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Causes of exotic bird establishment across oceanic islands

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The probability that exotic species will successfully establish viable populations varies between regions, for reasons that are currently unknown. Here, we use data for exotic bird introductions to 41 oceanic islands and archipelagos around the globe to test five hypotheses for this variation: the effects of introduction effort, competition, predation, human disturbance and habitat diversity (island biogeography). Our analyses demonstrate the primary importance of introduction effort for avian establishment success across regions, in concordance with previous analyses within regions. However, they also reveal a strong negative interaction across regions between establishment success and predation; exotic birds are more likely to fail on islands with species-rich mammalian predator assemblages.

Keywords: birds; introduction effort; invasions; islands; mammal predators

1. INTRODUCTION

Recent studies of the determinants of introduction success in exotic birds have identified regional differences in the probability that species will successfully establish non-native populations (Blackburn & Duncan 2001; Cassey *et al.* 2004). For example, Cassey *et al.* (2004) showed that 56% of avian releases succeeded in Hawaii, but only 35% in New Zealand. Similarly, Blackburn & Duncan (2001) found significant variation in introduction success across regions, with high probabilities of success in the Afro- and Neotropics, and low probabilities in South-east Asia and the Nearctic. In neither study did the ranking of establishment probability across regions imply an obvious cause of the variation observed. Although most data on regional differences in invasions concern numbers of established species rather than introduction success, regional variation in success has also been shown in fishes and mammals (Jeschke & Strayer 2005), suggesting that such differences may be a more general feature of biological invasions.

Why might some regions be harder for exotic birds to invade than others? Within regions, introduction effort now seems firmly established as a primary determinant of success; establishment is more likely if more individuals are released, or there are more separate release events (Duncan *et al.* 2003; Cassey *et al.* 2004; Cassey *et al.* 2005). However, the influence of introduction effort across regions is yet to be established. It is possible that the relationship between introduction effort and introduction success breaks down at this level, for example if regions differ in the slope and/or intercept of their relationship between effort and success. Cassey *et al.* (2004) found that introduction success was not related to

average effort across 13 regions. For example, the difference in introduction success between Hawaii and New Zealand pertains despite similar average numbers of individuals per species being liberated. These differences are not simply a consequence of each region receiving introductions from different sets of bird taxa, some of which may be good invaders and others poor (Cassey *et al.* 2004). Nevertheless, the generality of these results is unclear, as this is the only inter-regional comparison of introduction success in birds (or, as far as we are aware, any other taxon; see Lockwood *et al.* 2005) that includes effort data.

Other candidate explanations for regional variation in introduction success include natural enemies, resources and the physical environment (Shea & Chesson 2002). Since all exotic bird species must increase from relatively low numbers, their populations initially may be highly susceptible to extirpation through predation on adults, juveniles and nests (Thomson 1922; Duncan *et al.* 2003). Competition with other bird species already present at a site may have the same effect by depriving new colonists of access to resources (Elton 1958). More extreme or variable abiotic environments may be harder for species to establish viable populations in, suggesting that introduction success should be lowest at high latitudes (Elton 1958; Sax 2001; although this may depend on characteristics of the species released; Duncan *et al.* 2003). Alternatively, the greater array of habitats typically found in larger or more attitudinally diverse regions may increase the probability that an exotic species will find a location suitable (Smallwood 1994; Case 1996). Biotic and abiotic factors may also interact, since the numbers of predators and competitors is likely to be higher in regions with more amenable climates, more habitat diversity, and higher levels of resource production.

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Table 1. Hypotheses for why some regions are harder for exotic birds to invade than others, with associated predictions, assumptions and statistical tests. (The parameter estimates for the probability of establishment success in our linear models are an estimate of how much the odds (e^{estimate}) of a species establishing (compared to not establishing) would change for a unit increase of the given predictor variable. Thus, negative estimates indicate a lower probability of success associated with an increase in the predictor variable. For the test of hypothesis 1, 'levels' denotes the three logarithmic effort classes to which each introduction event was assigned for each island was categorized (see §2 for more details). Estimates here refer to the probability of success in comparison to success in the largest effort class. Test significance: † $p \approx 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.)

| hypothesis | prediction | assumption | test | | | |
|---|---|---|--|----------|------|----------|
| | | | levels | estimate | s.e. | t-value |
| (i) success is higher when introduction effort is greater | success should be positively related to introduction effort | more individuals released increases establishment probability | 1–10 | –3.03 | 0.64 | –4.73*** |
| | | | 11–100 | –1.56 | 0.49 | –3.16** |
| | | | > 101 | 0 | | |
| (ii) success is lower when the number of potential predators is higher | success should be negatively related to the number of introduced mammalian predator species | predation pressure on an island increases with the number of introduced predator species | estimate \pm s.e. = -1.57 ± 0.89 , $t = -1.78^\dagger$ | | | |
| | success should not be related to the number of introduced mammalian herbivore species | predation pressure is unrelated to the number of introduced herbivore species, even though numbers of predator and herbivore species are correlated | estimate \pm s.e. = -0.72 ± 0.42 , $t = -1.74^\dagger$ | | | |
| (iii) success is lower when the number of potential competitors is higher | success should be negatively related to the number of native birds | an introduced bird species is more likely to encounter a competitor on an island with more bird species in total | estimate \pm s.e. = -0.73 ± 0.41 , $t = -1.81^\dagger$ | | | |
| (iv) success is higher when human disturbance is greater | success should be positively related to human population size | higher human populations lead to greater levels of disturbance. Greater volumes of trade generated by larger populations may also increase opportunities for exotic species to be imported, and so increase introduction effort as a by-product | estimate \pm s.e. = 0.19 ± 0.11 , $t = 1.72^\dagger$ | | | |
| | success should be positively related to time since human colonization | a longer history of human presence on an island increases the likelihood of disturbance | estimate \pm s.e. = -0.12 ± 0.38 , $t = -0.32$ | | | |
| | success should be negatively related to island isolation | more isolated islands will have less human contact and disturbance | estimate \pm s.e. = -0.34 ± 0.33 , $t = -1.03$ | | | |
| (v) success is higher on islands with greater habitat diversity | success should be positively related to island area | smaller islands have fewer habitat types | estimate \pm s.e. = -0.18 ± 0.11 , $t = -1.62^\dagger$ | | | |
| | success should be positively related to island elevation | less elevated islands have lower range of habitat types | estimate \pm s.e. = -0.44 ± 0.33 , $t = -1.31$ | | | |
| | success should be negatively related to island isolation | more isolated islands have lower habitat diversities due to problems of colonization | estimate \pm s.e. = -0.34 ± 0.33 , $t = -1.03$ | | | |

A further feature of the environment that may influence the establishment success of exotic birds is the level of human disturbance (Rejmánek 1989; Case 1996; Cassey 2003). High levels of human disturbance may create habitat favourable for the establishment of introduced birds, as many of these have a long history of human commensalism. Case (1996) found that the best predictor of the establishment success of exotic birds on islands around the world was the number of native bird extinctions. He argued that this reflected the effect of human disturbance in terms of habitat destruction and associated intrusions of exotic predators. However, this analysis suffers from the lack of information on introduction effort, which we would expect *a priori* (and despite the results of Cassey *et al.* 2004) to be a good predictor of success (Duncan *et al.* 2003), and which is frequently well correlated with other putative predictors (Cassey *et al.* 2004).

In this paper, we address the question of why some regions are harder for exotic birds to invade than others, using an extensive dataset on avian introductions to oceanic islands around the world (cf. Case 1996). We test the following hypotheses for establishment success: (i) success is higher when introduction effort is greater; (ii) success is lower when the number of potential predators is higher; (iii) success is lower when the number of potential competitors is higher; (iv) success is higher when human disturbance is greater; (v) success is higher on islands with greater habitat diversity. We focus on islands because we can more easily quantify metrics for these more restricted areas that allow tests of predictions of each of these hypotheses.

2. MATERIAL AND METHODS

We collated data from published literature sources for 41 oceanic islands or archipelagos (hereafter referred to as islands). We scored an avian introduction as successful if it resulted in the establishment of a persistent or probably persistent population following release, and unsuccessful otherwise (introductions described as possible successes were ignored). Data (and sources) for the numbers of successful and unsuccessful introductions follow Cassey (2002) and Cassey *et al.* (2004). A generalized linear mixed model (GLMM) was used to account for the clustering of islands and archipelagos into four biogeographic regions (Atlantic, Caribbean, Indian Ocean and Pacific). GLMMs provide a framework for analysing data in which observations are likely to be correlated due to clustering and cannot, therefore, be treated as statistically independent units. GLMMs incorporate information on such clustering to provide estimates of standard errors corrected for this non-independence, which will generally be more conservative than estimates obtained if the clustering is ignored. We modelled the likely non-independence of introductions on islands in the same region by assuming a common positive correlation between introduction outcomes within the same region, but a zero correlation between outcomes involving different regions (a variance components model). The remaining predictor variables were included as fixed effects. The GLMM was implemented by the GLIMMIX macro in SAS (Littell *et al.* 1996). Avian introduction success for each island was modelled specifying a binomial error distribution and logit link function, with number of successes/total number of bird

introductions (the probability of success) as the response variable.

Success was explored in terms of the following predictor variables:

Introduction effort. We collated data for as many exotic bird species introductions as possible on the total number of individuals of each bird species released on each island (minimum estimate). Introduction effort was modelled by calculating, for every archipelago for which data were available, the number of success and failures in each of the three logarithmic effort classes (0–10, 11–100, >101 individuals introduced), and analysing effort as a class variable. Estimates for the levels of introduction effort, and their significance, are evaluated against the largest level (i.e. establishment success on islands decreases significantly with the introduction of fewer individuals).

Number of exotic mammal species. In most places, level of predation is difficult to assess as it derives from a variety of sources. However, oceanic islands were in most cases largely predator-free before human discovery, and most predation of bird species there can be attributed to introduced mammals. We collated data on all mammal species introduced to the islands in our set, and then classified them as herbivores if their diet was exclusively plant material (or almost so), or predators otherwise. Thus, omnivorous species known in some cases to be significant predators of birds or their eggs, such as rats (*Rattus* spp.) and pigs (*Sus scrofa*), were included as predators. Data sources are listed in Blackburn *et al.* (2004).

Number of native bird species. This includes the number extant and recently extinct (i.e. since European colonization). Data sources are listed in Blackburn *et al.* (2004).

Human population size (number of individuals), *island area* (km²), *maximum elevation* (m), *isolation from nearest continental landmass* (km), and *time since first human colonization* (years). The main sources for these data were Milberg & Tyrberg (1993), Anon. (1997), Biber (2002) and <http://islands.unep.ch/isldir.htm>.

3. RESULTS AND DISCUSSION

Table 1 describes how the data were used to test the five hypotheses for variation in establishment success across regions outlined in §1. This table also includes the results of univariate relationships between avian introduction success and the various predictor variables. Exotic bird establishment on islands is more likely where introductions involve the release of more individuals, on average ($F_{2,27} = 11.83$, $p < 0.01$, with effort classified as described in §2). This result, across islands, mirrors findings previously described within regions (Duncan *et al.* 2003; Cassey *et al.* 2004). None of the other hypothesized relationships with exotic bird introduction success are formally supported in the univariate tests (table 1), although the effects of number of mammalian predators, number of mammalian herbivores, number of native bird species and human population size all approach significance ($p < 0.1$), and would have been considered so had we employed more liberal one-tailed significance levels. Island area also approaches formal significance ($p < 0.1$), albeit in the opposite direction to that predicted.

We constructed a multivariate model of avian establishment success across islands using forward selection toward a final model that tested all the predictor variables in table 1.

Table 2. Multivariate model of exotic bird species establishment success on oceanic islands. (The sample size was only 30, as not all data were available for all archipelagos. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.)

| | level | estimate | s.e. | t-value |
|--|--------|----------|------|----------|
| intercept | | 5.29 | 2.05 | |
| no. of introduced predatory mammals | | -4.00 | 1.90 | -2.10* |
| introduction effort (no. of individuals) | 0-10 | -3.09 | 0.59 | -5.21*** |
| | 11-100 | -1.67 | 0.46 | -3.62** |
| | >101 | 0 | | |

The best fitting (final) model was that with the lowest Akaike Information Criterion, calculated in the SAS procedure NLMIXED, and is shown in table 2. Both introduction effort and number of mammalian predator species explain independent variation in introduction success in a multivariate model. In contrast, our final model identifies that success is not related to the number of mammalian herbivores, even though the numbers of predators and herbivores on islands are positively correlated ($r = 0.70$, $n = 38$, $p < 0.01$). Thus, exotic bird introductions are more likely to succeed when more individuals are released, but more likely to fail on islands where those individuals encounter more species of exotic mammalian predators.

Our analyses also do not support the influence of native bird community size on exotic bird success. We use native bird community size as an index of the probability that an exotic species will encounter and be excluded by a native competitor. This may be a poor index of the likelihood of encountering competition because exotics are more likely to be encountered in highly modified habitats, whereas native species are more likely to occur in native habitats (Diamond & Veitch 1981; Simberloff 1992; Smallwood 1994; Case 1996). However, in this case we would not expect exotics to be excluded by native competitors, and hence our conclusion that competition with natives does not limit exotic establishment success is unchanged. Competition could still be important in this situation if it was occurring between previously established exotics (e.g. Moulton & Pimm 1983; Lockwood *et al.* 1993; Moulton 1993; Brooke *et al.* 1995; Moulton *et al.* 2001, but see Duncan & Blackburn 2002). However, this would suggest that establishment probability should decline as number of established exotic species increases, while these two variables are unrelated across our islands (estimate \pm s.e. = -0.20 ± 0.31 , $p = 0.53$).

Neither do we find support for the hypothesis that exotic establishment success is facilitated by greater habitat diversity *per se*. Area, elevation and isolation are all thought to relate to island habitat diversity, but are unrelated to establishment success (table 1).

Finally, our analyses do not support the generality of earlier analyses that concluded that human activity through 'habitat destruction and deterioration' was an important correlate of successful establishment on islands for exotic birds (Case 1996; Cassey 2003). Although there is trend towards higher establishment success on islands with higher human population sizes (table 1), this disappears when introduction effort is controlled for.

Moreover, there is no relationship between establishment success and either time since human colonization or island isolation, whether effort is controlled for or not. Thus, we find no strong evidence that exotic bird species preferentially invade environments more disrupted by human activities.

In summary, of the five hypotheses set out in table 1, patterns of exotic bird establishment on islands are consistent with only two. Our data reinforce the importance of introduction effort for avian establishment success across, as well as within, regions. However, they also reveal a strong negative interaction across regions between ease of establishment and predation. Exotic birds fail in the face (and teeth) of large predator assemblages.

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