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Global patterns of introduction effort and establishment success in birds

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Theory suggests that introduction effort (propagule size or number) should be a key determinant of establishment success for exotic species. Unfortunately, however, propagule pressure is not recorded for most introductions. Studies must therefore either use proxies whose efficacy must be largely assumed, or ignore effort altogether. The results of such studies will be flawed if effort is not distributed at random with respect to other characteristics that are predicted to influence success. We use global data for more than 600 introduction events for birds to show that introduction effort is both the strongest correlate of introduction success, and correlated with a large number of variables previously thought to influence success. Apart from effort, only habitat generalism relates to establishment success in birds.

Keywords: birds; exotic species; introduction effort; propagule pressure

1. INTRODUCTION

Non-indigenous species are a major and growing component of human-induced environmental change, making understanding the causes of their successful establishment an important goal for ecology, environmental management and conservation biology (Elton 1958; Williamson 1996; Vitousek *et al.* 1997). A wide range of characteristics has been hypothesized to determine establishment success, including attributes of the exotic species (e.g. life-history traits), the location of introduction (e.g. climate, species richness), and the specific introduction event (e.g. date). Tests primarily using data from historical introductions have shown many of these characteristics to be correlated with success. However, in many cases, the amount of explained variation in success is low and studies frequently find contradictory results, sometimes even when they consider the same exotic assemblage (reviewed in Williamson 1996; Kolar & Lodge 2001; Duncan *et al.* 2003).

One factor that theory suggests should be a particularly important determinant of success is introduction effort (or propagule pressure) (Newsome & Noble 1986; Williamson 1996, 1999; Duncan *et al.* 2003). Introduction effort may be distributed idiosyncratically with respect to species and location, making the influence of other factors hard to determine. Alternatively, introductions of some species or to some locations may benefit from greater effort, causing species- or location-level effects to be confounded with effort (Duncan *et al.* 2003). Unfortunately, introduction effort is unknown for the vast majority of historical introductions. Most studies must therefore use proxies for effort (e.g. geographical range size) whose efficacy usually must be assumed (Blackburn & Duncan 2001), or ignore effort altogether. Either way, the results of such studies will be flawed if propagule pressure is not distributed at random with respect to traits found to predict success, or across recipient regions that hold different numbers of exotic invaders (Levine 2000; Wonham *et al.* 2000; Duncan & Blackburn 2002).

Here, we report an analysis of historical introduction success that includes direct measures of propagule pressure for a major animal group (birds) at the global scale. We use these data to assess the geographical and taxonomic distribution of introduction effort, to test whether effort is random with respect to species or location. We then test the ability of effort to explain establishment success, and the extent to which traits previously found to predict success may be confounded with effort.

2. METHODS

We define an introduction event as the release of individuals into a region to which their species is not native. Data on historical human-mediated avian introductions (excluding those for the purpose of conservation) are available for 1920 introduction events for 416 species (Cassey 2002*a*). We define a location as an island or a governmental state within a continental mainland to which individuals of a non-native species were introduced. Multiple releases of non-native individuals to the same island or state are counted as one introduction to that location. We collated data on propagule size or propagule number from the primary literature for as many of these events as possible. Propagule size is the total number of individuals released at each location, whereas propagule number is the number of separate releases. Both quantities are given as minimum estimates. We scored an 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). Introduction locations were clustered for analysis into the regions listed in table 1.

For each introduced species, seven variables that have been hypothesized to influence introduction success were recorded: body mass (grams; log transformed), native geographical range (range maps digitized and standardized for differences in map projections; log transformed), annual fecundity (the product of modal clutch size and average number of broods; log transformed), dietary generalism (number of seven major food types included in the diet of a species), habitat generalism (number of seven major habitat types included in a species range), sexual dichromatism (dichromatic if there are any differences between sexes in their colour and/or pattern of ornamentation) and migratory tendency (0, sedentary; 1, nomadic and/or local movements; 2, partial migrant; 3, migrant).

For each introduction event, five variables that have been hypothesized to influence introduction success were also recorded: whether the introduction was to a mainland or island location, latitude of introduction, the (log-transformed) difference between the latitudinal mid-point of the native range of the species and the latitude of

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Table 1. Estimates and their associated significance tests for log propagule size versus introduction success by the individual regions and taxonomic families.
(n, number of introduction events for regions, and number of species introduced (number of introduction events) for families. ${}^{*}p < 0.05$, ${}^{**}p < 0.01$, ${}^{***}p < 0.001$.)

	n	success	estimate	s.e.	χ^2	estimate	s.e.	χ^2
effort versus success by region						controlling for family		
New Zealand	133	0.35	1.73	0.31	30.35^{***}	2.64	0.42	39.07^{***}
Australia	81	0.33	1.18	0.37	10.07^{**}	0.79	0.42	3.85^{*}
Canada	25	0.32	3.45	1.43	5.81^{*}	4.48	1.56	8.22^{**}
USA	205	0.29	0.34	0.15	5.27^{*}	0.57	0.21	7.56^{**}
Hawaii	88	0.56	0.55	0.33	2.81	1.57	0.68	5.27^{*}
Oriental	9	0.67	4.42	3.09	2.05	—	—	—
Oceania	26	0.65	1.26	1.05	1.45	1.26	1.09	1.33
Africa	13	0.38	0.75	0.71	1.1	3.23	4.93	0.43
South America	6	0.67	1.76	2.41	0.53	—	—	—
West Indies	8	0.38	0.43	0.91	0.23	0.47	4.37	0.01
Europe	22	0.50	–0.22	0.47	0.22	–0.67	2.48	0.07
British Isles	18	0.22	0.28	0.75	0.14	—	—	—
St Helena	9	0.00	all introductions failed			—	—	—
effort versus success by family						controlling for region		
Phasianidae	37 (264)	0.30	0.51	0.12	15.73^{***}	0.74	0.16	22.38^{***}
Passeridae	18 (47)	0.51	2.33	0.72	10.43^{**}	2.74	0.75	13.45^{***}
Fringillidae	21 (57)	0.35	1.29	0.49	8.47^{**}	1.76	0.51	12.01^{**}
Anatidae	19 (42)	0.43	1.3	0.53	7.7^{**}	1.2	0.5	4.71^{*}
Sturnidae	5 (20)	0.70	2.1	1.07	5.34^{*}	3.63	1.12	5.69^{*}
Psittacidae	16 (21)	0.52	2.01	1.13	4.47^{*}	2.16	1.17	3.4
Muscicapidae	6 (27)	0.30	0.99	0.65	2.54	3.16	1.07	8.77^{**}
Sylviidae	6 (7)	0.29	2.27	1.9	2.02	—	—	—
Columbidae	13 (28)	0.39	1.34	1.08	1.69	2.04	1.61	1.61
Corvidae	8 (17)	0.59	0.58	0.74	0.63	0.53	0.78	0.47

introduction ('latitudinal difference') calculated without reference to hemisphere (i.e. an introduction from 50° N to 40° S has a latitudinal difference of 10°), and whether the introduction was intra-regional (introduction site and native range in the same biogeographic region) or inter-regional (in different biogeographic regions).

Non-randomness in the distribution of propagule size was assessed using contingency tests to compare the frequency of success between regions and families from the entire dataset of globally introduced birds, and from the reduced dataset that includes only events with data on propagule size. The distribution of variation in introduction effort among taxonomic levels was calculated using nested ANOVA. Interspecific relationships between propagule size and other continuous variables were modelled using Proc Genmod in SAS (SAS Institute, Inc. 1993). To account for clustering as a result of taxonomy and region, we used the Glimmix macro in SAS to fit generalized linear mixed models (GLMMs). GLMMs provide a framework for analysing data in which observations are likely to be correlated owing to clustering and cannot therefore be treated as statistically independent units. We modelled the likely non-independence of introductions of the same taxa by assuming a common positive correlation between introduction outcomes involving the same taxa (species, genera, families and orders), but a zero correlation between introduction outcomes involving different taxa (a variance components model). Clustering of introduction events within regions were similarly modelled. The remaining predictor variables were included as fixed effects. Propagule size was logarithmically transformed in all cases and modelled specifying a normal error distribution and an identity link. Success was modelled specifying a binomial error distribution and logit link function, with introduction outcome (success or failure) as the response variable.

3. RESULTS AND DISCUSSION

Historical records include information on propagule size ($n = 646$ events) or propagule number ($n = 305$ events) for 34% of reported bird introductions worldwide. Propagule size and number are highly correlated across events ($r = 0.71$, $n = 300$), and give similar results in the analyses reported here, but more data are available for the former. We therefore adopt propagule size as our metric of introduction effort. Events with propagule size data are a non-random subset of bird releases with respect to region of introduction (7–73% of introduction events per region include propagule size data), but are random with respect to the number of species per family represented ($\chi^2 = 13.82$, d.f. $= 9$, $p = 0.129$). Importantly, the establishment success of attempted introductions does not differ for events with or without propagule size data, both across families ($\chi^2 = 4.42$, d.f. $= 9$, $p = 0.882$) and across regions ($\chi^2 = 14.93$, d.f. $= 12$, $p = 0.245$). Thus, propagule size data are unbiased with respect to successful establishment within regions and families.

Propagule size itself is not randomly distributed with respect to regions ($\chi^2 = 258.13$, d.f. $= 12$, $p < 0.001$) or families ($\chi^2 = 178.23$, d.f. $= 9$, $p < 0.001$). Larger numbers of individuals were introduced to North America, New Zealand, Hawaii, Canada and Australia, and from the Phasianidae, Muscicapidae, Sturnidae and Fringillidae, compared with the other regions and families listed in table 1. This pattern reflects human bias towards transporting and releasing larger numbers of game birds, pets or biocontrol agents, and the colonial fervour of acclimatization societies or government-sponsored release programmes. Nevertheless, most variation in effort (58%) is clustered among introduction events within species (table 2). This is the same level at which most variation in introduction success is located (Blackburn & Duncan 2001; Cassey 2002*b*; Bessa-Gomes *et al.* 2003), suggesting both a link between the two and a reason why establishment success has sometimes been reported to be idiosyncratic

Table 2. Results of nested ANOVA showing the distribution of variation in introduction effort at different levels in the avian taxonomic hierarchy.
(Variance components were calculated using PROC NESTED in SAS.)

variance source: among (within)	d.f.	mean square error	% variance component
families (orders)	21	14.58	30.02
genera (families)	88	1.27	3.82
species (genera)	68	0.97	7.88
introduction events (species)	448	0.69	58.28

Table 3. Estimates and their associated significance tests for log-propagule size and biological traits often implicated as predictors of introduction success.
(The negative estimate for island or mainland indicates that mainlands receive a greater number of individuals per attempt than islands. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.)

	across species comparisons			controlling for phylogenetic relatedness		
	estimate	s.e.	χ^2	estimate	s.e.	χ^2
body mass	0.17	0.06	9.46^{**}	−0.12	0.06	4.66^{*}
geographical range	0.30	0.08	14.48^{***}	0.19	0.06	10.91^{***}
annual fecundity	1.48	0.16	90.15^{***}	0.44	0.14	10.39^{**}
diet generalism	0.18	0.04	25.60^{***}	0.03	0.03	1.22
habitat generalism	0.06	0.04	1.85	0.06	0.03	3.49
dichromatism	0.23	0.08	8.22^{**}	0.01	0.07	0.01
migratory tendency	−0.19	0.04	23.70^{***}	0.06	0.03	4.42^{*}
latitudinal difference	−0.42	0.06	42.11^{***}	−0.14	0.03	20.17^{**}
island or mainland	−0.79	0.08	109.56^{***}	−0.3	0.04	67.88^{***}

with respect to higher taxonomy (Blackburn & Duncan 2001). Introduction effort is indeed significantly associated with establishment success for introduced birds (estimate ± s.e. $= 0.35 \pm 0.08$, $n = 646$, $\chi^2 = 18.43$, $p < 0.001$).

Propagule size is also non-randomly distributed with respect to a range of other characteristics of non-indigenous species (table 3). This suggests that previously documented correlations between these variables and establishment success were confounded with propagule size. This conjecture is supported in birds by the minimum adequate model for success. Success is associated only with propagule size (estimate ± s.e. $= 0.96 \pm 0.13$) and habitat generalism (0.61 ± 0.14), when phylogenetic autocorrelation and the random effect of region are accounted for. When the same model is fitted excluding propagule size, greater establishment success is associated with greater habitat generalism (0.58 ± 0.14), broader geographical range (0.79 ± 0.30), introductions to islands (0.51 ± 0.19), less tendency to migrate (-0.35 ± 0.16), and less difference between donor and recipient latitudes (-0.50 ± 0.16). These are all variables that other studies have found to be correlates of establishment success (Newsome & Noble 1986; Williamson 1996; Kolar & Lodge 2001; Duncan *et al.* 2003), but usually without controlling directly for introduction effort.

The few previous studies that have included information on propagule size have found it to be the major correlate of success, but to date such studies have been either localized in extent (Newsome & Noble 1986; Veltman *et al.* 1996; Duncan 1997) or limited in scope (Beirne 1975; Dawson 1984; Greustad 1999). Our results show that propagule pressure is the primary determinant of introduction success for an entire higher taxon, where releases have occurred for a variety of reasons (e.g. hunting, aesthetics, biological control, accidental), at the global scale. They demonstrate the fundamental requirement of invasion research to account for non-random associations with propagule pressure, if other determinants of introduction success are to be identified and their influences properly understood (Levine 2000; Wonham *et al.* 2000). Our results also suggest that the best way to reduce subsequent invasions is simply to reduce the number of alien individuals released, though this will be difficult in an era of ever increasing international trade and travel (Levine & D'Antonio 2003).

Although success generally increases with effort, there are still examples of species that do not become established despite very high introduction effort (Duncan *et al.* 2003). Moreover, the precise form of the relationship differs among geographical regions and bird families (table 1). These differences are not a consequence of each region receiving introductions from a different set of families, or each family being introduced to a different set of regions: differences remain when regions are compared controlling for family, and families compared controlling for region (table 1). Mean success and mean propagule size are not correlated, either across regions ($r = -0.13$, $n = 13$) or across bird families ($r = -0.13$, $n = 10$). Our results show that increases in effort elevate success, but elevate it in an idiosyncratic manner across regions and taxa. We do not yet know the reason for this taxonomic and regional variation in success, but it seems likely to be an important avenue for subsequent investigation.

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