and event-level factors are likely to be confounded because selectivity means that introductions are nonrandom with regard to the taxonomy and characteristics of the species introduced and their locations of origin and introduction. For example, species that are more common in Britain were introduced in greater numbers to New Zealand (Blackburn & Duncan 2001b). Species that are common in Britain also possess traits that distinguish them from less common species (e.g., smaller body mass and typical niche position; Nee et al. 1991, Gregory & Gaston 2000). Hence, for introductions of British birds to New Zealand, factors at the species-level (certain life-history traits) and event-level (the number of individuals introduced) are confounded. The solution in this case is to identify confounding factors and to control for them statistically using techniques such as multiple regression.

The second issue is that, when we consider data from several introduction locations, each introduction event is unlikely to represent a statistically independent data point (Blackburn & Duncan 2001a,b). This is because species were often introduced to multiple locations, and multiple species were introduced to each location. If some species are better at establishing than others, or if it is easier to establish at some locations than others, then the outcome of introductions of the same species, or of introductions to the same location, will be correlated. In these circumstances, the introduction of 5 species to each of 10 different locations does not provide 50 independent pieces of evidence to assess how species- or location-level factors affect establishment (see also Hurlbert 1984, McArdle 1996).

Introduction events are unlikely to be independent if they can be clustered by both species and location. Furthermore, species and locations may themselves

cluster into higher-level units. In particular, closely related species are more likely to share life-history, morphological, and behavioral traits than are more distantly related species. If these shared traits affect the likelihood of establishment, then introduction outcomes will be clustered by phylogenetic or taxonomic relatedness.

Clustering, leading to correlated responses in groups of observations, typically violates a core assumption of standard statistical models: that the error terms in the model are independent (i.e., uncorrelated). This leads to standard error estimates that are smaller than the true values, resulting in overestimates of the significance of factors included in the model (a greater frequency of Type I errors). In plain terms, we are more likely to obtain models containing spuriously significant factors if we fail correctly to account for the clustering of observations in our data.

There are at least two approaches to dealing with this problem when analyzing historical introduction data. First, it is less of an issue if we consider introductions of multiple species to a single location (for example, the outcome of bird introductions to Tahiti), because these data are not clustered by species and location—we have only one event per species at a single location (likewise for introductions of a single species to multiple locations). While this tactic largely overcomes the problem, it limits the questions we can address, and we still have to consider non-independence owing to phylogenetic relatedness. Alternatively, there has been renewed interest in developing statistical models that deal directly with the problem of nonindependence in clustered data. These approaches include the use of generalized least squares, linear mixed models, generalized linear mixed models and generalized estimating equations (Diggle et al. 1994, Goldstein 1995). These approaches are appropriate for analyzing spatially, temporally, and phylogenetically clustered data that are regularly encountered in ecological studies. Generalized linear mixed models have been applied to a global analysis of establishment success in birds, to account for the clustering of introduction events by species, taxonomic groups, and geographic locations (Blackburn & Duncan 2001a). Clearly, problems of clustering and nonindependence in introduction data are not specific to birds, and comparative studies of invasion success in any taxonomic group should carefully consider these issues.

Event-Level Influences on Establishment Success

INTRODUCTION EFFORT A feature of introduced species is that they are typically released in low numbers and so start with small founding populations. Smaller populations are at greater risk of extinction from stochastic fluctuations owing to demographic, environmental, or genetic stochasticity (Pimm 1991). In addition, small populations may suffer from Allee effects (for example, an inability to find mates at low population densities) and are more prone to extinction from natural catastrophes (e.g., several populations of introduced birds appear to have died out as a result of hurricanes; see Long 1981). Given that they start out with small founding populations, it is not surprising that most introductions fail. For birds, 744 of 1466 (51%) introduction events in the global data set analyzed by Blackburn

& Duncan (2001a) did not result in establishment, and this success rate is high relative to other taxa (Williamson 1996, Williamson & Fitter 1996).

A straightforward explanation for the success of some introductions is that they involved the release of a greater number of individuals and so were more likely to escape the threats facing small founding populations. That is, establishment success increases with greater introduction effort, or propagule pressure. Because information on release sizes has been recorded in many cases, it is possible to use historical bird introductions to test this hypothesis. All studies that have addressed this question so far have shown that species introduced with greater effort (typically measured as the total number of individuals released) have a higher probability of establishment [Dawson 1984 (cited in Williamson 1996); Newsome & Noble 1986; Griffith et al. 1989; Pimm 1991; Veltman et al. 1996; Duncan 1997; Green 1997; Sol & Lefebvre 2000; Duncan et al. 2001, 2003; Cassey 2001b; Duncan & Blackburn 2002], although all but two of these studies use data from just two locations, New Zealand and Australia. Nevertheless, observational and experimental evidence in other animals has also shown that the size of the founder population increases the chance of establishment (e.g., Hopper & Roush 1993, Berggren 2001, Forsyth & Duncan 2001). These results are consistent with the hypothesis that small populations are less likely to establish owing to stochastic events and that these play a major role in invasions (Green 1997). Nevertheless, there are exceptions. Despite the introduction of over half a million common quail, *Coturnix coturnix*, to more than 30 states in North America between 1875 and 1958 (Bump 1970), no introduction succeeded (Lever 1987). Clearly, factors other than propagule pressure can be critical in determining the fate of introductions (see below).

The role of demographic stochasticity in avian introductions has been explicitly modeled by Legendre et al. (1999). Because demographic stochasticity can generate random fluctuations in sex ratio leading to difficulty in finding a mate, they constructed a two-sex model with an explicit mating system and calculated resulting extinction probabilities via Monte Carlo simulations. The results showed that demographic uncertainty imposes high extinction risk on monogamous as compared to polygynous birds, and on short-lived as compared to long-lived birds. The model fit reasonably well to the extinction probabilities calculated for passerine birds introduced to New Zealand.

Nevertheless, stochasticity is not the only mechanism that could explain the link between introduction effort and establishment success. A greater number of release attempts may improve establishment by increasing the chance that at least one release population encounters favorable conditions for population growth (Crawley 1986). Griffith et al. (1989) found that introductions involving releases over a greater number of years had a greater probability of establishing, independently of the number of individuals released, although Green (1997) failed to find a similar relationship for New Zealand bird introductions. In a more direct test, Veltman et al. (1996) reported that species successfully introduced to New Zealand were released at more localities than unsuccessful species, although the number of localities and the total number of individuals released are correlated in these data.

Green (1997) also suggested that the link between introduction effort and establishment success could arise indirectly if, for example, people directed more effort toward releasing species that seemed pre-adapted to the conditions they would encounter at their location of introduction. Similarly, introduction effort could be related to establishment success indirectly through relationships with abundance in the source location and associated species traits. Nevertheless, studies that have attempted to control for these indirect relationships by including species traits, environmental tolerances, and overseas range size in multiple regression models have consistently found that introduction effort remains by far the strongest independent explanation for establishment success in birds (e.g., Duncan et al. 2001).

CLIMATE/ENVIRONMENTAL MATCHING One of the most frequently stated hypotheses in the biological invasion literature is that species should have a better chance of establishing if the climate and physical environment at the location of introduction and in the species' natural range are closely matched (Brown 1989, Williamson 1996). Data from bird introductions provide some of the very few quantitative tests of the hypothesis that a close climate/environmental match between a target and source location enhances establishment success. We include climate/environmental matching under event-level effects because this is a feature unique to each introduction event.

Avian establishment success is significantly greater when the difference between a species' latitude of origin and its latitude of introduction is small (Blackburn & Duncan 2001a, Cassey 2001b), 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 region (Blackburn & Duncan 2001a, Cassey 2003). Likewise, for re-introductions, Wolf et al. (1998) found that species re-introduced in the core of their original range had greater establishment success than species released in the periphery. Regions at similar latitudes or within the same biogeographic region are likely to be similar in climatic and habitat conditions. Hence, these results support the hypothesis that introduction success is enhanced if species are matched with suitable environments (Brown 1989).

Also related to the idea that climate/environmental matching is important is the finding in some studies that bird species with larger geographic ranges are more likely to establish following introduction (Moulton & Pimm 1986, Blackburn & Duncan 2001a, Duncan et al. 2001). Species may have large geographic ranges because they can exploit a broad range of conditions (they have large niche breadth), or use conditions that are themselves widespread (they have a typical niche position; Gaston 1994). In a similar vein, it has been suggested that being native to a relatively variable abiotic environment could also enhance establishment success (Ehrlich 1989), because species that survive in such environments can generally cope with a wide range of environmental conditions (see also Stevens 1989). Any of these situations would increase the chance that a species introduced to a new location would encounter conditions favorable to its survival, although only the range size effect has received empirical support.

Location-Level Influences on Establishment Success

Three characteristics of a location are likely to influence establishment: enemies, resources, and the physical environment (Shea & Chesson 2002). Establishment should be favored at locations where there are fewer enemies (predators, parasites, or diseases), more available resources (owing to higher resource availability or an absence of competitors), or a more benign environment. It is difficult to identify precisely which enemies, resources, or aspects of the physical environment influence establishment, so studies of location-level effects often consider features of the environment that ought to be correlated with these characteristics. For example, species richness is commonly used as a surrogate for the number of enemies, competitors or vacant niches likely to be present at a location (Shea & Chesson 2002). Species richness itself tends to co-vary with latitude and whether or not the location is an island (Elton 1958).

In fact, there is little evidence from bird introductions to support the hypothesis (Elton 1958) that species-poor locations are easier to invade than species-rich locations. Case (1996) showed that the number of established bird species does not vary significantly with the richness of the native avifauna nor the variety of potential mammalian predators. Whereas New Zealand has fewer native but a greater number of exotic bird species than Australia, there is no difference in establishment probability for birds introduced to these locations (Sol 2000a). Likewise, a global analysis of bird introductions failed to find a relationship between establishment success and latitude of introduction, implying no significant effect of resident species richness on establishment (Blackburn & Duncan 2001a).

Islands are often viewed as more vulnerable to invasion because of lower species richness, but also owing to factors such as an absence of certain functional groups, reduced competitive ability of island species, intensive human exploitation, or reduced habitat diversity (e.g., Vitousek 1988, Dalmazzone 2000). In support of this notion, Newsome & Noble (1986) reported a higher failure rate for bird species introduced to mainland Australia compared with bird species introduced to Australia's offshore islands. However, this result could be an artifact of differences in invasive ability between the species introduced to mainlands and islands. A species-by-species examination of introduced birds in two independent island-mainland comparisons (New Zealand versus Australia, and Hawaiian Islands versus U.S. mainland) found no evidence that islands were easier to invade (Sol 2000a). This result has been generalized in global analyses of bird introductions that failed to find a relationship between establishment success and whether the introduction was to a mainland or island location (Blackburn & Duncan 2001a, Cassey 2003). The high proportions of exotic bird species found on islands appears primarily to be a consequence of the many attempts to introduce birds to islands (see above *To Which Locations Were Birds Introduced?*) rather than any inherent feature of islands that make them easy to invade (Sol 2000a, Blackburn & Duncan 2001a).

Correlative studies testing for a relationship between species richness and invasion success have been criticized because variation in species richness may be

confounded with variation in other factors that affect establishment, making it difficult to isolate species richness effects (Shea & Chesson 2002). For birds, the studies described above suggest that factors other than resident species richness are overwhelmingly important in determining the outcome of introductions, even after statistically controlling for confounding factors. This lack of an effect is probably real. Competition between native and introduced birds does not appear to regulate establishment because most exotic birds establish in habitats highly modified by humans, such as farmland and urban areas, which are little used by native species (Diamond & Veitch 1981, Simberloff 1992, Smallwood 1994, Case 1996). Such modified habitats may favor pre-adapted invaders through release of resources and enemy reduction (Mack et al. 2000, Shea & Chesson 2002). Thus, many introduced birds may succeed because they exploit either vacant niches created by human activities or existing niches that humans have expanded.

Some authors have suggested that establishment is more likely for species that can exploit niche opportunities left by extinct or declining native species (Herbold & Moyle 1986, Case 1996, Mack et al. 2000). This is less likely if native and exotic species show strong habitat segregation. Nevertheless, Cassey (2001b) showed that, whereas extinct bird species in New Zealand tend to be larger-bodied than extant species, they do not differ in size from established exotic species. He suggested that some established invaders could be occupying the niches of extinct species. Case (1996) likewise reported a positive relationship between the numbers of established and recently extinct bird species at locations around the world. This relationship does not arise because introduced birds cause the extinction of native species: Most extinctions occurred prior to bird introductions. More likely, high extinction rates are associated with high levels of human disturbance, which in turn creates habitat favorable for the establishment of introduced birds (Case 1996).

Habitat segregation suggests that competition between native and exotic species has little role in determining whether or not introduced birds establish. However, it leaves open the question as to whether interactions with native species can prevent introduced species from spreading into more pristine habitats. Diamond & Veitch (1981) reported that, in New Zealand, exotic birds that are abundant on the main islands are virtually absent from unmodified forests on offshore islands, despite having ample opportunities to colonize these. There is no evidence that this segregation results from competitive interactions. More likely, introduced species establish in habitats to which they are pre-adapted but to which many native species are not, and vice versa (Case 1996, Sax & Brown 2000).

Whereas competition between exotic and native bird species does not appear to influence establishment, it is possible that competition between the introduced species may be important at locations with many introductions. In a series of studies, Moulton and coworkers (e.g., Moulton & Pimm 1983; Moulton 1985, 1993; Lockwood et al. 1993; Lockwood & Moulton 1994; Brooke et al. 1995; Moulton & Sanderson 1999; Moulton et al. 2001b) have used two lines of evidence to argue that this is the case. First, for passerine introductions to Hawaii and Saint Helena, the probability that a species will establish declines through time

as the number of established species accumulates. Moulton and coworkers argue that it is harder for progressively later introductions to establish because they face increasing competition from a greater number of already established species. Second, at several locations successfully established species overlap less in their morphological characteristics than would be expected if a random selection of the introduced species had established. Moulton and coworkers argue that this pattern arises because species are more likely to fail due to competition with other introduced species of similar morphology, leading to a pattern of morphological overdispersion among the established species.

However, these conclusions have been questioned by studies showing that the same patterns could arise through various artifacts (Simberloff & Boecklen 1991, Duncan 1997, Duncan & Blackburn 2002). Whereas later introductions of passerine birds to New Zealand faced a greater number of already established species and were less likely to succeed, this relationship was confounded by introduction effort (Duncan 1997). Later introductions tended to be of fewer individuals and so were less likely to succeed for that reason. Similarly, Duncan & Blackburn (2002) showed that significant morphological overdispersion among gamebirds established in New Zealand (Moulton et al. 2001b) could not have resulted from competition, but could be explained by greater effort being applied to the introduction of species that were morphologically different from one another. In addition to facing a greater diversity of already established birds, later introductions to New Zealand, and probably elsewhere, would also have faced a greater diversity and abundance of introduced predators, making it impossible to isolate the effect of competition (Duncan et al. 2003). These results for New Zealand do not rule out the importance of inter-specific competition in other introduced bird assemblages, but they do question the evidence presented in support of this mechanism. Overall, there is little unequivocal support for the hypothesis that competition affects the outcome of bird introductions.

The idea that establishment is affected by competitive and predatory interactions has suggested at least three further hypotheses. First, social foraging species should be better invaders than solitary species (Mayr 1965, Ehrlich 1989), because social foraging can increase the probability of detecting predators, locating food, and learning about new food sources. This hypothesis has not received empirical support (Sol 2000b, Duncan et al. 2001). Second, ground-nesting birds should have lower probabilities of establishing than canopy-, shrub-, or hole-nesters, because nest predation is generally higher in ground-nesters (see Reed 1999). There is some support for this hypothesis (Newsome & Noble 1986; McLain et al. 1999; but see Sol et al. 2002). Third, herbivores have been predicted to invade new habitats more easily than carnivores (Hairston et al. 1960, Crawley 1986), because competition is thought to be less intense among herbivores than among carnivores. The hypothesis has not received empirical support for birds (e.g., Veltman et al. 1996), and its assumptions are questionable (Crawley 1986).

A further location-level factor proposed to influence establishment is the area of suitable habitat (Smallwood 1994, Case 1996). Larger areas can support more

individuals and are thus more likely to maintain self-sustaining populations in the long-term. However, this fact may be of little relevance to establishment when populations generally start out small. Indeed larger areas may result in more dispersed founding populations and a lower probability of success owing, for example, to greater difficulty finding mates. Case (1996) found a weak, but significant, positive correlation between island area and the number of species introduced, but no correlation with establishment success. Site invasibility was not found to decrease with area in California's nature reserves (Smallwood 1994).

Finally, in a global analysis of bird introductions, Blackburn & Duncan (2001a) found significant variation in establishment rate among biogeographic regions after having controlled for other confounding factors such as latitude. It is unclear what underlies such large-scale geographic variation in establishment probability.

Species-Level Influences on Establishment Success

The widespread success of certain introduced birds, such as the starling (*Sturnus vulgaris*), house sparrow (*Passer domesticus*), and rock dove (*Columba livia*; Long 1981), suggests that some species may simply be good at establishing in novel environments. Whether species differ inherently in their probability of establishing, and if so, what characteristics regulate this difference, are two questions that have long interested ecologists (Mayr 1965, Ehrlich 1989).

DO SPECIES DIFFER IN THEIR PROBABILITY OF ESTABLISHING? Simberloff & Boecklen (1991) noted what they termed an all-or-none (AON) pattern for bird introductions to the Hawaiian islands. Bird species tended to establish successfully or to fail repeatedly on all islands to which they were introduced, with mixed outcomes, where species established on some but not other islands, being rare (but see Moulton 1993; Brooke et al. 1995; Moulton & Sanderson 1996, 1999; Duncan 1997; Duncan & Young 1999). Such a pattern would suggest that species-level attributes are a key determinant of establishment. Some species are particularly good invaders, and so succeed everywhere they are introduced, while other species are poor invaders and fail regardless of the location.

A brief perusal of any compendium of avian introductions (e.g., Long 1981, Lever 1987) is enough to show that birds do not follow a strict AON pattern. This is expected even if species-level attributes strongly influence establishment success (Duncan & Young 1999). Species are unlikely to be either absolutely good or poor invaders because event- and location-level factors will also affect establishment. Hence, even an exceptionally good invader might occasionally fail because of unfavorable circumstances, and vice versa. The key question is whether there is significant variation in establishment probability among introduced species, the alternative being that all species establish with equal probability. In testing this hypothesis, we need to control for confounding factors—an inherently poor invader might appear better than it really is if introduced to locations that are easy to invade. Fitting a mixed model to data on global bird introductions, and having controlled

for location- and event-level factors likely to affect establishment, Blackburn & Duncan (2001a) showed that there are highly significant differences among species in establishment probability. Given this variation, do certain attributes of the species themselves distinguish the good from the poor invaders?

WHICH TRAITS INFLUENCE ESTABLISHMENT SUCCESS? The idea that certain species attributes influence establishment success is supported by comparative studies linking the outcome of historical bird introductions to behavioral, life history, and morphological traits (e.g., Newsome & Noble 1986, McLain et al. 1995, Veltman et al. 1996, Green 1997, Cassey 2001a, Sol 2003). However, two problems make it difficult to draw firm general conclusions from the studies to date. First, some studies present results from univariate statistical models while other studies present results from multivariate models. Multivariate models are more powerful in correlative studies because they reduce the likelihood that a significant relationship between two variables results from their correlation with a third variable, assuming that important confounding variables have been included in the analysis. Second, some studies suffer from the problems of non-independence we discussed above. In particular, the importance of traits in explaining establishment is often assessed by fitting a generalized linear model with establishment included as either a binary outcome (the result of each introduction event coded as success or failure) or a binomial outcome (the number of successful events / the total number of introduction events for each species). In either model, a species is represented in the analysis as many times as it has been introduced. However, when the data include multiple introductions of the same species to different locations, then each event will not represent an independent data point because the outcomes of introductions of the same species to different locations are almost certainly correlated. In these circumstances, it is important to consider extensions of generalized linear models (such as generalized linear mixed models or generalized estimating equations) that take into account the clustering of events and minimize the problem of inflated type I error rates.

The traits identified as influencing establishment success are of three types: (a) traits that preadapt species to the new environment, (b) traits that favor population increase from a low level, and (c) traits that constrain establishment success.

Preadaptations to establishment One reason for failing to establish is that a species fails to find a suitable niche in the new environment, either because the niche does not exist or because it is occupied by other species. The chance of finding a favorable niche will depend on the presence of preadaptations to exploit the resources and escape enemies in the new environment.

A generalist species with a wide niche breadth should have, on average, a better chance of finding appropriate resources and environmental conditions wherever it is introduced than a more specialized species (Ehrlich 1989, Forsy & Allen 1999). A problem with testing this hypothesis is the difficulty in quantifying niche breadth (Gaston 1994). Using a coarse measure of dietary breadth, McLain et al.

(1999) found that, for 132 passerine species introduced to nine islands, those with a broader dietary range were more likely to establish (see also Wolf et al. 1998, Cassey 2001b). Similarly, Brooks (2001) found that introduced birds categorized as habitat specialists were less likely to establish successfully. However, other studies have failed to find such relationships (Veltman et al. 1996, Sol et al. 2002), and it is difficult to determine if these discrepancies result from a weak influence of niche breadth or reflect the noise associated with using coarse measures to quantify breadth.

A species released into a new environment will face a variety of novel challenges for which it may not be well adapted (Sol 2003). Animals may partly compensate for this lack of adaptive fit by inventing new behaviors or adjusting established behaviors to the novel conditions (Klopfer 1962, Plotkin & Odling-Smee 1979, Morse 1980, Arcese et al. 1997, Brooker et al. 1998, Berger et al. 2001, Lefebvre et al. 2003, Sol 2003). This behavioral flexibility may aid establishment through, for example, the ready adoption of unexploited new food resources, the adjustment of breeding to the prevailing breeding conditions, or rapid behavioral changes to avoid novel enemies (Sol 2003). Because behaviorally flexible species are believed to be more exploratory (Greenberg & 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 enhance survival and reproduction in the new environment. The hypothesis that behavioral flexibility enhances establishment (Mayr 1965) is supported by the finding that established birds tend to have a larger brain size per unit body mass and to show more innovative behaviors in their region of origin than failed species (Sol & Lefebvre 2000, Sol et al. 2002).

Certain traits associated with generalist behavior may enhance establishment for some species, whereas other traits may preadapt species to specific habitats. The latter may explain why birds that inhabit human-modified habitats in their native range and those with a history of close association with humans tend to be successful invaders (Sol et al. 2002; see also Mayr 1965, Brown 1989, Sax & Brown 2000).

Securing the bridgehead Most introduced populations start off small and face the threat of stochastic extinction. One argument is that species with higher rates of population growth should have a higher probability of establishing because they can more quickly escape the risks associated with remaining at small population size (Moulton & Pimm 1986, Pimm et al. 1988, Pimm 1991). Because population growth rates are difficult to measure, most studies that test this hypothesis use life-history traits known to be correlated with population growth rate as surrogates. Thus, species with small body mass, short development times, multiple broods per season, and large clutch sizes are expected to have higher establishment. However, small-bodied species with high rates of population growth also tend to have more variable population sizes, which could increase their risk of extinction because population densities will drop to low levels more often (Pimm 1991). In these

circumstances, larger-bodied, longer-lived, species with slower rates of population growth that are relatively unaffected by environmental fluctuations are expected to have higher establishment (Legendre et al. 1999, Forsyth & Duncan 2001).

These contradictory theoretical predictions are mirrored in empirical findings. Whereas some studies report a positive relationship between clutch size and establishment success (Green 1997, Cassey 2001b), others have reported negative relationships or no relationship at all (Veltman et al. 1996, Duncan et al. 2001). Cassey (2001b) found that birds with longer generation times were more likely to establish following introduction to New Zealand, but Griffith et al. (1989) reported higher establishment success for re-introduced species classified as “early breeders” than for those considered “late breeders.” Results for body mass are similarly equivocal (e.g., Veltman et al. 1996, Green 1997, Sol & Lefebvre 2000, Blackburn & Duncan 2001b, Sol et al. 2002). Moreover, the relationship between body mass and establishment appears to depend on the taxonomic level considered. Cassey (2001a) found that global introduction success is significantly negatively related to body size across species, families, and higher family nodes. However, within taxa, larger-bodied species are more likely to establish.

Population growth rate has also been invoked in the suggestion that colonial species should establish less readily than noncolonial. Colonial species may have, at low population densities, a reduced per capita growth rate owing to the Allee effect, which would increase the probability of stochastic extinction (Reed 1999). The only study that has examined this prediction failed to find support for it (Sol 2000b).

Constraints on success Some traits may lower establishment probability regardless of other traits the species possess. The two most commonly cited such traits are migratory behavior and sexual color dimorphism. In New Zealand, migratory species are less likely to establish than nonmigratory species (Veltman et al. 1996, Duncan et al. 2003; but see Duncan et al. 2001, Sol et al. 2002). The reasons for this result are unclear, but they could be related to physiological costs associated with preparing for migration, or because suitable habitats to migrate to are not available or cannot be found from the new location (Veltman et al. 1996). In birds, sexual dimorphism in plumage color appears to be the result of sexual selection, and in some studies sexually dimorphic species are less likely to establish following introduction than sexually monomorphic species (McLain et al. 1995, 1999; Sorci et al. 1998; Sol et al. 2002; but see Sol & Lefebvre 2000; Duncan et al. 2001, 2003). The reasons for this may be associated with the cost to males of producing and maintaining secondary sexual characters (A.P. Møller, M.C. Gontard-Danek, unpublished manuscript).

TAXONOMIC VARIATION IN ESTABLISHMENT PROBABILITY Given that species differ significantly in establishment probability, how is this variation partitioned among different levels in the taxonomic hierarchy? If significant variation resides at high levels in the hierarchy, say among families, then it should be possible to

predict establishment from knowledge of a species' taxonomic status alone (Daehler & Strong 1993). In addition, knowing which families, or other higher taxa, have a high establishment rate may suggest traits shared by members of those groups that contribute to their success.

Applying methods such as nested ANOVA and mixed models to bird introduction data reveals that most variation in establishment probability resides at low rather than high taxonomic levels (Blackburn & Duncan 2001a, Sol et al. 2002). That is, closely related species are likely to differ substantially in their probability of establishment. Nevertheless, the extent to which at least some variation in establishment resides at higher taxonomic levels remains unclear. Sol et al. (2002) reported that 21% of variation in establishment rate was found at order level. Having controlled for variation in location-level effects, Blackburn & Duncan (2001a) found no similar significant effect in their global analysis of bird introductions. In Australia, introduced gamebirds (order Galliformes) were significantly less likely to establish than other species (Duncan et al. 2001), with similar low rates of establishment observed in New Zealand and the United States. This observation could, in part, reflect hunting pressure, although in the United States long moratorium periods were implemented before the hunting of gamebird species commenced (Long 1981). Moulton et al. (2001a) also reported lower establishment success in Galliformes and Columbiformes relative to Passeriformes.

The general pattern of variance partitioning suggests that interspecific variation in establishment probability is driven primarily by traits that vary among closely related species. It follows that traits shared by closely related species, including phylogenetically conserved life history traits such as body mass and clutch size, should poorly explain establishment. The equivocal results reported for many such traits, along with their failure significantly to explain establishment for global bird introductions (Blackburn & Duncan 2001a), bear this out. The general failure to identify life history traits that consistently explain establishment may reflect the overwhelming importance of factors such as introduction effort or environmental matching. Equally, however, there may be no simple set of traits that favor establishment. Instead, different traits may enhance establishment under different conditions, and at any one location there may be establishment opportunities for species possessing a variety of trait combinations.

SPREAD

The European starling (*Sturnus vulgaris*) established following introduction to New York state in the late nineteenth century and has subsequently spread to become among the most widely distributed and abundant birds in North America. At about the same time, the crested myna (*Acridotheres cristatellus*) was introduced and became established in Vancouver. This close relative of the starling became reasonably numerous but spread little, remaining largely confined to Vancouver and its environs, with the population now having dwindled to low numbers. Relative to

other taxa, birds are generally good dispersers. Why then, following establishment, do bird species differ so markedly in the rate at which they spread and the final extent of their distribution?

Because birds are well studied, sufficient records exist quantitatively to model range expansion in several introduced species (Hengeveld 1989, Van den Bosch et al. 1992, Veit & Lewis 1996, Williamson 1996, Shigesada & Kawasaki 1997, Lensink 1998, Gammon & Maurer 2002, Silva et al. 2002). Whereas these models allow us to examine factors affecting the rate of expansion in a few typically widespread species, no study has yet quantified or examined the reasons underlying interspecific variation in rate of spread.

Three studies have nevertheless examined the determinants of current geographic range size in two introduced avifaunas: New Zealand (Duncan et al. 1999) and Australia (Duncan et al. 2001, Williamson 2001). The extent of habitat or environmental conditions suitable for an introduced species should ultimately constrain its distribution in a new location. This hypothesis is supported by data from both avifaunas. In New Zealand, the species with the largest geographic ranges were those whose preferred habitat was most widespread, specifically species that use extensive human-modified habitats such as farmland. On the larger and more climatically varied continent of Australia, species with larger geographic ranges were those with a greater area of more climatically suitable habitat available, with this variable explaining 69% of the variation in range sizes.

All three studies show that species with a larger native geographic range size achieved a larger range size in the location of introduction (Duncan et al. 1999, 2001; Williamson 2001). At least two explanations could underlie this relationship. First, as we have discussed, species with larger native ranges may have broader environmental tolerances or use more widespread resources, enhancing success at both establishment and spread. We suspect this is the primary cause of this relationship. The second explanation follows from the finding that species with larger native range sizes tend to be introduced more often and in greater numbers (Blackburn & Duncan 2001b). In New Zealand, the species introduced with greater effort were not only more likely to establish but were also more likely to spread and achieve a larger geographic range size (Duncan et al. 1999). One explanation for this finding is that species with large founding populations might be able to capture a greater proportion of shared resources from species with smaller founding populations. This initial advantage could have compounded itself—those species initially able to capture a greater share of resources would have had faster population growth and rate of spread, allowing them further to pre-empt resources at newly colonized sites as their ranges expanded. As we would expect, this effect is most pronounced among closely related species that are more likely to compete for similar resources (Duncan et al. 1999). This explanation implies that competition may play a role in limiting the range sizes of established species but not in influencing establishment success (see above). Nevertheless, it requires further testing even to establish if the relationship between introduction effort and range size holds more generally (it does not for Australia; Duncan et al. 2001).

Finally, several life history traits consistently relate to the geographic range size of established species in New Zealand and Australia (Duncan et al. 1999, 2001; Cassey 2001b; but see Williamson 2001). More widespread species tend to be those with life history traits associated with high population growth rates, characteristically small-bodied, rapidly developing species with high fecundity. It has been suggested that species with fast population growth rates have larger ranges because they may be less vulnerable to local extinction when colonizing unoccupied sites (Gaston 1988).

FUTURE DIRECTIONS

Throughout this review, we have emphasized how the quantity and quality of data on historical bird introductions have provided opportunities to test key hypotheses about the factors underpinning invasion success. We finish by highlighting five promising research directions.

First, attempts to analyze data on bird introductions have highlighted issues that are likely to be a feature of all historical introduction data: confounding of explanatory variables and non-independence of observations. Given that historical introduction data provide us with opportunities to test hypotheses that we cannot test experimentally (because of cost or ethical considerations), a priority is to identify and apply appropriate statistical methods to analyzing such data for all taxonomic groups. Undoubtedly, the degree and type of non-independence will depend on the circumstances surrounding the transport and introduction of different taxa. Birds and plants selected for transport and introduction, for example, probably show different patterns of taxonomic clustering. Analyses that do not consider issues of non-independence should be interpreted with caution.

Second, while comparative studies of bird introductions have provided useful tests of several invasion hypotheses, others remain for which bird introductions appear ideally suited. For example, the “enemy release” hypothesis posits that some invaders do better in their location of introduction than in their native range owing to a lack of natural enemies (e.g., competitors, predators, and pathogens). Because birds are well studied, a considerable amount of detailed information exists on the factors regulating the populations of many bird species in their native ranges. Similarly detailed studies identifying the factors regulating populations of the same species that have established at new locations could test, for example, whether release from predation or competition is the explanation underlying enhanced success in the new location.

Third, measuring and explaining the impact of invaders remains a major unresolved issue in invasion biology (Ricciardi et al. 2000). The impacts of bird invaders have generally received less attention than those associated with other taxa (see, e.g., Ebenhard 1988). One possible reason is the perception that, because most avian invaders occur in human-modified habitats rather than in pristine habitats (Case 1996), their ecological impact should be relatively less important

(e.g., Diamond & Veitch 1981). However, birds have also been reported to generate serious ecological impacts on recipient communities, including hybridization and introgression with native species (Rhymer & Simberloff 1996), transmission of diseases (van Riper et al. 1986), competition and predation (Penny 1974; but see Koenig 2003), and habitat alteration (Ebenhard 1988). In addition, introduced birds have major economic impacts in many locations (Lever 1994, Bomford & Sinclair 2002). Defining and measuring precisely what we mean by impact remains a challenging task, but one that is critical to setting priorities for managing invasive species (Parker et al. 1999; Smith et al. 1999; Williamson 1999, 2001; Ricciardi et al. 2000). Assuming that we can quantify impacts, we can, in principle, apply comparative methods to identify why some species have greater impact than others, as has been done for other invasion transitions, and use this information in explanatory models. Here again it will be important to consider how attributes of the invader and characteristics of the community interact to determine impact. For example, islands are hypothesized to be more vulnerable to the impacts of exotic invaders because island species have not been exposed to mainland selective pressures (Loope et al. 1988, Simberloff 1995). Data on introduced birds may provide opportunities to test these and related hypotheses.

Fourth, the field of invasion ecology has been criticized for drawing a distinction between invasions resulting from human-caused introductions and natural invasions (as we do in this study) when the underlying processes may be very similar and mutually informative (Davis et al. 2001). Because many natural bird invasions have been well documented (e.g., Hengeveld 1989, Clegg et al. 2002), birds provide opportunities to compare these invasion pathways and to assess whether an understanding of invasion dynamics gleaned from human-caused introductions can reliably inform us of natural invasion processes, and vice versa. We caution that this need not be the case. In particular, introduced birds are a distinctly non-random subset of the world's birds so that conclusions about how these species behave may not transfer to other bird groups.

Finally, species introduced to novel habitats provide unique opportunities to investigate the evolutionary process (Mooney & Cleland 2001). Established populations of many introduced species are isolated from source populations and may diverge rapidly from their ancestors through a combination of divergent natural selection, genetic drift and divergence under uniform selection (e.g., Selander & Johnston 1967, Baker & Moeed 1987, Baker 1992, Reznick & Ghalambor 2001, Badyaev et al. 2002). In their classic studies on geographic variation in house sparrows introduced to North America, Selander & Johnston (1967) found major geographic divergence in coloration and morphometric characters within less than 100 years following establishment. More recent studies in other birds have also demonstrated rapid genetic and life history differentiation in introduced populations (e.g., Baker & Moeed 1987, Baker 1992, Badyaev et al. 2002). Given the well-documented history of many bird introductions, often detailing dates and numbers of individuals released, and the range of locations at which some species have established, populations of introduced birds provide a

remarkable and largely untapped resource for addressing questions about evolutionary change.

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