Evolutionary Ecology Research, 2003, **5**: 1011–1021

A comparative analysis of the relative success of introduced land birds on islands

Phillip Cassey*

Laboratoire d'Ecologie, Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris cedex 05, France

ABSTRACT

It has been suggested that more species have been successfully introduced to oceanic islands than to mainland regions. This suggestion has attracted considerable ecological interest and several theoretical mechanisms have been proposed. However, few data are available to test the hypotheses directly, and the pattern may simply result from many more species being transported to islands rather than mainland regions. Here I test this idea using data for global land birds and present evidence that introductions to islands have a higher probability of success than those to mainland regions. This difference between island and mainland landforms is not consistent among either taxonomic families or biogeographic regions. Instead, introduction attempts within the same biogeographic region have been significantly more successful than those that have occurred between two different biogeographic regions. Subsequently, the proportion of introduction attempts that have occurred within a single biogeographic region is thus a significant predictor of the observed variability in introduction success. I also show that the correlates of successful island introductions are probably different to those of successful mainland introductions.

Keywords: biogeographic regions, introduction success, islands, land birds, mainland continents.

INTRODUCTION

Humans have introduced land bird species to many different regions of the world (Long, 1981). Some of these introductions have been successful and sustainable populations have been established, whereas many others have failed (Lockwood, 1999; Blackburn and Duncan, 2001a; Cassey, 2002a). Many conceptual models exist that predict varying influences of species-level, location-level and event-level properties (*sensu* Blackburn and Duncan, 2001a) for the outcomes of species introductions (Mooney and Drake, 1989; Williamson, 1999; Kolar and Lodge, 2001). Many of the empirical hypotheses associated with the success of non-native species date from the natural history observations and writings of Elton (1958). In his book, *The Ecology of Invasions by Animals and Plants*, Elton argued that 'the balance of relatively simple communities of plants and animals is more easily upset than that of richer ones; that is more subject to destructive oscillations

---

* e-mail: cassey@biologie.ens.fr

in populations . . . and more vulnerable to invasions' (p. 145). He supported this argument with observations that islands are simple ecosystems that frequently exhibit high vulnerability to biological invasions. Surprisingly, these observations have proven difficult to test (Levine and D'Antonio, 1999).

The geographic isolation of islands can present great dispersal difficulties to naturally colonizing species and, therefore, acts as a filter on what can reach an island (Mueller-Dombois *et al.*, 1981). In evolutionary and ecological terms, this results in islands being characterized by both 'impoverishment' and 'disharmony', having fewer species than equivalent mainland areas and higher degrees of endemism (Williamson, 1981). These features are generally more pronounced for oceanic islands for which the filter of isolation is more severe. Recently, island systems have been exposed to much higher rates of global disturbance, of which human colonization is the dominant perturbation factor (Chown *et al.*, 1998).

A general pattern that has emerged from syntheses of global introductions is that the number of non-native species established on oceanic islands is greater than for continental islands and mainland regions (Drake *et al.*, 1989; Williamson, 1996). This observation is consistent with the natural impoverishment of these islands. However, this pattern may also be caused if more species have been introduced to oceanic islands compared with other regional landforms (Pimm, 1991; Simberloff, 1995). For example, of the nearly 2000 recorded land bird introduction attempts that have been compiled by the author and described elsewhere (Cassey, 2002b), less than a third have been to mainland regions. In contrast, the five archipelagoes of Hawai'i, New Zealand, the Mascarenes, Society Islands and West Indies together received more than 40% of all introduction attempts, including 75% of all land bird species that are known to have been introduced outside their native geographic ranges. For comparisons between continental Australia and the New Zealand archipelago, and continental North America and the Hawaiian archipelago, Sol (2000) found that there was no difference in introduction success between islands and continents when he controlled for differences in the invading capacities of different avian species. Blackburn and Duncan (2001a) found the same for a global data set of bird introductions.

In this paper, I extend previous analyses of the relative success of land bird species introduced to island regions around the globe. First, I test for differences in the success of introductions to islands versus mainland regions, using an updated global list of introduction events and distinguishing between oceanic and continetnal islands. Second, I examine the prediction that, for any given family, introductions that occur within a biogeographic region will be more successful than those occurring between different biogeographic regions (e.g. the abiotic suitability hypothesis *sensu* Simberloff, 1989; and examined by Blackburn and Duncan, 2001a). Third, I use statistical models to determine whether the variation in introduction success among mainland regions and islands can be explained by chance alone, or whether introduction success is related to species-level, location-level and event-level variables.

DATA SOURCES

By land birds I mean species that are considered to have long-term terrestrial populations and are not dependent on the ocean for feeding. Less than 5% of all land bird introductions are of species that breed only on islands (Long, 1981). Hence, for comparability, all analyses were conducted using only 'mainland' breeding species. Following Ebenhard (1988), I have defined an introduced species as one that is recorded to have been transported and introduced free-living outside its naturally occurring geographic range. The enumeration of attempted land bird introductions consists of 416 species from 1960 separate introduction attempts and follows the methods that are described in Cassey (2002a). The data used in the analyses and the bibliography for the sources from which I drew them may be accessed through the Australian Digital Theses project and Griffith University at http://www.gu.edu.au/ins/catalogue/grifflink/ (Cassey, 2002b).

To control for the confounding influences of taxonomy (Lockwood, 1999) and biogeography (Blackburn and Duncan, 2001b), introductions were pooled within avian families as well as the biogeographic regions to which they were introduced. Species were assigned to families according to the taxonomic classification of Sibley and Monroe (1990, 1993) using the application Nomina (Andrew, 1998). Biogeographic regions and landforms (mainland, mainland island and oceanic island) were classified into the following categories, following Wallace (1876) and Ebenhard (1988): Nearctic (including Alaska, North America and Canada, Eastern Pacific and Hawai'i, West Indies); Neotropical (including Central America, Southern America, Western Antarctic, Northern Pacific); Australasia (including Australia, Central Pacific and New Zealand, Western Pacific, Southern Antarctic); Oriental (including Indian subcontinent, Wallacea, Japan); Ethiopian (including Southern Africa, Central Atlantic, Central Antarctic Seas, West Indian Ocean); Palearctic (including Europe, Northern Atlantic Ocean, Mediterranean Sea, Northern Africa). Analyses were restricted to taxonomic families, biogeographic regions and major landforms that have experienced at least five introduction attempts.

Data were collected from the literature for the 55 islands that have experienced at least five introduction attempts and are annually inhabited by human populations. My indices of island characteristics were island size (ln[square kilometres]), isolation from nearest mainland region (ln[kilometres]), human density (population per square kilometre) and human environment (developed land as a share of total land area). Great circle distance between donor and recipient regions for each introduction attempt (ln[kilometres]) was measured as an index of environmental similarity and introduction effort.

STATISTICAL ANALYSES

All data analyses were conducted in SAS 6.12 and used the procedures IML, NESTED or GENMOD (SAS Institute, 1996). Logistic regression analyses were used to determine whether the outcome of introduction success has varied significantly between land bird introductions to mainland regions and those to oceanic and continental islands. Introduction success was measured as the number of successful introduction attempts divided by the total number, since proportions provide an intuitively obvious basis for comparison. Arcsine square-root transformations were used to normalize the residuals of proportion data (Sokal and Rohlf, 1995). To avoid possible pseudoreplication, *F*-tests are presented to account for both within- and between-landform sources of random variation in introduction success (Elston, 1998; Littell *et al.*, 1999). Significance of differences between landforms was assessed using planned orthogonal contrasts.

To test the abiotic suitability hypothesis, I calculated differences in introduction success and relative biogeographic effort (RBE; the proportion of introductions for a family that occurred between different biogeographic regions rather than within a single biogeographic region). Contrasts were constructed between mainland and island introductions across separate taxonomic families. Contrasts in introduction success (ΔY) were always calculated in the same direction as positive differences in RBE (ΔP), where ΔY is the difference in the two proportions (each given by: no. of successes/total no. of introductions for a given family).

To determine whether the variability in introduction success has been randomly distributed among islands, I conducted a Monte-Carlo simulation of the random distribution of successful introductions from the 1068 introductions that have occurred on islands with at least five introduction events. A computer program to conduct these simulations was written in SAS procedure IML (SAS Institute, 1996). At the end of each iteration I noted which island the randomly assigned successful introductions were from, and calculated the proportion of introduction attempts that had been picked in this way. The simulation was repeated with 10,000 iterations and a relative frequency histogram was drawn of the average number of islands in each proportion class across all 10,000 iterations. The null hypothesis that the observed distributions were not significantly different from random were tested using ordered χ^2 tests (Zar, 1999).

Multiple logistic regression, with a logit link function and binomial errors (McCullagh and Nelder, 1990), was used to examine how well the six variables (taxonomic constraint, island isloation, island size, human density, human environment and great circle distance) predicted the introduction success of land birds to islands. I used sequential stepwise deletion tests manually to assess and remove non-significant terms from a model containing all the remaining predictor variables (Olden and Jackson, 2000). The resulting change in deviance was compared to a χ^2 distribution using the appropriate degrees of freedom.

RESULTS

The predicted proportion of successful land bird introductions was greater for introductions to both continental islands (mean success [95% CI] = 0.52 [0.47, 0.58]; $n = 358$) and oceanic islands (mean success [95% CI] = 0.53 [0.50, 0.57]; $n = 772$) than for introductions to mainland regions (mean success [95% CI] = 0.39 [0.35, 0.44]; $n = 549$). There was no difference in the predicted proportion of successful land bird introductions between continental and oceanic islands (Proc GENMOD; SAS Institute, 1993). Introduction success varied significantly with the interactions between taxonomic family and landform (Table 1; $F_{22,288} = 3.47$, $P < 0.001$) and between biogeographic region and landform (Table 2; $F_{10,303} = 2.49$, $P = 0.007$).

Introduction attempts that have occurred within the same biogeographic region have been significantly more successful than those that have occurred between two different biogeographic regions for pooled introduction attempts ($F_{1,306} = 32.35$, $P < 0.001$). Independent contrasts between mainland and island introductions show a strong negative relationship, across families, between the proportion of introduction attempts that occurred between biogeographic regions and their resulting success (Fig. 1a). For a given family, introductions to mainland regions have been significantly more likely to succeed if they occurred within a biogeographic region (Fig. 1b). For introductions to islands, although the trend remains for introductions to be more likely to succeed if they occurred within a biogeographic region, the relationship is non-significant (Fig. 1c).

The successful introduction of land bird species on islands has significantly differed from a random allocation of introduction attempts to islands ($\chi^2 = 29.34$, $n = 1679$, $P < 0.001$) (Fig. 2). Notably, the modes of the two distributions are different and there is a higher

Table 1. Successful (failed), and proportion of successful, land bird introduction attempts for mainland regions, and oceanic and continental islands, by taxonomic family

Introduction attempts of land bird families							
Family name	Common name	Mainland regions		Continental islands		Oceanic islands	
Passeridae	Sparrows	38 (10)	**0.79**	93 (74)	0.56	40 (34)	0.54
Corvidae	Crows and allies	12 (4)	**0.75**	11 (12)	0.48	3 (2)	0.60
Columbidae	Pigeons and doves	23 (10)	**0.70**	37 (50)	0.43	13 (8)	0.62
Numididae	Guineafowl	2 (5)	0.29	13 (10)	**0.57**	3 (9)	0.25
Odontophoridae	New World Quails	5 (14)	0.26	17 (16)	**0.52**	12 (19)	0.39
Muscicapidae	Flycatchers	5 (23)	0.18	13 (14)	**0.48**	1 (4)	0.20
Phasianidae	Pheasants	43 (166)	0.21	74 (101)	**0.42**	34 (63)	0.35
Pycnonotidae	Bulbuls	2 (3)	0.40	8 (2)	0.80	8 (1)	**0.89**
Sturnidae	Starlings	14 (6)	0.70	34 (13)	0.72	16 (4)	**0.80**
Anatidae	Ducks and geese	20 (11)	0.65	13 (23)	0.36	12 (5)	**0.71**
Psittacidae	Parrots	34 (38)	0.47	30 (26)	0.54	30 (14)	**0.68**
Fringillidae	Finches	15 (46)	0.25	37 (51)	0.42	15 (8)	**0.65**

Note: Data are for the 12 families with at least five introduction attempts to each of mainland regions and oceanic and continental islands. These 1679 introduction attempts constitute 86% of all land bird introductions recorded by the author. Proportions in **bold** indicate the landform with the greatest introduction success for each family.

Table 2. Successful (failed), and proportion of successful, land bird introduction attempts for mainland regions, and oceanic and continental islands, by biogeographic region

Introduction attempts to biogeographic regions						
Biogeographic region	Mainland regions		Continental islands		Oceanic islands	
Oriental	7 (2)	**0.88**	53 (36)	0.60	26 (12)	0.68
Australasian	51 (64)	**0.46**	13 (27)	0.33	140 (173)	0.45
Ethiopian	24 (16)	0.65	20 (5)	**0.80**	90 (69)	0.57
Palearctic	47 (37)	0.58	30 (45)	0.40	7 (0)	**1.00**
Neotropical	15 (14)	0.59	9 (9)	0.50	11 (4)	**0.73**
Nearctic	59 (213)	0.22	74 (82)	0.47	141 (130)	**0.52**

Note: Data are for the six biogeographic regions with at least five introduction attempts to each of mainland regions and oceanic and continental islands. These 1755 introduction attempts constitute 90% of all land bird introductions recorded by the author. Proportions in **bold** indicate the landform with the greatest introduction success for each biogeographic region.

frequency of observed islands with greater proportions of successful introduction than expected by chance processes alone. Following manual selection through multiple logistic regression, predictor variables were identified that adequately predicted introduction success to mainland regions and islands (Table 3). Among islands, introduction success was significantly associated with variability in taxonomic constraint, decreased human population density, increased human environment, and decreased great circle distance between the donor and recipient regions.

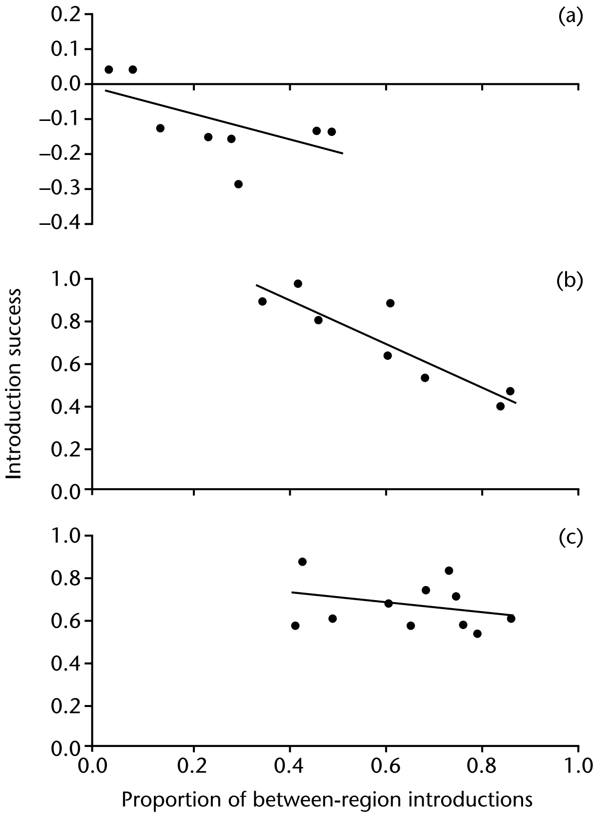

Fig. 1. (a) The relationship between the contrasts in introduction success and relative biogeographic effort (RBE) between island and mainland introductions for land bird families with at least five introduction attempts to both mainland regions and islands. The least-squares linear regression slope is estimated through the origin ($r^2 = 0.56$, slope = −0.386, $n = 8$, $P = 0.020$). (b) The relationship between RBE (the proportion of introduction attempts occurring among biogeographic regions) and introduction success for families with at least five introduction attempts to mainland regions ($r^2 = 0.81$, slope = −0.928, $n = 8$, $P = 0.002$), and (c) families with at least five introduction attempts to islands ($r^2 = 0.26$, slope = −0.519, $n = 11$, $P = 0.109$).

DISCUSSION

As expected from natural history observations (Darwin, 1845; Elton, 1958), I found that the success of land bird species has been significantly greater for introductions to islands than for introductions to mainland regions. Notably, this result is independent of the fact that there have been twice as many introductions to islands as there have been to mainland regions. Is this evidence, therefore, for the hypothesis that island biotas will be more vulnerable to the successful establishment of introduced species than mainland biotas?

My analyses show that introduction attempts, among taxonomic families (Table 1) and biogeographic regions (Table 2), do not consistently support the pattern of more successful establishment of non-native species on oceanic islands (see also Simberloff, 1995; Levine

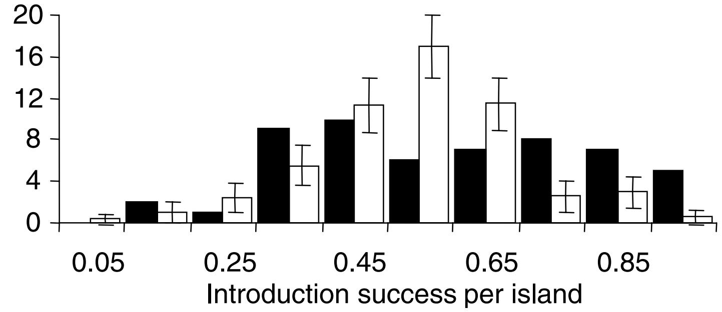

Fig. 2. Frequency distribution across islands of the proportion of introduction attempts to an island that are recorded as successful ($n = 55$ islands; solid bars) and the predicted frequency distribution based on 10,000 simulations (open bars). Error bars on the predicted distribution represent 95% confidence limits around the mean.

Table 3. Results of multiple logistic regression for variables used to predict the probability of introduction outcome[a] for land birds introduced to islands.

Level	Variable	Category	Coefficient	Type III
Species	Taxonomic constraint			24.89***
		Anseriformes	0.047	
		Galliformes	0.881	
		Ciconniformes	1.373	
		Psittaciformes	−0.279	
		Columbiformes	−0.301	
		Passeriformes	0	
Location	Isolation		0.014	0.97
	Island size		0.080	1.53
	Human density		−0.169	4.96*
	Human environment		1.117	6.69**
Event	Great circle distance		−5.651	14.43***

Note: Coefficient estimates and Type III significance tests are presented for the change in deviance associated with dropping a variable last from the model ($n = 55$ islands).
[a] Introduction outcome: 0 = failed; 1 = successful.

and D'Antonio, 1999; Sol, 2000; Blackburn and Duncan, 2001a). Instead, within a family, the proportion of introductions that occur between biogeographic regions was a significant predictor of the observed differences in introduction success between islands and mainland regions (see also Blackburn and Duncan, 2001a). In my analyses, the percentage of introductions occurring within a biogeographic region ranged from 63% for mainland introductions of Columbidae to 12% for island introductions of Pycnonotidae.

Bird species are largely distinguished by their ability to disperse (Lack, 1969). Between different biogeographic regions, related species are separated by greater habitat and environmental differences (Maurer, 1999). In addition, evolutionary differences are more extreme and often strongly contrasted across biogeographic boundaries (Cox and Moore, 2000). It is therefore likely that non-native species from within a single biogeographic region have combinations of traits that are better suited to the variability of the environment than non-native species from another region (Sax and Brown, 2000; Blackburn and Duncan, 2001a,b). For land bird introductions, there can also be a significant reduction in the practical human effort required to transport species numbers and propagules between donor and recipient regions with decreasing distance (Thomson, 1922).

When introduction attempts are pooled across landform types and biogeographic regions, I have previously found that life-history and ecological attributes (notably increased habitat generalism, lack of migratory tendency, and sexual monochromatism) together explain significant variation in the successful establishment of introduced land bird species (Cassey, 2002a). When studying the variability in establishment success among introduction attempts, it is apparent that species-level, location-level and event-level effects are often confounded (Blackburn and Duncan, 2001a,b). Spatial variation in introduction success can arise because of differences in the invasibility of recipient environments (location-level), because species introduced at different locations differ in their ability to invade (species-level), or because the number or quality of individuals released at different locations differs (event-level). A framework is currently being developed to allow for robust statistical analyses where the effects of introduction success are confounded (see, for example, Blackburn and Duncan, 2001a). Future analyses will be able to incorporate the results from this study.

In the present analysis, a significant amount of variability in the success of individual families between islands and continents can be explained by the proportion of introductions that have occurred among biogeographic regions (Fig. 1a). Clearly this difference only explains part of the difference between islands and mainlands, and when the landform types are separated the same relationship is only significant among mainland regions. Similarities, therefore, within a single biogeographic region (and differences between different biogeographic regions) are greater, and less variable, for mainland regions than islands. Most importantly, the overall lower success of mainland introductions is due, in large part, to the few non-native introductions that have occurred between acclimatization regions within mainland biogeographic regions. This is, of course, related to the fact that introduced species are also often those that are abundant and widespread (Blackburn and Duncan, 2001b). Nevertheless, across individual families the result is robust. Figure 1a shows that the smaller predicted mean proportion of introduction successes to mainland regions is largely due to the variability of whether mainland introductions have been attempted either within or between biogeographic regions.

Interestingly, the variability in introduction success of land bird species on islands is not explained by introduction patterns among biogeographic regions. I found strong evidence that the observed variation in introduction success among islands is not simply a result of chance processes alone. Most notably, there were far too many islands for which success has been significantly greater than expected for introduction attempts to be distributed randomly among islands. These results support the idea that it is worth seeking correlates of introduction success among islands. Interestingly, there was no difference in the success of land birds introduced to oceanic versus continental islands. Nevertheless, my analysis confirms that indices of species-level (taxonomic constraint), location-level (human density and human environment) and event-level (great circle distance) properties are influential in determining the success of introduction attempts between islands (see Table 3).

The percentage of human-modified environment was important as a predictor of introduction success on islands. Interestingly, this was correlated with both decreasing island size and human density in the same direction as its relationship with introduction success. When human environment is entered into the model, however, neither island size nor human density are significant predictors of introduction success. Smaller islands have a much greater ratio of coastline per unit area and, because human populations tend to cluster around the coast, the degree of human perturbation can be greater for the smaller islands that are annually inhabited by human populations.

Like other taxa, successful land bird introductions may be characteristic of disturbed and human-dominated habitats (Sax and Brown, 2000). Previous studies have reported negative relationships between changes in the species richness of recipient land bird biotas on islands and the success of introduced species (Diamond and Veitch, 1981; Case, 1996; Chown *et al.*, 1998). In other words, habitats with decreasing native species richness have a greater number of successfully introduced species (i.e. the biotic resistance hypothesis *sensu* Elton, 1958). Similarly, Case (1996) found that native species extinctions were the most important correlate of success. He concluded, however, that this reflected the degree of human activity and 'habitat destruction and deterioration' rather than any advantage through the release of avian competitors. His conclusion is supported by the results presented here.

Decreasing great circle distance was a significant predictor of introduction success among islands. This result reflects the previous trend that species that are transported and released close to their native range are more likely to establish than those that are transported to more distant locales and released. It has previously been shown that in New Zealand, at least, great circle distance is strongly correlated with the maximum size of propagules released (Cassey, 2001). As the distance between the recipient and donor regions is reduced, it is likely that the effort with which species can be transported and released is potentially much lower, and that their individual health increases. Over half of the land bird introductions to islands occurred before 1914 and the survival of propagules, transported by ship and in different stages of development, could be extremely poor with instances of complete mortality not uncommon (e.g. Thomson, 1922).

There is an urgent need to identify the variables associated with the success of introduced species (Vitousek *et al.*, 1997; McKinney and Lockwood, 1999; Kolar and Lodge, 2001). My analyses have revealed that, on average, the greater success of introduced land birds on islands is due to the fact that a large proportion of mainland introductions occurred between biogeographic regions. Notably, mainland introductions for a given family were more likely to succeed if they occurred within the same biogeographic region (e.g. the abiotic suitability hypothesis *sensu* Simberloff, 1989). The remaining variability in introduction success is probably due to differences that are characteristic of island and mainland environments, as well as differences in the efforts of the acclimatization societies themselves. I found that introduction success among islands is significantly associated with decreased island size, increased human population density, and decreased great circle distance between the donor and recipient regions. These results support regional analyses (e.g. Duncan *et al.*, 2001) and global analyses (e.g. Blackburn and Duncan, 2001a; Cassey, 2002a) that have shown that an understanding of introduction success is in fact possible.

ACKNOWLEDGEMENTS

I thank Rebecca Boulton, Marcel Cardillo, John Ewen, Rohan Clarke, Wade Hadwen, Robert King, Stuart Pimm, Carla Catterall and Stuart Bunn for their contributions to this research. Ian Owens, Julie Lockwood, Peter Bennett, Dave Forsyth, Salit Kark, Tim Blackburn, Michael Rosenzweig and an anonymous reviewer made comments that greatly improved the manuscript. This work was initially supported by Griffith University, GUPRS and ICTG scholarships while P.C. was visiting the Ornithology and Avian Conservation Laboratory, La Trobe University. For the completion of this work P.C. acknowledges assistance from the French Ministry of Education and Research, Action Concertee Incitative 'Jeunes Chercheurs 2000', awarded to the group 'Eco-Evolution Mathematique' and the French Ministry for Environment, Action Concertee Incitative 'Invasions Biologiques'.

REFERENCES

Andrew, P. 1998. *Nomina: Global Bird Dictionary* [relational taxonomies computer software]. Melbourne: CSIRO.

Blackburn, T.M. and Duncan, R.P. 2001a. Determinants of establishment success in introduced birds. *Nature*, **414**: 195–197.

Blackburn, T.M. and Duncan, R.P. 2001b. Establishment patterns of exotic birds are constrained by non-random patterns in introduction. *J. Biogeogr.*, **28**: 927–939.

Case, T.J. 1996. Global patterns in the establishment and distribution of exotic birds. *Biol. Conserv.*, **78**: 69–96.

Cassey, P. 2001. Determining variation in the success of New Zealand land birds. *Global Ecol. Biogeogr.*, **10**: 161–172.

Cassey, P. 2002a. Life history and ecology influences establishment success of introduced land birds. *Biol. J. Linn. Soc.*, **76**: 465–480.

Cassey, P. 2002b. Comparative analyses of successful establishment among introduced land birds. Doctoral dissertation, Griffith University, Australia.

Chown, S.L., Gremmen, N.J.M. and Gaston, K.J. 1998. Ecological biogeography of southern ocean islands: species–area relationships, human impacts, and conservation. *Am. Nat.*, **152**: 562–575.

Cox, C.B. and Moore, P.D. 2000. *Biogeography: An Ecological and Evolutionary Approach*. Oxford: Blackwell Scientific.

Darwin, C. 1845. *Journal of Researches into the Natural History and Geology of the Countries Visited During the Voyage of H.M.S. 'Beagle' Round the World, Under the Command of Capt. Fitz Roy, R.N.*, 2nd edn. London: John Murray.

Diamond, J.M. and Veitch, C.R. 1981. Extinctions and introductions in the New Zealand avifauna: cause and effect? *Science*, **211**: 499–501.

Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M. and Williamson, M., eds. 1989. *Biological Invasions: A Global Perspective*. Chichester: Wiley.

Duncan, R.P., Bomford, M., Forsyth, D.M. and Conibear, L. 2001. High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for climate. *J. Anim. Ecol.*, **70**: 621–632.

Ebenhard, T. 1988. Introduced birds and mammals and their ecological effects. *Swedish Wildlife Res. Viltrevy*, **13**: 1–107.

Elston, D.A. 1998. Estimation of denominator degrees of freedom of *F*-distributions for assessing Wald statistics for fixed-effect factors in unbalanced mixed models. *Biometrics*, **54**: 1085–1096.

Elton, C.S. 1958. *The Ecology of Invasions by Animals and Plants*. London: Methuen.

Kolar, C.S. and Lodge, D.M. 2001. Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.*, **16**: 199–204.

Lack, D. 1969. The numbers of bird species on islands. *Bird Study*, **16**: 193–209.

Levine, J.M. and D'Antonio, C.M. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, **87**: 15–26.

Littell, R.C., Milliken, G.A., Stroup, W.W. and Wolfinger, R.D. 1999. *SAS System for Mixed Models*. Cary, NC: SAS Institute.

Lockwood, J.L. 1999. Using taxonomy to predict success among introduced avifauna: relative importance of transport and establishment. *Conserv. Biol.*, **13**: 560–567.

Long, J.L. 1981. *Introduced Birds of the World*. London: David & Charles.

MacArthur, R.H. and Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

Maurer, B.A. 1999. *Untangling Ecological Complexity*. Chicago, IL: University of Chicago Press.

McCullagh, P. and Nelder, J.A. 1990. *Generalized Linear Models*. London: Chapman & Hall.

McKinney, M.L. and Lockwood, J.L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.*, **14**: 450–453.

Mooney, H.A. and Drake, J.A. 1989. Biological invasions: a SCOPE program overview. In *Biological Invasions: A Global Perspective* (J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson, eds), pp. 491–508. Chichester: Wiley.

Mueller-Dombois, D., Bridges, K.W. and Carson, H.L., eds. 1981. *Island Ecosystems: Biological Organization in Selected Hawaiian Communities*. US/IBP Synthesis Series #15. Stroudsburg, PA: Hutchinson-Ross.

Olden, J.D. and Jackson, D.A. 2000. Torturing data for the sake of generality: how valid are our regression models? *Ecoscience*, **7**: 501–510.

Pimm, S.L. 1991. *The Balance of Nature?* Chicago, IL: University of Chicago Press.

SAS Institute. 1993. *SAS/STAT Software: The GENMOD Procedure, Release 6.09*. Technical Report P–243. Cary, NC: SAS Institute Inc.

SAS Institute. 1996. *SAS Proprietary Software Release 6.12*. Cary, NC: SAS Institute Inc.

Sax, D.F. and Brown, J.H. 2000. The paradox of invasion. *Global Ecol. Biogeogr.* **9**: 363–371.

Sibley, C.G. and Monroe, B.L. 1990. *Distribution and Taxonomy of Birds of the World*. New Haven, CT: Yale University Press.

Sibley, C.G. and Monroe, B.L. 1993. *A Supplement to Distribution and Taxonomy of Birds of the World*. New Haven, CT: Yale University Press.

Simberloff, D. 1989. Which insect introductions succeed and which fail? In *Biological Invasions: A Global Perspective* (J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson, eds), pp. 61–75. Chichester: Wiley.

Simberloff, D. 1995. Why do introduced species appear to devastate islands more than mainland areas? *Pacific Sci.*, **49**: 87–97.

Sokal, R.R. and Rohlf, F.J. 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*. New York: W.H. Freeman.

Sol, D. 2000. Are islands more susceptible to be invaded than continents? Birds say no. *Ecography*, **23**: 687–692.

Thomson, G.M. 1922. *The Naturalisation of Animals and Plants in New Zealand*. Cambridge: Cambridge University Press.

Vitousek, P.M., D'Antonio, C.M., Loope, L.L. and Rejmanek, M. 1997. Introduced species: a significant component of human-caused global change. *NZ J. Ecol.*, **21**: 1–16.

Wallace, A.R. 1876. *The Geographical Distribution of Animals*. London: Macmillan.

Williamson, M. 1981. *Island Populations*. Oxford: Oxford University Press.

Williamson, M. 1996. *Biological Invasions*. London: Chapman & Hall.

Williamson, M. 1999. Invasions. *Ecography*, **22**: 5–12.

Zar, J.H. 1999. *Biostatistical Analysis*, 4th edn. Englewood Cliffs, NJ: Prentice-Hall.