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Determinants of establishment success in introduced birds

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A major component of human-induced global change is the deliberate or accidental translocation of species from their native ranges to alien environments^{1,2}, where they may cause substantial environmental and economic damage^{3,4}. Thus we need to understand why some introductions succeed while others fail. Successful introductions tend to be concentrated in certain regions², especially islands and the temperate zone, suggesting that species-rich mainland and tropical locations are harder to invade because of greater biotic resistance^{1,5–9}. However, this pattern could also reflect variation in the suitability of the abiotic environment at introduction locations for the species introduced^{13,9–11}, coupled with known confounding effects of non-random selection of species and locations for introduction^{8,12–14}. Here, we test these alternative hypotheses using a global data set of historical bird introductions, employing a statistical framework that accounts for differences among species and regions in terms of introduction success. By removing these confounding effects, we show that the pattern of avian introduction success is not consistent with the biotic resistance hypothesis. Instead,

success depends on the suitability of the abiotic environment for the exotic species at the introduction site.

Historical records provide a valuable resource for investigating reasons for introduction success or failure, but firm conclusions have proved difficult to draw from such data^{3,8,13} for two reasons¹⁴. First, patterns of success are confounded because species were not randomly assigned to introduction locations, and because some locations will have received disproportionately more invaders, or more good or poor invaders. Second, individual introductions cannot be regarded as independent data points in a statistical analysis. Instead, introduction outcomes are likely to be correlated because the same species was frequently introduced to many locations, and because most locations were subject to several introductions^{15,16}.

To overcome these problems, we modelled the success or failure of all known historical bird introductions using a generalized linear mixed model (GLMM), including as random effects variables that coded for the clustering of introduction events within species, higher taxa and biogeographic region of introduction (Methods). This allows us to control for differences in introduction success rate among species and regions, and to account for the non-independence of introductions by modelling the covariance among introductions of the same species to different locations, among introductions of species within higher taxa, and among introductions to the same biogeographic region.

Having controlled for the above effects, there is no relationship between introduction success and either the latitude of introduction or whether the introduction was to an island or mainland location (Table 1, fixed effects). Thus, within biogeographic regions, species-rich locations (for example, low latitude, mainland) are as easy to invade as species-poor locations (for example, high latitude, island)^{8,17}. There was significant variation in success rate among biogeographic regions (Table 1, random effects) but the ordering of regions by their ease of invasibility was not consistent with the biotic resistance hypothesis (Table 2). Two of the most species-rich regions, the Afrotropics and Central/South America were ranked among the easiest to invade. Hence, our results find no support for

Table 1 Fixed-effect and random-effect parameters

Fixed effect		Category	Parameter estimate	Standard error	Type III, F	P
Biogeographic region	Between		-0.8477	0.1822	21.7	<0.0001
	Within		0			
	Latitudinal difference		-0.0366	0.0075	23.8	<0.0001
	Log ₁₀ (geographic range)		0.5906	0.1502	15.5	<0.0001
	Latitude of introduction		-0.0099	0.0067	2.2	0.140
Island/mainland	Island		0.0074	0.1743	0	0.966
	Mainland		0			
Random effect		Estimated variance component	Standard error	Likelihood ratio test	P	
Among orders		0.0107	0.0399	0.6	0.439	
Among families (Order)		0	—	—	—	
Among genera (Family)		0.2667	0.2507	0.2	0.655	
Among species (Genus)		1.5238	0.3201	226.9	<0.0001	
Among biogeographic regions		0.1676	0.1244	22.5	<0.0001	

Parameters are estimated in a multivariate generalized linear mixed model (GLMM) with introduction success or failure as the response variable for global bird introductions. For the fixed effects, positive parameter estimates mean that larger values of the fixed effect are associated with a higher probability of introduction success, accounting for non-independence in the data owing to the clustering of introductions modelled by the random effects. For binary variables (within or between regions, island or mainland), parameter estimates are calculated relative to one of the two categories, which thus has an estimate of zero in each case. For the random effects, the likelihood ratio is a test for zero variance in the random effect with everything else in the model. Similar results are obtained for the random effects if these are modelled alone: this is effectively a nested analysis of variance (ANOVA) of introduction success across taxonomic levels¹⁵, confirming that most variation is among species within genera, and hence that the success of a species cannot be predicted from that of its relatives. The biotic resistance hypothesis predicts that introduction success should be higher on islands and lower at low latitudes¹: these are both falsified. The abiotic suitability hypothesis predicts that introduction success should be higher when translocations are to similar latitudes¹⁸, within biogeographic regions⁶, and for species that have larger geographic ranges²²: these are all supported. F, test statistic; P, probability.

an effect of biotic resistance on introduction success^{8,13}. The traditional perception, that species-poor islands and temperate locations are easy to invade, probably reflects the greater total number of avian introductions to these locations¹⁴.

Introduction success was significantly greater when the difference between a species latitude of origin and its latitude of introduction was small, and when species were introduced to locations within their native biogeographic region (Table 1, fixed effects). Locations at similar latitude and in the same biogeographic region are more likely to share climatic and habitat features in common^{6,18}, showing that introduction success is enhanced if species are matched with suitable environments¹⁹. All else being equal, species with larger geographical range sizes should have a wider environmental tolerance²⁰, or use more widespread resources²¹, and so have a higher probability of encountering an abiotic environment at a new location that allows successful introduction²². Consistent with this prediction, geographical range size is also a significant correlate of introduction success for global bird introductions (Table 1, fixed effects). These results support the view that physiological tolerances are likely to be at least as important as biotic interactions in determining the responses of species to global climate change^{23,24}.

Variation in introduction success unaccounted for by the fixed effects in the model can be decomposed into variation due to differences among species at different levels of the taxonomic hierarchy, differences among biogeographic regions (see above) and residual variation. This decomposition revealed significant unexplained variation among species, but not among taxonomic groups at the genus level or higher (Table 1, random effects). This shows that unmeasured species-level traits associated with introduction success must be phylogenetically labile, varying even among closely related species. By the same token, characteristics typically shared by related species, including several life history traits hypothesized to predict introduction success (body mass, generation time and population growth rate^{3,25–27}), can explain only a small and non-significant amount of variation in global introduction success. To check this, we ran our analysis again, including family-typical values for three traits (body mass, clutch size and incubation period; see Methods) as fixed-effect predictors in the model. None of these family-level traits were significant determinants of introduction success, as predicted by the decomposition of unexplained variance among avian taxonomic levels (Table 1, random effects).

In addition to variation in specific characteristics that affect invasibility, significant differences among species in introduction success will almost certainly reflect variation in introduction effort (the number of releases or individuals released at each location)³. Although data are not available for most locations, our analyses account for variation in effort in two ways. First, species with a larger geographical range size tend to have been introduced more often and in greater numbers because they were more readily obtained for introduction^{14,22}. Hence, the significant effect of geographical range

size on introduction success may reflect introduction effort in addition to abiotic tolerance, both of which are required to account for the significant relationship between geographical range size and success in Australian bird introductions²². Second, coding species identity as a random effect in the model controls for differences among species, including variation in introduction effort.

Determining the causes of introduction success is important for improving our ability to identify and screen out environmentally and economically damaging biological invaders^{3,28}. Our results show that for birds the outcome of introductions is not predicted by general features of locations related to biotic resistance (such as latitude), and that the success of a species cannot be predicted from that of its relatives. Instead, the importance of phylogenetically labile species-specific factors, such as geographical range size, and event-level effects related to environmental suitability, such as the match between latitudes of origin and introduction, suggest that success depends on the particular combination of species and location. This may help to explain why general features of invaders have been hard to characterize^{3,13,26}, but shows that an understanding of introduction success is possible nonetheless. □

Methods

Data

We included all known historical human-mediated introductions (excluding natural colonizations and subsequent unassisted colonizations from introduced populations) except for introductions undertaken for conservation purposes, giving a total of 1,466 introduction events (of a species to a particular location) for 389 species. We define a location as an island or a country on a continental mainland to which a species was introduced. Multiple releases to the same island or country are counted as one introduction to that location. 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). For each introduction event, five variables were recorded in addition to success: whether introduction was to a mainland or island location, the latitude of introduction, the difference between the latitudinal midpoint of the native range of the species and the latitude of introduction ('latitudinal difference') calculated without reference to hemisphere (that is, an introduction from 50° N to 40° S has a latitudinal difference of 10°), whether the introduction was intraregional (introduction site and native range in the same biogeographic region) or interregional (in different biogeographic regions), and the geographical range size ($\log_{10}(\text{latitudinal range} \times \text{longitudinal range})$) of the species introduced. Latitude and longitude were measured in degrees. For each bird family with at least one introduced species, we calculated geometric mean values of body mass, clutch size and incubation period. All data sources are listed in the Supplementary Information.

Analyses

We used the GLIMMIX macro in SAS²⁹ to fit a generalized linear mixed model (GLMM) specifying a binomial error distribution and logit link function, with introduction outcome (success or failure) as the response variable. GLMMs provide a framework for analysing binary response data (success or failure of introduction) in which observations are likely to be correlated owing to clustering and cannot therefore be treated as statistically independent units³⁰. GLMMs incorporate information on the clustering to provide estimates of standard errors corrected for this non-independence, which will generally be more conservative than estimates obtained if the clustering is ignored. GLMMs also allow the variance explained at different levels of a clustering hierarchy to be decomposed, providing an upper limit to the amount of variation that could be explained by unobserved variables associated with each level of the hierarchy³⁰. We modelled the likely non-independence of introductions of the same species by assuming a common positive correlation between introduction outcomes involving the same species, but a zero correlation between introduction outcomes involving different species (a variance components model). Clustering of introduction events within higher taxonomic levels (genera, families and orders) and biogeographic regions were similarly modelled. On the logit scale, the effects for each clustering variable are assumed to be a random sample taken from a larger population of normally distributed values, rather than being a set of fixed values, so that inferences about the importance of these 'random effects' apply to the wider population from which those observations derive. The remaining predictor variables were modelled as fixed effects.

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Table 2 Parameter estimates and standard errors

Biogeographic region	Parameter estimate	Standard error
Afrotropics	0.5620	0.2809
Palearctic	0.3435	0.2464
Central/South America	0.3098	0.2915
Caribbean	0.1308	0.2508
Malagasy	0.0345	0.2346
Pacific	-0.0210	0.1942
Antarctic	-0.0533	0.3887
Australasia	-0.2054	0.1949
Nearctic	-0.2516	0.2343
Southeast Asia	-0.2589	0.2677
Atlantic	-0.5905	0.2745

The biogeographic regions were included as random effects in a multivariate GLMM with introduction success or failure as the response variable for global bird introductions. Regions with more positive parameter estimates were associated with a higher probability of introduction success, accounting for the fixed effects (in Table 1) and non-independence in the data owing to the clustering of introductions by species.

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Distance determined by the angular declination below the horizon

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A biological system is often more efficient when it takes advantage of the regularities in its environment^{1,2}. Like other terrestrial creatures, our spatial sense relies on the regularities associated with the ground surface^{2–6}. A simple, but important, ecological fact is that the field of view of the ground surface extends upwards

from near (feet) to infinity (horizon)². It forms the basis of a trigonometric relationship wherein the further an object on the ground is, the higher in the field of view it looks, with an object at infinity being seen at the horizon. Here, we provide support for the hypothesis that the visual system uses the angular declination below the horizon for distance judgement. Using a visually directed action task^{7–10}, we found that when the angular declination was increased by binocularly viewing through base-up prisms, the observer underestimated distance. After adapting to the same prisms, however, the observer overestimated distance on prism removal. Most significantly, we show that the distance overestimation as an after-effect of prism adaptation was due to a lowered perceived eye level, which reduced the object's angular declination below the horizon.

Figure 1a illustrates the relationship between the angular declination below the horizon (α) and the absolute distance (d) of an object on the ground from the observer. Assuming that the observer's eye height (h) is known¹¹, the object distance can be determined by obtaining the angular declination below the horizon: $d = h/\tan(\alpha)$ (refs 2–4). To test this 'angular declination hypothesis', that the visual system can access the information regarding the angular declination below the horizon for distance perception, consider the consequence of viewing through a pair of base-up prisms that deviate light by δ degrees (Fig. 1b). Predictably, the angular declination below the horizon will increase to $\alpha + \delta$, and, accordingly, the perceived distance, $h/\tan(\alpha + \delta)$, will decrease. Next, suppose that the observer continually views the visual environment through the base-up prisms, and eventually removes the prisms to reveal the after-effect of prism adaptation^{12–14}. If we assume that prism adaptation induces a recalibration of the eye level downward, the angular declination below the horizon will also reduce. Thus, we

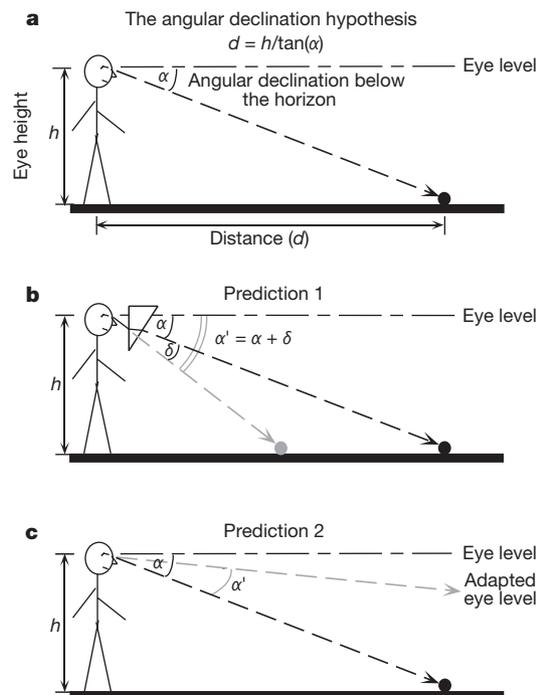


Figure 1 The angular declination hypothesis. **a**, The hypothesis describes how the visual system can compute distance (d) from the eye height (h) and the angular declination below the horizon (α), with the trigonometric relationship $d = h/\tan(\alpha)$. **b**, Prediction 1. A base-up prism increases the object's angular declination from α to $\alpha + \delta$, reducing computed distance. **c**, Prediction 2. The after-effect of base-up prism adaptation is a downward shift of the eye level. Because the eye level serves as a reference for computing the angular declination below the horizon, and the object's angular declination (α) is reduced to (α'), distance is overestimated.