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Establishment patterns of exotic birds are constrained by non-random patterns in introduction

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Abstract

Aim Species transported to and introduced into non-native environments, termed 'introductions', constitute a growing component of many regional floras and faunas, yet not all such species successfully establish. Investigations into why some introductions succeed while others fail are often based on analyses of the outcome of historical introductions. Such 'experiments in nature' have the drawback that the effects of interest may be confounded because they have not been randomized with respect to each other, and because the species and locations chosen for introduction may not be a random subset of the available species or locations. Our aim is to quantify this non-randomness using a global data set of bird introductions, and examine the factors associated with introduction probability in two subsets of these data, one taxonomic (order Anseriformes) and one geographical (British birds).

Location Global.

Methods Statistical analyses of the distributions among taxa and locations for 1378 introduction events for 426 bird species across the world, and statistical analyses of the characteristics of Anseriform and British bird species selected for introduction.

Results Global introductions of birds have been highly non-random with respect to taxon, location of origin, and location of introduction. Most introductions involve species in just five families (Phasianidae, Passeridae, Psittacidae, Anatidae and Columbidae), and most introductions have been to temperate and island locations. Within the taxonomic and geographical subsets, the species chosen for introduction tend to be abundant species that would have been relatively easy to obtain.

Main conclusions The characteristics of the species and locations chosen for introduction are not representative of species and locations in general, which limits our ability to draw general conclusions from historical records, and generates problems of confounding and non-independence in statistical analyses of introduction success. We suggest possible solutions for these problems.

Keywords
Anseriformes, birds, British birds, introductions, population size.

INTRODUCTION

Four steps can be identified in the process of the invasion of a region by an exotic species as a result of human activity (Williamson, 1996). First, the species must be transported from its native geographical range to the alien environment. Secondly, the species must be released (or escape) from captivity into that environment. Thirdly, the species must succeed in establishing following release. Finally, species that establish successfully may spread beyond the release point, the extent of which defines the geographical range size in the new environment. We term these stages as transport,

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introduction, establishment, and spread (see also Lockwood, 1999; Kolar & Lodge, 2001).

Humans have intentionally or accidentally introduced numerous species to locations at which they were previously absent, but only a proportion of these introductions have resulted in the establishment of new populations (Elton, 1958; Long, 1981; Drake *et al.*, 1989; Williamson, 1996). In many cases, species successfully established in new locations have caused huge environmental damage, and such species are one of the principal means by which biodiversity is presently being eroded (Elton, 1958; Williamson, 1996; Vitousek *et al.*, 1997; McKinney & Lockwood, 1999; Mack *et al.*, 2000). Increasingly, however, introductions are being used for conservation purposes (Griffith *et al.*, 1989), with the aim of re-establishing species in areas from which they have been extirpated. In both situations there is a strong incentive to understand what determines whether or not species will succeed in establishing following introduction, termed 'introduction success'. Despite this incentive, our understanding of the factors underlying variation in introduction success and our ability to predict successfully the outcome of any given introduction is poor (Drake *et al.*, 1989; Gilpin, 1990; Williamson, 1996, 1999; Williamson & Fitter, 1996; Smith *et al.*, 1999; but see Daehler & Carino, 2000; Duncan *et al.*, 2001).

For most taxa, manipulative experiments are impractical or unethical on the scales required to test hypotheses about the factors affecting introduction success. Consequently, the commonest way in which introduction success is investigated is through analysing the outcome of historical introductions, which constitutes a classic 'experiment in nature' (Diamond, 1986; Case, 1996): a change in a system brought about as the intentional or accidental product of human activities, which can be used to test a scientific hypothesis. For birds alone, Long (1981) documents 1378 instances of introduction, involving 426 species, providing abundant data with which to investigate the causes of introduction success (see, for example, Moulton & Pimm, 1983, 1986; Newsome & Noble, 1986; Simberloff, 1992; Brooke *et al.*, 1995; Veltman *et al.*, 1996; Duncan, 1997; Legendre *et al.*, 1999; Dean, 2000; Sol & Lefebvre, 2000; Duncan *et al.*, 2001).

As with all methodologies, experiments in nature have limitations (McArdle, 1996) and we can identify two major shortcomings. First, those species that get introduced into alien environments are unlikely to be a random subset of all species in the taxonomic group of interest (Crawley *et al.*, 1997; Daehler, 1998; Pysek, 1998; Lockwood, 1999; McKinney & Lockwood, 1999; Lockwood *et al.*, 2000) and introduction locations are unlikely to be a random subset of all available locations (e.g. data in Long, 1981; Case, 1996; Vitousek *et al.*, 1997; Mack *et al.*, 2000). As species can only establish if they have been introduced, this may limit our ability to draw general conclusions about the characteristics of species or locations associated with successful establishment. Secondly, species will have been introduced into differing numbers of locations, locations will differ in the number of introductions they have received, and the choice of which species to introduce into which locations will not have been made at random (see e.g. Long, 1981; Simberloff, 1989; Crawley *et al.*, 1997). This raises two problems for statistical analysis and inference: (1) individual observations (e.g. of introduction success or failure) may not constitute independent data points for statistical analysis and (2) because species have not been randomly assigned with respect to location, location-level and species-level effects may be confounded. For example, a species could have a high rate of introduction success because it was inherently a good invader or because it was consistently introduced to locations that were easy to invade. In addition, introduction protocols ('event-level' effects, including, for example, the number of individuals introduced) will vary from introduction event to introduction event, typically will be unknown for most events (Simberloff, 1989; Williamson, 1989, 1996; Lawton, 1990), and may be confounded with location- or species-level effects. Certain species, for example, may have been consistently introduced to locations in greater numbers than other species. These short-comings limit our ability to make strong inferences about the factors affecting introduction success from analyses of historical records.

Given these likely problems, a useful first step in an analysis of historical invasions is to quantify the patterns of non-randomness of introduction in the data. This would enable us to assess the likely significance of the above problems, and to devise strategies for the analysis and interpretation of the data that recognize and, ideally, account for these problems. While historical records of avian introductions provide one the richest sources of data for testing hypotheses about factors affecting introduction success (see above), there has been no systematic assessment of the degree to which non-randomness in the species or locations involved in introductions might affect the results of statistical analyses, or their interpretation. Here, we analyse a global data set of historical bird introductions to provide a wide-ranging assessment of the patterns of non-randomness in these events. We also present two case studies, using Anseriformes (wildfowl) and the British avifauna, in which we examine in more detail the characteristics of species associated with introduction to new locations.

METHODS

Of the four stages in the process of invasion via human agency, we are concerned here only with introductions of species to locations at which they were previously absent. Long (1981) provides a comprehensive summary of global bird introductions, recording 1454 separate introduction events (the introduction of a species to a particular location) for 427 different bird species. However, some of these events were natural colonizations, which we excluded from our analysis because these were not human-mediated introductions and because Long (1981) recorded only successful natural colonizations while many such colonization attempts must have failed and remain unrecorded. Excluding natural colonizations leaves 1378 introduction events for 426 species, although missing data for some events mean that sample sizes in some of our analyses are less than this maximum. The majority of events involve introductions of species to locations outside their native geographical range, but we also included introductions for conservation purposes, where the aim is to re-establish populations in areas of a species' native range from which it has been extirpated. Conservation-related introductions comprise of only a small percentage of the total number of events ($<5\%$).

We classified the locations to which species were introduced in three ways. First, locations were classified either as mainland, if they lay on one of the continental land masses (mainland North America, South America, Asia, Africa or Australia), or as island otherwise. Second, locations were assigned to one of the following biogeographical regions: Palaearctic (including Europe, North Africa, and temperate latitudes across Asia, and Japan), South-east Asia (including the Indian subcontinent and southern China), Afrotropics (Africa south of the Sahara), Arabia, Malagasy (Madagascar and nearby islands, including the Seychelles, Mascarenes, and Chagos), Australasia (including New Guinea, New Zealand, and islands in between), Antarctic (including sub-Antarctic islands, such as Kerguelen), Pacific (Melanesia, Micronesia, Polynesia), Nearctic (North America south to Mexico), Central/South America, Caribbean, and Atlantic (islands not closely associated with any land mass, e.g. St Helena). Thirdly, locations were classified into geopolitical units, following national boundaries wherever possible, but lumping or splitting units when this was sensible (e.g. we separate the Hawaiian Islands and Alaska from the USA).

The latitude of each introduction event was determined from the information in Long (1981) and The Concise Times Atlas of the World (Anonymous, 1997). Where the location of an introduction was given imprecisely (e.g. 'France', 'Australia'), the event was assigned the latitudinal mid-point of the region identified. This serves to cluster introductions somewhat with respect to latitude, but does not affect the general trends. Southern latitudes are arbitrarily designated to be negative.

The location from which introduced species were taken for introduction was also recorded for each event in two ways. First we determined the latitudinal mid-point of each species' natural geographical range from the range maps in Long (1981). Secondly, we identified the biogeographical region from which the species was derived, with widespread species, which occupy several regions, classified as either Holarctic, New World, or multi-regional. Some introductions were to the same biogeographical region in which the species naturally occurs. We term these 'intraregional' introductions, all other events were termed 'inter-regional' (Simberloff, 1989).

Species were classified following the taxonomy of Sibley & Monroe (1990, 1993). We used the simulation approach described in Lockwood *et al.* (2000) to test for differences between the observed and expected number of introduced species in each bird family. Each iteration of the simulation involved picking 426 species at random, and without replacement, from the total global avifauna (9702 species) and summing the number of these randomly chosen species in each family. A total of 50,000 iterations of the simulation procedure were run, and the observed number of introduced species in any given family was judged significantly greater than expected if at least S% of the randomly derived values for that family were less than the observed, where $S = (\beta/2) \times 100$. The β is calculated by applying a sequential Bonferroni correction to α, and $\alpha = 0.05$.

We examined in more detail the characteristics of introduced species in one taxonomic and one geographical subset of birds. The taxonomic subset was the order Anseriformes (wildfowl). Species in this order are classified into the families Anatidae (ducks, geese and swans, 148 species), Anhimidae (screamers, three species), Anseranatidae (magpie goose, one species), and Dendrocygnidae (whistling ducks, nine species) (Sibley & Monroe, 1990). Twenty-nine of these 161 species (18%) have been introduced at least once (Long, 1981). The geographical subset was British birds. A total of 214 bird species comprise the normal British breeding and wintering avifauna (see Gaston & Blackburn, 2000; Appendix III), of which 58 (27%) have been introduced at least once (Long, 1981).

For wildfowl, we tested if the species introduced at least once differ from those that have never been introduced in the following characteristics: global population size (number of individuals), breeding geographical range size [number of occupied squares on the WORLDMAP (Williams, 1992, 1993) grid], body mass (g), latitudinal mid-point of breeding geographical range (distance from the equator in degrees of latitude), and whether the species range is centred in the northern or southern hemisphere. Continuous variables were log-transformed for analysis, except for latitudinal range mid-point. Missing data mean that sample sizes for analyses are 154 species. Data sources and more detailed definitions of the variables are given in Gaston & Blackburn (1996).

For British birds, we compared the following characteristics: British population size (number of individuals), British geographical range size (number of occupied 10×10 km squares on the British National Grid), body mass (g), and whether the species was resident in Britain, principally a summer migrant (breeding in Britain but wintering elsewhere), or principally a winter migrant (wintering in Britain but breeding elsewhere). The British population size and geographical range size for a species was taken to be the higher of the values for the summer or winter population. Continuous variables were log-transformed for analysis. Only species native to Britain were included in the analyses. Data, sources and more detailed definitions of the variables are given in Appendix III of Gaston & Blackburn (2000).

Although we can identify species that have been introduced at least once and that are part of the British avifauna, Britain was almost certainly not the source of all individuals involved in the introductions. This should not substantially affect our conclusions, as other populations of these species will have similar body sizes and migratory strategies to those in Britain, while geographical range sizes and abundances tend to be positively correlated across regions (e.g. species widespread and abundant in Britain will also be widespread and abundant across Europe; Gaston, 1994; Gregory & Blackburn, 1998). Nevertheless, to address the problem that introductions of species in the British avifauna may not have derived from Britain, we also compared the characteristics of British species that have or have not been introduced to New Zealand. Britain was the source for most individuals of the 37 bird species introduced to New Zealand that are part of the British avifauna (Thomson, 1922).

We fit a generalized linear model (GLM) with a logit link function and binomial error distribution (using PROC GENMOD; SAS Institute, 1990) to identify which characteristics of wildfowl or British birds predicted whether or not species were introduced. The significance of predictor variables was assessed using the change in model deviance (distributed approximately χ^2). For British birds, we also identified which characteristics predict the total number of introduction events for each species (from data in Long, 1981) by fitting a GLM with a log link function and Poisson error distribution (appropriate for count data). Finally, for British birds introduced to New Zealand, we tested which species characteristics could predict the total number of introduction events and the total number of individuals introduced to New Zealand, in each case fitting a GLM with an identity link and normal error distribution. The data on number of introduction events and the total number of individuals introduced to New Zealand were taken from Veltman *et al.* (1996), and were log-transformed for analysis.

Characteristics of the wildfowl and British bird species included in the analyses are not independent. Population size and geographical range size, for example, are strongly correlated in both groups (Gaston & Blackburn, 1996; Blackburn *et al.*, 1997). Such correlations can make it difficult to determine which of a set of predictor variables has the strongest influence on a response variable. We, therefore, used hierarchical partitioning (Chevan & Sutherland, 1991) to identify the extent to which each predictor variable was independently related to a response variable. Hierarchical partitioning involves calculating the independent contribution of a variable to the fit of a model for all of the models containing all possible combinations of predictor variables that include the variable of interest. The average of these 'independent contributions' provides a measure of the independent effect of that variable on the response, relative to the effects of other variables analysed. This approach overcomes a limitation of standard multiple regression in which a single 'best fit' model is obtained and where the independent contribution of each predictor variable depends on which other predictor variables happen to be included in that model (Chevan & Sutherland, 1991; Mac Nally, 1996, 2000). Hierarchical partitioning was implemented using a purpose-written macro in SAS (SAS Institute, 1990).

RESULTS

Global patterns of bird introductions

Bird introductions have occurred to most latitudes with ice-free land (Fig. 1). Mean introduction latitude is 4°N, but relatively few introductions actually occur close to the equator. Instead, the pattern of variation is bimodal, with peaks between latitudes 10° and 40° on both sides of the equator. This pattern contrasts with the distribution of ice-free land, which has its greatest extent in the tropics (Rosenzweig, 1992).

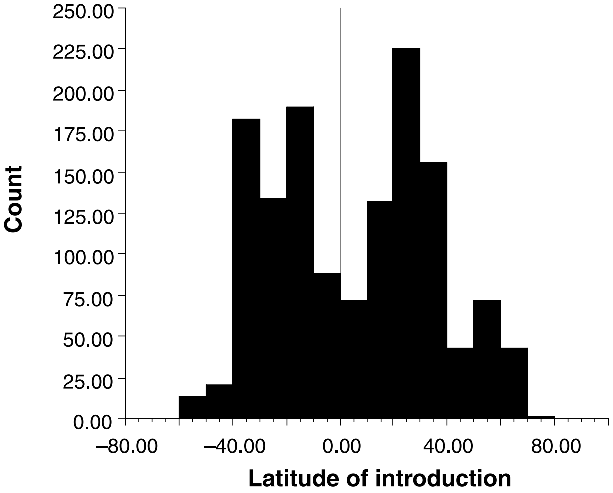

Figure 1 The frequency distribution of latitude of introduction for all 1378 avian introduction events.

The geopolitical units with the most introduction events are the Hawaiian Islands (163), New Zealand (146), the USA (excluding Alaska and the Hawaiian Islands) (125), Australia (113), the Mascarenes (65) and the Society Islands, including Tahiti (56). This pattern results in a predominance of introductions to the Pacific and Australasian biogeographical regions (Table 1). Nevertheless, except for the Antarctic region, all biogeographical regions have had at least 40 introduction events.

By far the majority of introductions have been to islands (953 events) compared with mainland locations (425 events), despite the fact that islands comprise of only about 3% of ice-free land area (Mielke, 1989). Slightly over half of all introductions to islands occurred in the Pacific (271) and Australasian regions (216), followed by the Malagasy (125) and Caribbean (97). The greatest number of mainland introductions were in the Nearctic (154) followed by the Palaearctic (83) and Australasia (70).

The overall bimodal pattern of introduction events by latitude (Fig. 1) actually results from a series of distinct introduction peaks at different latitudes for island and mainland introductions (Fig. 2). For islands, the peak north of the equator results primarily from introductions to the Hawaiian Islands and the Caribbean, while the two peaks south of the equator result from introductions to the Society Islands (especially Tahiti) and islands in the Malagasy region (especially the Mascarenes and Seychelles), and introductions to New Zealand and islands around Australia. The two mainland peaks result primarily from introductions to the Nearctic and to Australia. There have been few introductions

Table 1 Region of introduction × region of origin for the 1378 introduction events. The numbers in parentheses by region of origin are used to reference region of introduction. For clarity, intraregional introduction events are in bold

	Region of introduction											
Region of origin	1	2	3	4	5	6	8	10	12	13	14	Total
Afrotropics (1)	**20**	0	22	17	15	1	24	7	33	13	0	152
Antarctica (2)	0	**0**	0	0	0	0	0	0	0	1	0	1
Atlantic (3)	0	0	**1**	0	0	0	0	0	0	0	0	1
Australasia (4)	1	0	0	**103**	1	1	1	4	44	6	9	170
Caribbean (5)	0	0	0	0	**8**	0	0	0	1	0	0	9
Central/S. America (6)	1	1	0	1	35	**14**	0	22	32	6	0	112
Holarctic (7)	0	2	0	5	0	1	0	4	3	13	0	28
Malagasy (8)	2	0	1	0	0	0	**32**	0	0	0	0	35
Multi-regional (9)	13	2	6	26	5	10	26	14	26	22	15	165
Nearctic (10)	2	0	1	17	17	5	0	**48**	30	16	0	136
New World (11)	0	0	0	0	6	1	0	3	2	0	0	12
Pacific (12)	0	0	0	0	0	0	0	0	**16**	0	0	16
Palaearctic (13)	8	0	3	70	3	6	4	49	23	**57**	3	226
South-east Asia (14)	10	0	7	47	7	9	38	29	61	27	**80**	315
Total	57	5	41	286	97	48	125	180	271	161	107	

to tropical mainland regions, particularly south of the equator. Tropical islands have received more introductions, although the number of events within 10° of the equator is still relatively low.

The frequency distribution of the latitude of origin of species for all introduction events is shown in Fig. 3(a). This distribution is significantly left-skewed (skewness = –0.196, $t = -2.97$, d.f. $= \infty$, $P < 0.05$; significance test as described by Sokal & Rohlf (1995) and the mean latitude of origin is 13.6°N, significantly greater than zero ($t = 18.9$, d.f. = 1375, $P < 0.0001$). Thus, most introduction events involve species that have their latitudinal mid-point in the northern hemisphere, with two peaks at 10–20°N and 30–40°N. However, many species were introduced more than once (see below). If latitude of origin is compared across species, with each species included only once, the mean value shifts towards the equator, although it still lies in the northern hemisphere (8.95°N), and is significantly greater than zero ($t = 6.6$, d.f. = 423, $P < 0.0001$). The frequency distribution is now no longer significantly skewed (Fig. 3(b); skewness = 0.101, $t = 0.85$, d.f. $= \infty$, $P > 0.05$).

Considering all introduction events, the species involved originated primarily in south-east Asia followed by the Palaearctic (Table 1). Very few events involved species originating from the Pacific, Caribbean or Malagasy regions, in contrast to the number of introduction events to these regions. When region of origin is examined by species rather than by event, five regions stand out as being the source for the majority of introduced species: the Palaearctic, South-east Asia, Central/South America, Australasia and the Afrotropics. Slightly over one quarter (379) of introduction events were intraregional (Table 1), including 53 of the 56 events listed as conservation introductions in Long (1981).

The species chosen for introduction are not a random sample of birds with regard to family membership. Instead, species in the families Phasianidae, Passeridae, Psittacidae, Anatidae and Columbidae are significantly over-represented after applying Bonferroni correction for multiple statistical tests (Table 2). A further seven families have more species introduced than expected at the $\alpha = 0.05$ level, but do not exceed expectation once the Bonferroni correction is applied. A total of 829 of the 1378 introduction events (60%) involve species from the five families that are significantly over-represented in the data (Table 3), despite these families containing only 14% of the world's bird species (following Sibley & Monroe, 1990).

Case study I. Wildfowl

The order Anseriformes (wildfowl) includes the family Anatidae, which contains significantly more introduced species than expected given the total number of species in the family (Table 2, see also Lockwood, 1999). When considered individually, four variables significantly predict whether or not a wildfowl species has been introduced. Introduced species tend to have larger population sizes, larger geographical range sizes, larger body mass, and to have their ranges centred in the northern hemisphere, compared with non-introduced species (Table 4). Several of these predictor variables are correlated, however, and hierarchical partitioning identifies only large population size and large body mass as having a strong independent association with introduction probability.

In addition, the squared term for population size is a significant predictor of wildfowl introduction when added to a model that already includes population size and body mass (change in deviance = 4.3, $P = 0.04$). Hierarchical partitioning further indicates that this term has an independent influence on introduction probability (mean change in deviance = 9.0). Hence, wildfowl with both large and small population sizes have a higher probability of introduction. The effect at small population size is weaker and arises because four rare wildfowl species have been introduced for conservation purposes. When conservation introductions are

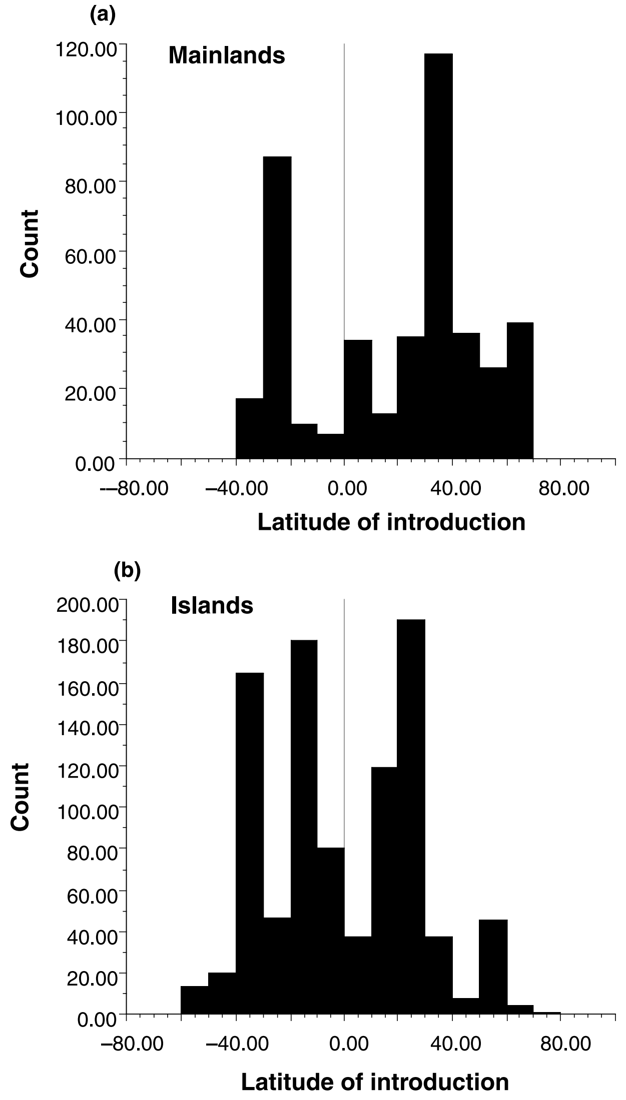

Figure 2 The frequency distribution of latitude of introduction for (a) all introduction events to mainland locations ($n = 425$), and (b) all introduction events to islands ($n = 953$).

excluded, the squared term for population size is no longer a significant predictor when added to the model after population size and body mass (change in deviance = 0.7, $P = 0.39$).

Case study II. British birds

A high proportion of birds in the normal breeding and wintering avifauna of Britain have been introduced elsewhere – 27% compared with just 4.4% of all bird species. When considered individually, population size and geographical range size were significantly positively associated with introduction probability, and resident species were more likely to be introduced than either summer or winter migrants (Table 5). Hierarchical partitioning supports this, showing that all three variables are independently associated with introduction probability but that population size has by far the strongest influence.

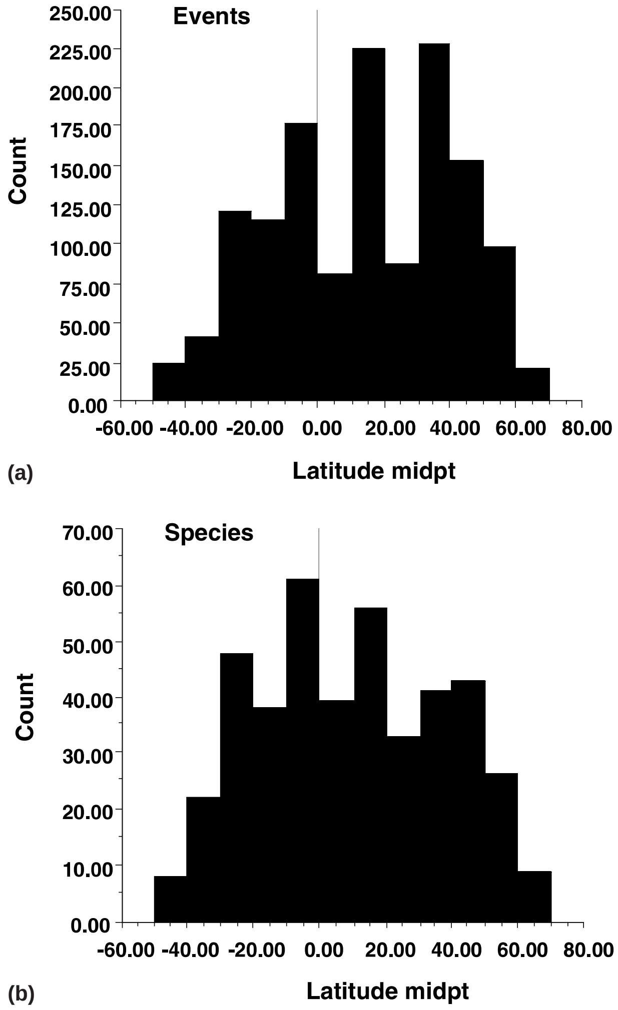

Figure 3 The frequency distribution of latitudinal mid-point of range of species involved in introduction events (a) by event (each introduction constitutes a single data point for this histogram ($n = 1378$), so some species are included more than once), and (b) by species [each species constitutes a single data point for this histogram ($n = 426$)].

We obtain similar results if we restrict our analysis to those 37 species introduced from Britain to New Zealand (Table 6). In this case, body mass is also a significant predictor in univariate analysis but has little influence in the hierarchical partitioning, suggesting that the significant effect of body mass derives indirectly from correlations with other variables. British population size is again the strongest independent predictor in the hierarchical partitioning.

All four variables (British population size, geographical range size, migratory category and body mass) also predict the total number of introduction events worldwide for the 58 British species introduced at least once, when each variable is considered alone (Table 7). However, hierarchical

Table 2 The number of species introduced from a family (from Long, 1981), the total number of species in the family (following Sibley & Monroe, 1990, 1993), and the probability (P_{sim}, calculated using random simulation) of observing as many or more introductions from that family given the number of species in the family and the proportion of the world's bird species that have been introduced. Bold type indicates probabilities that are significantly lower than expected ($\alpha = 0.05$), once a sequential Bonferroni correction for multiple statistical tests (Rice, 1989) has been applied. Only families for which $P_{\mathrm{sim}} < 0.05$ are shown

Family	No. spp. introduced	No. spp. in family	P_{sim}
Phasianidae	56	176	**< 0.0001**
Passeridae	56	388	**< 0.0001**
Psittacidae	51	360	**< 0.0001**
Anatidae	27	148	**< 0.0001**
Columbidae	31	313	**< 0.0001**
Odontophoridae	7	31	0.0008
Fringillidae	63	995	0.004
Rheidae	2	2	0.005
Pteroclidae	4	16	0.009
Apterygidae	2	3	0.011
Casuariidae	2	4	0.023
Cracidae	6	50	0.045

Table 3 Number of avian introduction events by family and region of origin. Anat = Anatidae, Col = Columbidae, Pass = Passeridae, Phas = Phasianidae, Psitt = Psittacidae

	Family					
Region of origin	Anat	Col	Pass	Phas	Psitt	Other
Afrotropics	6	3	69	7	10	57
Antarctica	0	0	0	0	0	1
Atlantic	0	0	0	0	0	1
Australasia	9	22	25	5	40	69
Caribbean	0	3	0	0	1	5
Central/South America	3	1	0	0	29	79
Holarctic	13	0	0	14	0	1
Malagasy	2	6	12	2	8	5
Multi-regional	0	56	48	7	18	36
Nearctic	21	1	0	39	0	75
New World	0	6	0	0	0	6
Pacific	1	0	1	0	8	6
Palaearctic	19	4	2	93	0	108
South-east Asia	0	21	69	118	7	100
Total	74	123	226	285	121	549

partitioning identifies only population size, geographical range size and migratory status as important independent predictors of the number of introduction events. British species with a larger population size, a larger geographical range size, and resident in Britain were introduced more often.

For the 37 species introduced from Britain to New Zealand, the number of introduction events and number of individuals introduced are both predicted by British population size, geographical range size and migratory category (Table 8). Resident species with a larger population and geographical range size in Britain were introduced to New Zealand more often and in greater numbers. Hierarchical partitioning identifies only British population size and migratory category as strong independent predictors of both the number of individuals and the number of introduction events in New Zealand.

DISCUSSION

Introduction patterns

The locations at which attempts have been made to introduce birds are not evenly distributed across the globe. Instead, introductions tend to be concentrated in relatively few, predominantly temperate and island, locations, although nowhere has escaped introductions entirely. In large part (but not entirely: Table 1) this non-randomness reflects the pattern of settlement by Europeans (Long, 1981; di Castri, 1989; Crosby, 1993; Mack *et al*., 2000), and especially the British, during the 18–20th centuries, who were responsible for many if not most of the introductions. The three regions which have had the greatest number of introductions (in order: Australasia, Pacific and Nearctic) are regions where settlement in this period was dominated by European colonists. This is even more apparent when we consider that 547 introduction events (40%) were to just four geopolitical areas: Hawaii, New Zealand, USA and Australia, the last three of which were British colonies. Not surprisingly, therefore, the large majority of birds that originated in the Palaearctic and that were introduced outside that region, were introduced to the Australasian, Pacific and Nearctic regions (Table 1).

These apart, most other introductions tended to involve species that originated in the same or a nearby region. Hence, excluding species with widespread origins, introductions to the Atlantic region were dominated by species originating in the Afrotropics, introductions to the Caribbean region were dominated by species originating in Central/South America and introductions to the Malagasy region were dominated by species originating in the Malagasy, South-east Asia and the Afrotropics (Table 1). This pattern suggests that many historical bird introductions were opportunistic: people tended to introduce birds that were accessible near the location of introduction, rather than having a pre-determined set of birds that they desired for introduction.

While they may have been somewhat opportunistic, people nevertheless preferentially selected certain types of birds for introduction. The over-representation of species in certain families undoubtedly reflects the introduction of birds in new locations primarily for hunting (especially Phasianidae and Anatidae) or aesthetic purposes (especially Psittacidae and Passeridae; albeit many introductions of species in this latter group were probably accidental) (Long, 1981; Lever, 1987; Lockwood, 1999; Lockwood *et al*., 2000).

Despite the regional patterns, latitudes between 30°S and 50°N have contributed about evenly to the list of introduced

Table 4 Relationships between the probability that a wildfowl species has been introduced somewhere in the world (binomial variable, introduced or not) and the variables in the first column. Univariate results are from logistic regression (PROC GLM in SAS, with logit link function and binomial error distribution). Hierarchical partitioning results show the effect of adding each variable to all possible models with the other variables (see Methods for more details)

	Univariate		Hierarchical partitioning
Variable	Parameter estimate	Change in deviance	Mean change in deviance
Log population size	0.733	13.7***	13.0
Log geographical range size	1.190	6.9**	3.9
Log body mass	1.627	7.2**	12.3
Latitudinal range mid-point	0.001	0.0	4.5
Hemisphere			
Southern	−0.754	3.2*	2.4
Northern	0		

$n = 154$;*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 5 Relationships between the probability that a British bird species has been introduced somewhere in the world (binomial variable, introduced or not) and the variables in the first column. Univariate results are from logistic regression (PROC GLM in SAS, with logit link function and binomial error distribution). Hierarchical partitioning results show the effect of adding each variable to all possible models with the other variables (see Methods for more details)

	Univariate		Hierarchical partitioning
Variable	Parameter estimate	Change in deviance	Mean change in deviance
Log population size	0.613	27.3***	18.3
Log geographical range size	1.141	16.8***	7.6
Log body mass	−0.065	0.1	0.5
Migration			
Resident	1.203	14.4***	8.7
Summer	−0.049		
Winter	0		

$n = 214$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 6 Relationships between the probability that a British bird species has been introduced to New Zealand (binomial variable, introduced or not) and the variables in the first column. Univariate results are from logistic regression (PROC GLM in SAS, with logit link function and binomial error distribution). Hierarchical partitioning results show the effect of adding each variable to all possible models with the other variables (see Methods for more details)

	Univariate		Hierarchical partitioning
Variable	Parameter estimate	Change in deviance	Mean change in deviance
Log population size	1.032	39.8***	26.8
Log geographical range size	1.859	21.5***	10.1
Log body mass	−0.478	3.8*	2.2
Migration			
Resident	0.795	10.6**	6.5
Summer	−0.740		
Winter	0		

$n = 214$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

bird species, with a modal peak at low southern latitudes. This pattern does not mirror the general latitudinal trend in bird species richness, which exhibits a much more marked peak at low latitudes (e.g. Dobzhansky, 1950; MacArthur & Wilson, 1967; Cook, 1969; Tramer, 1974; Haffer, 1988; Blackburn & Gaston, 1996; Gaston & Blackburn, 2000). It appears that introduced species are not a random sample from the world's avifauna with regard to the latitudinal mid-points of their native ranges: temperate species are over-represented. For northern temperate species, this over-representation is especially marked when individual introduction events are considered (Fig. 3(a)). Both patterns reflect the importance of the Palaearctic as a source for avian introductions (Table 1).

While the broad pattern of introduction appears to reflect the patterns of European settlement, the proximity of species to introduction locations and the desirability of species in certain families, people nevertheless made decisions (consciously or unconsciously) about which species in a particular family or from a certain geographical region should be introduced. Given that wildfowl were introduced for hunting purposes, which species of wildfowl were chosen? Given that British settlers introduced birds to their new colonies, which species did they

Table 7 Relationships between the total number of introduction events associated with those British bird species that have been introduced somewhere in the world and the variables in the first column. Univariate results are from logistic regression (PROC GLM in SAS, with log link function and Poisson error distribution). Hierarchical partitioning results show the effect of adding each variable to all possible models with the other variables (see Methods for more details)

	Univariate		Hierarchical partitioning
Variable	Parameter estimate	Change in deviance	Mean change in deviance
Log population size	0.345	34.7***	16.7
Log geographical range size	0.921	30.5***	13.0
Log body mass	−0.219	5.2*	1.8
Migration			
Resident	1.137	21.5***	12.4
Summer	0.575		
Winter	0		

$n = 58$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Table 8 Relationships between the total number of introductions and the total number of individuals introduced and the variables in the first column for those British bird species that have been introduced from Britain to New Zealand. Univariate results are from logistic regression (PROC GLM in SAS, with identity link function and normal error distribution). Hierarchical partitioning results show the effect of adding each variable to all possible models with the other variables (see Methods for more details)

	Univariate		Hierarchical partitioning
Variable	Parameter estimate	Change in deviance	Mean change in deviance
Number of introductions			
Log population size	0.248	16.2***	11.1
Log geographical range size	0.450	8.8**	4.3
Log body mass	−0.054	0.3	0.4
Migration			
Resident	0.238	10.5**	8.1
Summer	−0.409		
Winter	0		
Number of individuals			
Log population size	0.453	11.9***	7.1
Log geographical range size	0.832	6.7**	3.0
Log body mass	−0.194	0.8	1.0
Migration			
Resident	0.601	11.5**	9.5
Summer	−0.770		
Winter	0		

$n = 37$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

introduce? Our results show that people tended to introduce the species most readily available to them (with the exception of introductions for conservation purposes which involve rare species).

For British birds, the species with the highest probability of introduction were species available all year round (residents) with both a large population size and large geographical range size (see also Moulton & Pimm, 1986; Crawley, 1987; Ehrlich, 1989; Hanski & Cambefort, 1991; Williamson, 1996; Wonham *et al*., 2000), all factors that increase the ‘availability’ of birds for capture and transport to new locations. The total number of introduction events to which each introduced species was subject was likewise predicted by these same availability factors. Furthermore, for birds introduced to New Zealand from Britain, two of these availability factors, population size and resident status, also predict the number of individuals introduced and the number of introduction events in New Zealand. All of these outcomes point to the same scenario. While certain types of birds (such as wildfowl or gamebirds) were preferentially chosen for introduction, the species introduced were nevertheless those that were the most readily available and easily obtained. Because they were easily obtained, such species were also introduced to a greater number of locations and were introduced in greater numbers to any one location. This last outcome is important because introduction effort (measured as the total number of individuals introduced or the number of introduction events) is a strong predictor of avian introduction success at locations where these data are available (Newsome & Noble, 1986; Ehrlich, 1989; Griffith *et al*., 1989; Veltman *et al*., 1996; Williamson, 1996; Duncan, 1997; Green, 1997; Duncan *et al*., 2001). Consequently, abundant, widespread species will tend to be introduced to more locations and to have greater introduction success as a result of greater introduction effort brought about by their ready availability for capture, transport and introduction (Duncan, 1997; Duncan *et al.* 2001).

There is anecdotal evidence to support the idea that the birds captured for introduction were often those that were the most easily obtained for capture. Introductions to New Zealand, for example, often comprised birds that 'captains [of ships] could obtain easily and cheaply in Great Britain' (McDowall, 1994), while opposition from English farmers and the Small Birds Protection Act of 1872 made all but the most common birds difficult to obtain (Ashby, 1987). All of these findings highlight again the rather opportunistic nature of bird introductions. People tended to introduce birds that they could obtain readily in source locations, which were frequently located close to the point of introduction (Table 1).

The same result holds for wildfowl; the probability of introduction is most strongly predicted by population size, which again most likely reflects availability. Interpretation of this result is complicated, however, by the fact that the global population size estimates for wildfowl include individuals in populations established following introduction. Hence, there is a risk of circularity: introduced species may have larger population sizes because their populations have expanded following introduction to new areas. We think this effect is unlikely to be important for two reasons. First, introduced populations often make up only a small proportion of the total population size (e.g. ruddy ducks in Britain vs. the New World). Secondly, the same problem applies to geographical range size, yet this is not a strong predictor of introduction probability in wildfowl, suggesting that the population size effect is more than simply an artefact. Body mass is also a strong predictor of introduction probability in wildfowl. Wildfowl were introduced primarily for hunting and ornamental purposes (Long, 1981), and in both cases larger-bodied species are likely to have been favoured.

Implications for the analysis and interpretation of introduction success

The global data set of bird introductions is a valuable resource for studying the factors underlying introduction success and failure. However, the value of this resource may be compromised by two features associated with the non-random nature of introductions (see Introduction). Our results allow us to assess the likely importance of these features.

First, the characteristics of the species and locations chosen for introduction are not representative of species and locations in general, which limits our ability to draw general conclusions. In the first instance, this non-representativeness may bias our perception of the factors affecting introduction success. For example, it is often hypothesized that islands are easier to invade than mainlands because lower species richness on islands means that invaders will face reduced competition (Elton, 1958; Moulton & Pimm, 1983; Simberloff, 1986, 1989; Lever, 1987; Brown, 1989; Pimm, 1989). Consistent with this hypothesis is the disproportionately large number of invasive species found on islands. Our results show that this outcome could simply reflect the disproportionate number of introductions to Islands vs. mainlands, rather than any intrinsic differences in invasibility (see also Duncan & Young, 1999; Lockwood, 1999; Lonsdale, 1999; Sol, 2000). The solution to this problem is to consider the rate of introduction success, but the original limitation still holds: because most historical bird introductions involve common, widespread species introduced to relatively few locations, conclusions about the factors affecting introduction success based on these historical records may not apply to species and locations in general. This is an inherent limitation of the data. It is also one that is likely to apply to introductions of species in other less conspicuous and less well-documented taxa.

Secondly, the spatial and taxonomic clumping of introductions generate problems of confounding and non-independence in statistical analyses of introduction success. In the first case, location-, species- and event-level effects may be confounded because these effects have not been assigned at random with respect to each other. For example, species that are more common in Britain were introduced in greater numbers to New Zealand (Tables 7 & 8). Species that are common in Britain also possess certain life history traits that distinguish them from less common species (smaller body mass, for example: Nee *et al.*, 1991; Gregory & Blackburn, 1995; Blackburn *et al.*, 1996). Hence, for introductions of British birds to New Zealand, and most likely for introductions elsewhere, species-level (life history traits) and event-level (introduction effort) effects will be confounded. Identifying the independent contribution of effects at each level requires that we gather the appropriate data and then use appropriate analytical techniques, such as partial correlation, multiple regression or hierarchical partitioning, to separate out these effects on introduction success (McArdle, 1996).

In the second case, introductions to the same, or even nearby, locations do not represent independent data points, and introductions of the same species to different locations do not represent independent data points, for statistical analysis. This is an example of pseudoreplication (Hurlbert, 1984; McArdle, 1996): outcomes at one level of replication (individual introduction events) are correlated because they are clustered into higher level units (species or locations in this case). An analysis that ignores this clustering would be inappropriate because the errors associated with events in the same cluster would most likely be correlated, thereby violating an assumption of most statistical analyses (that the errors are independent). However, introduction events can be validly analysed as independent observations if this non-independence can be explicitly incorporated into the model. There are now several approaches available to do this that will also handle data requiring various distributional assumptions, including Generalized Linear Mixed Models (Goldstein, 1995) and Generalized Estimating Equations (Waclawiw & Liang, 1993). Because individual introduction events are invariably clustered into higher level units (e.g. Tables 1 & 2) these, or similar, approaches should be standard in any analysis of introduction outcomes at this level. We are currently applying such an approach to investigate causes of success for global bird introductions.

Overlaying these issues is one key point: species cannot succeed in establishing in an alien environment if they do not arrive there. Hence, while there may be intrinsic differences in the ability of species to invade new locations and differences in the inherent invasibility of locations, an over-riding factor determining the number of introduced species found at a location is likely to be 'introduction pressure' – the number of species introduced at that location (Case, 1996; Williamson, 1996; Lockwood, 1999; Lonsdale, 1999). Because introduction pressure varies markedly between locations for birds (Table 1; Figs 1 & 2), and most likely for other taxa, so too will the numbers of successfully introduced species found at those locations.

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