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Research

Bergmann's rule in alien birds

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Native bird species show latitudinal gradients in body size across species (Bergmann's rule), but whether or not such gradients are recapitulated in the alien distributions of bird species are unknown. Here, we test for the existence of Bergmann's rule in alien bird species worldwide, and investigate the causes of the observed patterns. Published databases were used to obtain the worldwide distributions of established alien bird populations, the locations of alien bird introductions, and bird body masses. Randomisation tests and linear models were used to assess latitudinal patterns in the body masses of introduced and established alien bird populations. Established alien bird species exhibit Bergmann's rule, but this is largely explained by where alien bird species have been introduced: latitudinal variation in the body masses of established alien bird species simply reflects latitudinal variation in the body masses of introduced species. There is some evidence that body mass is implicated in whether or not established species' alien ranges spread towards or contract away from the Equator following establishment. However, most alien bird ranges are encompassed by the latitudinal band(s) to which the species was introduced. Bergmann's rule in alien birds is therefore a consequence of where humans have introduced different species, rather than of natural processes operating after population introduction.

Keywords: biological invasion, body mass, latitude

Introduction

Bergmann (1847) was the first to propose that species of homeothermic animals living in cold climates should be larger-bodied than phylogenetic close relatives living in warm climates, and hence that there should be latitudinal gradients in body size in such taxa (Blackburn et al. 1999). The relationship that this posits has come to be generally known (and will be known here) as Bergmann's rule, although debate rumbles on as to whether spatial variation in body size should be analysed across or within species (cf. Watt et al. 2010, Meiri 2011). Bergmann's rule in its interspecific form has received considerable attention in the macroecological research community (Meiri and Dayan 2003, Meiri et al. 2007, Torres-Romero et al. 2016, Faurby and Araújo 2017). For birds, the relationship is generally well supported, with regional and global analyses of the distribution of avian body masses finding a general trend of

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larger body masses at high latitudes (Blackburn and Gaston 1996a, Olson et al. 2009). Evidence suggests that this pattern is a consequence in part of turnover among lineages, and in part of adaptation to temperature gradients and resource availability within lineages (Olson et al. 2009).

The existence of a latitudinal gradient in the body masses of native bird species raises the question of whether the same pattern is reconstituted amongst alien bird species. Aliens are species deliberately or accidentally translocated by direct human agency to areas outside their normal geographic ranges, where they may establish persistent viable populations, and then may spread widely across the new environment (Richardson et al. 2011). Populations of alien bird species are now found widely across the globe (Dyer et al. 2017a), and while most alien bird range sizes are small (median = ca 10 000 km^2), several species have an alien range size spanning more than 1×10^6 km^2 (Dyer et al. 2016). One key characteristic determining the success of alien bird species appears to be the match between the environment natively encountered by the species and that in the alien range: species introduced to areas that are not environmentally suitable will fail to establish, while species that can establish will not spread into areas that are environmentally unsuitable (Blackburn and Duncan 2001a, Duncan et al. 2001, 2003, 2014, Strubbe et al. 2013). Bergmann's rule in native bird species suggests that body size is one factor that mediates, or reflects, that environmental match. If so, we might expect to see Bergmann's rule recapitulated in the distributions of alien bird species, for example if small-bodied bird species cannot establish or spread at higher latitudes. As far as we are aware, no one has tested directly for Bergmann's rule in alien birds (although for an intraspecific test, see Cardilini et al. 2016).

The existence or otherwise of Bergmann's rule in alien bird species could potentially provide useful information on the drivers of the pattern, for example on whether the pattern is likely to arise as a consequence of short-term ecological interactions or longer term evolutionary selection. However, before any such conclusions can be drawn, a more prosaic explanation for spatial variation in alien bird body sizes must be ruled out – the influence of the set of species that have been introduced to an area (Lockwood et al. 2009, Dyer et al. 2017a). Patterns in the distributions of alien species (and their traits) could potentially arise because of where humans have tended to introduce species, rather than because of the environmental responses of those species. For example, Blackburn et al. (2008) showed that alien bird species richness is higher on more isolated islands because more alien bird species had been introduced to those islands, rather than through any effect of natural processes operating across islands. Likewise, spatial variation in alien bird body masses could arise as a consequence of which species have been introduced to different locations, rather than how the environment at those locations interacts with body mass.

Here, we explore latitudinal patterns in the body sizes of alien bird species, using a global database on alien bird distributions (GAVIA: Dyer et al. 2016, 2017a, b). GAVIA includes information on the geographic locations of species that were introduced but failed to establish, as well as maps of the established distribution of alien birds. This information allows us to explore the extent to which latitudinal patterns in alien bird body sizes are a consequence of where species are introduced versus where species succeed in establishing and spreading. We then use this information to assess whether there is evidence for effects of body size on alien bird distributions beyond the effects of where species are introduced.

Methods

We mined the GAVIA database to extract two types of information for bird species at the global scale: First, the locations of introduction and second, the locations with established alien populations. Established populations are those considered in the GAVIA database to be self-sustaining (Dyer et al. 2017b); this status was normally ascribed by the source from which GAVIA obtained the information for that population, with the caveat that no population (alien or native) persists indefinitely. The established location data are not the same as the introduction data as many species have spread since introduction to new latitudes, away from their original site of introduction. For the introduction data, we only included introduction records for which there was clear evidence of actual introduction at that location: these were available for a total of 711 species. For data on where species are established, we used the distributions of 359 species for which alien ranges were sufficiently well described to have been mapped in GAVIA. Four of the species with established population records do not have information on locations of introduction, even though they must have been introduced; therefore, 355 species have data on both locations of introduction and establishment, 356 species have data on locations of introduction but no recorded established populations (711 – 355), and we have distributional information (introduction and/or establishment) on 715 species in total (711 with locations of introduction plus 4 established but without locations of introduction).

We used this location information to identify 27 latitudinal bands to which bird species have been recorded as introduced as aliens, and/or in which they have established alien populations. These bands each span 5° of latitude, with the northernmost band analysed covering 70–75°N, and the southernmost band covering 55–60°S. There are a total of 2125 distinct species introduction × latitudinal band records (i.e. the 711 species have been introduced to ca 3 latitudinal bands on average) and a total of 1284 distinct species establishment x latitudinal band records (i.e. the 359 species are established in ca 3.5 latitudinal bands on average). These data allow us to plot the body sizes of alien species extant in each latitudinal band, but also the body sizes of alien species that have been introduced in each latitudinal band (which may or may not have established). If latitudinal variation in alien bird body sizes is primarily determined by where species have been introduced, these patterns should be very similar. Conversely, if latitudinal variation in alien bird body sizes is a consequence of interactions between species and the novel environment, which determines the ability of alien species to establish and spread, these patterns should be different.

Our analytical approach ('Stevens' method' sensu Blackburn and Gaston 1996b) potentially suffers from autocorrelation between bands, but we use it for three reasons. First, our analysis requires that we identify latitudes at which species have been introduced and either have or have not succeeded in establishing viable alien populations. Neither the mid-point nor comparative methods, which summarise a species' latitudinal span as a single point (the extant range midpoint), can deal with this requirement of the analysis. Stevens' method is unique in incorporating information on the range sizes of all species occurring at each latitude. Second, alien ranges (introduced or established) tend to be highly fragmented. For example, the yellowhammer *Emberiza citrinella* has been introduced to southern Australia, New Zealand and near Cincinatti in the USA (Long 1981), and so other methods (e.g. the 'mid-point' and 'comparative' methods sensu Blackburn and Gaston 1996b) are much more likely to assign species ranges to latitudes at which they do not occur than is the case for native distributions. Third, we are more interested in describing patterns of variation than in assigning significance to relationships. Autocorrelation is a consequence of pattern, not a cause, and so is less relevant in this situation. Moreover, autocorrelation does not affect our analyses of body size frequency distributions, or changes in range post-introduction, and so does not impinge on most of our results. Nevertheless, the fragmentation of alien ranges means that the likelihood of autocorrelation is reduced.

We obtained data on the body masses of the 715 species in our analysis from the database of amniote life history information (Myhrvold et al. 2015), the CRC Handbook of avian body masses (Dunning 2007, 2013), or from Handbook of birds of the world alive (<www.hbw.com/species>). Eight species for which masses were not available from these sources had their masses estimated as the means from other species in the genus with mass data (or for *Fregilupus varius*, from other species in the family). Species introduction × latitudinal band records, species establishment × latitudinal band records, and associated body masses, are included as Supplementary material Appendix 1–3. We used the same taxonomy as Dyer et al. (2017b). Logarithmic transformations of mass were always to base 10.

We first tested whether introduced species were a random sample of all birds in terms of their body mass, by drawing 715 species at random from the 9802 species with masses given by Myhrvold et al. (2015), calculating the geometric mean mass of the random sample, and repeating the process 10 000 times to generate a distribution of expected mean masses. We also ran this test constraining the family level composition of the list of randomly chosen species in each iteration of the model to be the same as that of the species actually introduced. We also used the permutation approach to test whether established species were a random sample of introduced birds in terms of their body mass, but drawing 359 species at random from the 715 species we know to have been introduced.

We used data on locations of introduction and the distributions of established species to calculate the geometric mean (and its standard deviation) body mass of all bird species recorded as introduced and all bird species established in each 5° latitudinal band. We then used plotted second order polynomial regressions of these means versus latitude to characterise latitudinal variation in alien bird body masses.

For the 355 species for which there are both established and introduction records, we compared the numbers of latitudinal bands with introduction records versus those with established populations for each species. We used paired t-tests to assess whether each species was introduced to or established in more latitudinal bands. We also carried out randomization tests to assess whether the pattern of changes in the latitudinal distributions of established species after introduction is related to body mass. For each group of n species for which established populations showed the same pattern of expansion or contraction relative to the equator or poles, we compared the median mass to the distribution of 100 000 random median masses generated by sampling n species without replacement from the set of 355 established species.

We used generalised linear models (GLM) with a Gaussian error function to test whether body mass predicts the extent to which alien species have established populations in bands closer to or further from a Pole than introduction records. This will show, for instance, whether the birds with larger body masses have been able to move towards higher latitudes since their introduction. The response variable here is the latitudinal difference between the midpoint of the band closest to a Pole with an introduction record and the midpoint of the band closest to a Pole with an established population recorded (one data point per species). Low phylogenetic correlation in the extent of Pole-ward spread or contraction (using the 'caper' package in R (Orme et al. 2015) applied to a Hackett all species phylogeny (Jetz et al. 2012), lambda [95% confidence intervals] = 0, [0, 0.18]) means that phylogenetic generalised least square (PGLS) models give identical answers; hence we report only the GLM results. We repeated these comparisons analysing only those species for which the highest latitudinal band of recorded introduction differs from the highest latitudinal band with an established population, and converting this difference into a binary variable (1 = species that have established populations in bands closer to a Pole than introduction records; 0 = species that have introduction records in bands closer to a Pole than established populations). We tested whether body mass predicts into which category a species falls using a GLM with binomial errors. We then repeated all of these analyses to test for the extent to which alien species have established populations in bands closer to or further from the Equator than introduction records. Low phylogenetic correlation (lambda = 0.13 [0.03, 0.29]) meant that GLM and PGLS models give very similar answers, and so we again report only the GLM results. All analyses were carried out using R ver. 3.4.2 (R Core Team).

Data deposition

Data available from Univ. College London (UCL) open access repository: <https://rps.ucl.ac.uk/viewobject.html?cid=1&id=1564443>.

Results

The frequency distributions of body masses for the introduced and established bird species in our analysis are given in Fig. 1. The mean mass of introduced species (140.1 g, n = 715) is significantly greater than a random sample of all bird species, falling outside the range of means obtained from all 10 000 iterations of the simulation (mean of 10 000 simulations = 51.9 g; range of the simulated distribution = 41.5–64.4 g). The same holds if the random samples are constrained so that the number of species in each family is the same as for the set of introduced species (mean of 10 000 simulations = 128.1 g; range of the simulated distribution = 118.2–139 g). However, the mean mass of established bird species (125.4 g, n = 359) does not differ from a random sample of introduced bird species (mean of 10 000 simulations = 140.0 g, 2.5–97.5% percentiles of the simulated distribution = 122.2–159.8 g).

The mean mass of the established bird species in latitudinal bands varies substantially with latitude, being lowest around the equator and increasing with latitude in both the southern and northern hemispheres (Fig. 2). A second order polynomial regression for log mass versus latitude explains 49% of the variation ($F_{2,24} = 13.3$, $p < 0.001$; Table 1). However, the mean mass of introduced bird species in latitudinal bands is also lowest around the equator, increases with latitude in both the southern and northern hemispheres (Fig. 2), and differs little from the pattern for established species. Indeed, the mean log mass of established species is highly positively correlated across bands with the mean log mass of species with introduction records in the same band ($r = 0.76$, $n = 25$, $p < 0.001$). A second order polynomial regression for log mass versus latitude for introduced species gives a stronger fit to that for established species, explaining 72% of the variation ($F_{2,22} = 31.5$, $p < 0.0001$; Table 1). Established species have been recorded from two high northern latitudinal bands for which there are no records of introduction; repeating the analysis for established records excluding these bands results in a very similar relationship to that for introduced species ($R^2 = 0.73$, $F_{2,22} = 33.5$, $p < 0.0001$; Table 1, Fig. 2b).

On average, established alien bird species have introduction records from slightly more latitudinal bands (mean ± SD = 4.4 ± 3.9) than bands with records of establishment (mean ± SD = 3.5 ± 3.8), and this difference is significant (paired t test, $t = 8.5$, $df = 354$, $p < 0.001$). Thus, post-introduction spread to new latitudinal bands is less common than post-introduction population extinction from latitudinal bands.

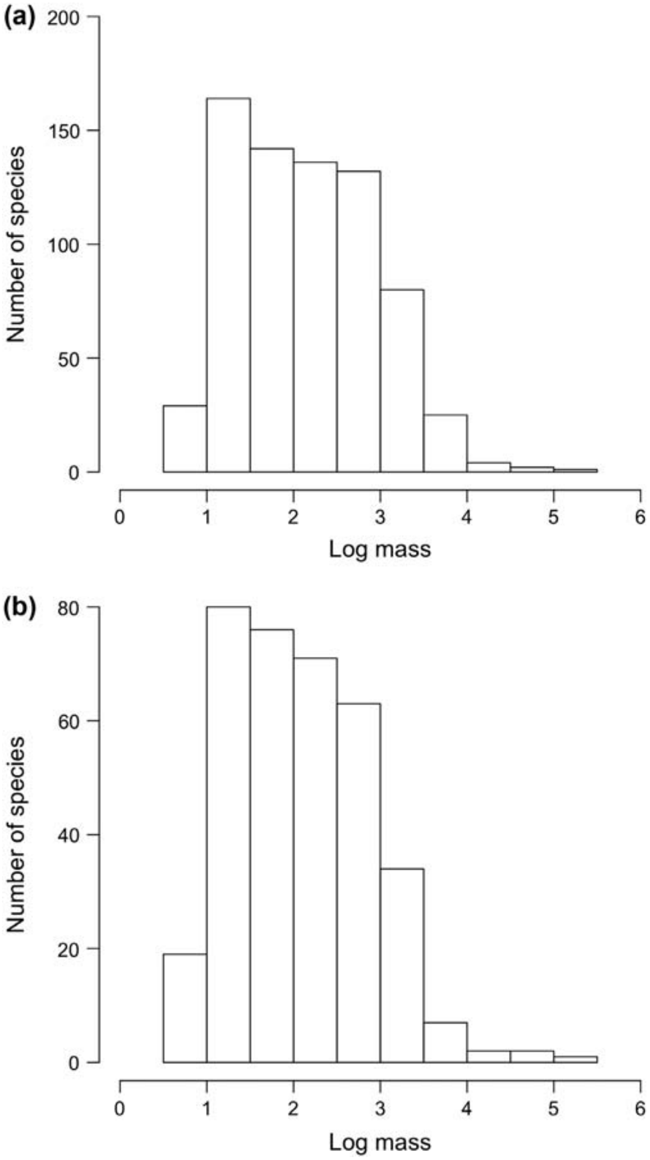

Figure 1. The frequency distribution of $\log_{10}$ body masses for (a) introduced (n = 715) and (b) established (n = 359) bird species.

The pattern of changes in the latitudinal distributions of established species after introductions is shown in Fig. 3. The most frequent outcome is that the highest and lowest absolute latitudinal bands of establishment are the same as the highest and lowest absolute latitudinal bands of introduction (Fig. 3, outcome A). Thirty-one alien species have established populations in bands closer to a Pole than introduction records (Fig. 3, outcomes E–G), while 105 alien species have been introduced to higher latitude bands than any in which they are established (Fig. 3, outcomes B–D). For the remaining 219 species, the highest latitude band in which they are established is also the highest latitude band in which they were recorded as introduced (Fig. 3, outcomes A, H, I).

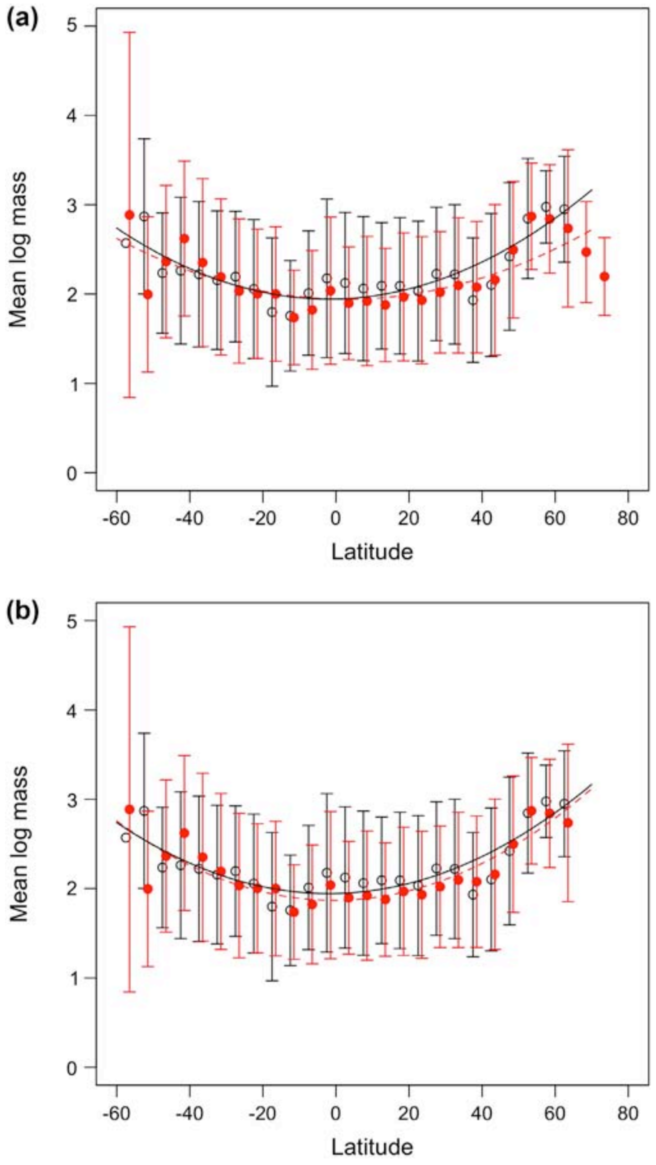

Figure 2. (a) The relationship between mean $\log_{10}$ body mass (grammes, ± standard deviation) of species in a latitudinal band and the latitudinal midpoint of that band (degrees), for introduced (black points and lines) and established (red points and lines) alien bird species. (b) The same relationships plotted across just those latitudinal bands in common to both groups. The coefficients of the regression lines are given in Table 1. Negative latitudes are in the southern hemisphere.

Twenty-four alien species have established populations in bands closer to the Equator than introduction records (Fig. 3, outcomes D, G, H), while 93 alien species have been introduced to lower latitude bands than any in which they are established (Fig. 3, outcomes B, E, I). For the remaining 238 species, the lowest latitude band in which they are established is also the lowest latitude band in which they were recorded as introduced (Fig. 3, outcomes A, C, F). Thus, overall, species introduced ranges tend to contract away from either the closest Pole or the Equator (or both), such that established locations occupy less extreme high or low latitudes than locations of introduction. Only a single species (the dunnock *Prunella modularis*) extended its range into both lower and higher latitudinal bands post-introduction (Fig. 3, outcome G). Randomization tests show that the median masses of species in two groups are larger than expected, and in three groups are smaller than expected (Fig. 3). However, there is no obvious association between these differences and whether or not species extended their ranges towards (or contracted their ranges away from) the equator or poles.

Body mass does not predict the extent to which alien species have established populations in bands closer to a Pole than introduction records (Gaussian GLM on Log mass: estimate ± SE $= 0.902 \pm 0.56$, $t = 1.61$, $p = 0.11$; Fig. 4a). Considering only those species for which the highest latitudinal band of recorded introduction differs from the highest latitudinal band with an established population, body mass does not differ for alien species that may have expanded Pole-ward following introduction (i.e. those which have established populations in bands closer to a Pole than introduction records) versus those that may have contracted away from the Pole (Binomial GLM with Log mass versus expansion towards/contraction from the Pole as categories: estimate ± SE $= 0.10 \pm 0.27$, $z = 0.39$, $p = 0.7$).

Body mass is related to the extent to which alien species have established populations in bands closer to the Equator than introduction records (Gaussian GLM on Log mass: estimate ± SE $= 2.68 \pm 0.52$, $t = 5.1$, $p < 0.001$): larger bodied bird species are more likely to have been introduced to lower latitude bands than any in which they are established (Fig. 4b). The same is true if we also consider only those species for which the lowest latitudinal band of recorded introduction differs from the lowest latitudinal band with an established population: body mass is lower for alien species that may have expanded towards the equator than those that may have contracted away from it (Binomial GLM with Log mass versus expansion towards/contraction from the Equator as categories: estimate ± SE $= 0.82 \pm 0.31$, $z = 2.63$, $p = 0.009$).

Discussion

Alien bird species exhibit Bergmann's rule. The mean body mass of species with established populations in different 5° bands of latitude varies more than tenfold, from a minimum of 54 g between 10 and 15°S, to a maximum of 771 g between 55 and 60°S. Mean alien bird body mass is < 200 g in most tropical bands (Fig. 2). However, the great majority of this variation can be accounted for simply by variation in the body masses of the bird species introduced. This is highly positively correlated with mean established mass across latitudinal bands, and shows virtually the same spatial pattern of latitudinal variation (Table 1, Fig. 2). Humans have tended to introduce smaller-bodied bird species to lower latitudes, and larger-bodied bird species to higher latitudes, and latitudinal variation in establishment success and subsequent population

Table 1. Coefficients for the second order polynomial regressions of body mass versus latitudinal band for established and introduced alien bird species records. For established records, 'All' refers to analysis on all 27 latitudinal bands with records of established bird species, while 'Common' refers to analysis just across the 25 latitudinal bands that also have introduced alien bird species records.

Species	Coefficients:	Estimate	Std. Error	t	p
Established					
All	Intercept	2.20	0.047	47.19	< 0.0001
(n = 27 bands)	First order	0.33	0.243	1.34	0.19
	Second order	1.21	0.243	4.98	< 0.0001
Common	Intercept	2.20	0.036	60.61	< 0.0001
(n = 25 bands)	First order	0.28	0.181	1.52	0.14
	Second order	1.46	0.181	8.05	< 0.0001
Introduced	Intercept	2.32	0.037	63.00	< 0.0001
(n = 25 bands)	First order	0.90	0.217	4.30	0.0003
	Second order	1.66	0.217	7.65	< 0.0001

spread has been effectively neutral with respect to body mass, and so barely modified that pattern. Thus, the fact that alien birds apparently exhibit an ecogeographic pattern qualitatively and quantitatively similar to that in native birds (e.g. compare our Fig. 2 with Fig. 1e in Olson et al. 2009) can be entirely due to human actions in introducing different species to different areas with no recourse to the ecology or evolution of the species concerned.

Humans have been moving bird species for millennia, but most introductions have occurred in the last 150 yr, with the rate increasing markedly after World War II (Dyer et al. 2017a, Seebens et al. 2017). Introductions in the century from 1850 were largely focussed on movements of perceived beneficial species between the European colonial powers and their colonies, and included many large-bodied game and ornamental species such as pheasants, partridges, ducks, geese and pigeons. Post-war introductions have been driven much more as an accidental side-effect of the cage bird trade, with south-east Asia and near Asia being particular hotspots, and smaller-bodied taxa such as starlings, finches and other passerines featuring prominently (Dyer et al. 2016). Latitudinal variation in the body masses of introduced alien birds may therefore reflect how the reasons for, and foci of, translocation have changed over time: large-bodied game and ornamental species to higher latitude European countries and their higher latitude colonies in both hemispheres (e.g. Canada, the U.S., South Africa, Australia, New Zealand), followed by smaller-bodied cage birds to trade centres at lower latitudes in the far and near East (e.g. Singapore, Hong Kong, Taiwan, the Emirates).

About half of the species for which we have data on locations of introduction have no recorded established distributions in our data. We find little evidence that the latitudinal pattern in disappearance is related to body mass, as evidenced by the closely congruent patterns for introduced and established records in Fig. 2. Nevertheless, there is some evidence that body mass is implicated in whether or not established species' alien ranges spread towards or contract away from the Equator following establishment (Fig. 4b). Thus, species with established populations in latitudinal bands closer to the Equator than any latitudinal bands with introduction records tend to be smaller-bodied than species with introduction records closer to the Equator than any established records. The implication is that large-bodied alien bird species are less likely to establish in bands they have been introduced to close to the Equator (or possibly that their ranges shift Pole-ward following establishment). Conversely, small-bodied alien bird species are more likely to be found in latitudinal bands closer to the Equator than any to which they are known to have been introduced. This may suggest that small-bodied alien bird species shift their ranges Equator-ward following establishment.

It is important to note however, that the presence of an introduction record in a latitudinal band, but no established population known there, can be taken to imply a species was introduced there but did not establish. However, the presence of an established population in a latitudinal band but not an introduction record cannot be taken to be indicative of spread – it may also indicate a missing introduction record. Certainly, the existence of a handful of established species with no records of introduction in our database shows that introduction records can be missing. We have no way of knowing for certain whether latitudinal range spread occurs after introduction in most cases (though it certainly does in some), only latitudinal range contraction. Thus, the tendency shown in Fig. 4b for small-bodied alien bird species to be more likely to be found in latitudinal bands closer to the Equator than any to which they are known to have been introduced, may in fact reflect a systematic lack of introduction records rather than that small-bodied alien bird species shift their ranges Equator-ward.

Either way, no such trend with body mass is noted for spread towards or contraction away from the Poles following establishment (Fig. 4a). Large body mass does not seem to be an advantage at higher latitudes, as it might have been expected to from Bergmann's rule. It may be that the tendency for introduced species to be significantly larger-bodied than expected by chance (see Results and Blackburn and Duncan 2001b, Blackburn et al. 2009), and for larger-bodied bird species to be introduced at higher latitudes (Fig. 2) means that they are pre-selected to benefit from whatever advantages large size brings to native birds at higher latitudes (Olson et al. 2009). Thus, body mass has no further influence on whether or not species will establish at (or even spread beyond) the highest latitudes to which they have been introduced (Fig. 4a). The general pre-selection for large body size in introduced bird species may also be why size does seem to have some effect at low latitudes, given that smaller body size appears to be advantageous at low latitudes for native bird species.

In fact, regardless of any effect of body mass, established alien bird species show rather little tendency to spread far beyond their latitudes of introduction. Indeed, most species are established in fewer latitudinal bands than the number to which they were introduced (3.5 versus 4.4). Most species do not have established populations in latitudinal bands closer to either the Equator or Poles than any to which they were introduced, such that established locations occupy less extreme high or low latitudes than locations of introduction. This all reflects the fact that many avian introduction attempts end in failure (Dyer et al. 2017b). While there are a number of high profile alien bird species that have spread extensively following establishment (e.g. the European starling *Sturnus vulgaris* in North America; Long 1981), most alien bird range sizes are small (Dyer et al. 2016) and clearly in general encompassed by the 5° latitudinal band(s) (each ca 550 km north–south) to which the species was introduced. Only 13% of alien bird species have established populations in more latitudinal bands than the number to which they were introduced.

The tendency for introduced species to be larger-bodied than expected by chance is also found for amphibians (Tingley et al. 2010) and mammals (Capellini et al. 2015, Blackburn et al. 2017), although we currently await analyses of spatial variation in alien body mass for these taxa. As far as we are aware, the only other study to explore Bergmann's rule in the context of alien species is by Blanchet et al. (2010) for fish assemblages worldwide. Blanchet et al. found that established alien fish species were larger-bodied than a random sample of fish species, and tended to increase the mean body size of the assemblages in which they established. The addition of alien fish species actually transformed a non-significant relationship between mean body size and latitude in the Southern Hemisphere into the positive relationship expected from Bergmann's rule. However, it is unclear both whether established alien fish assemblages themselves show Bergmann's rule, or whether the patterns in alien fish species

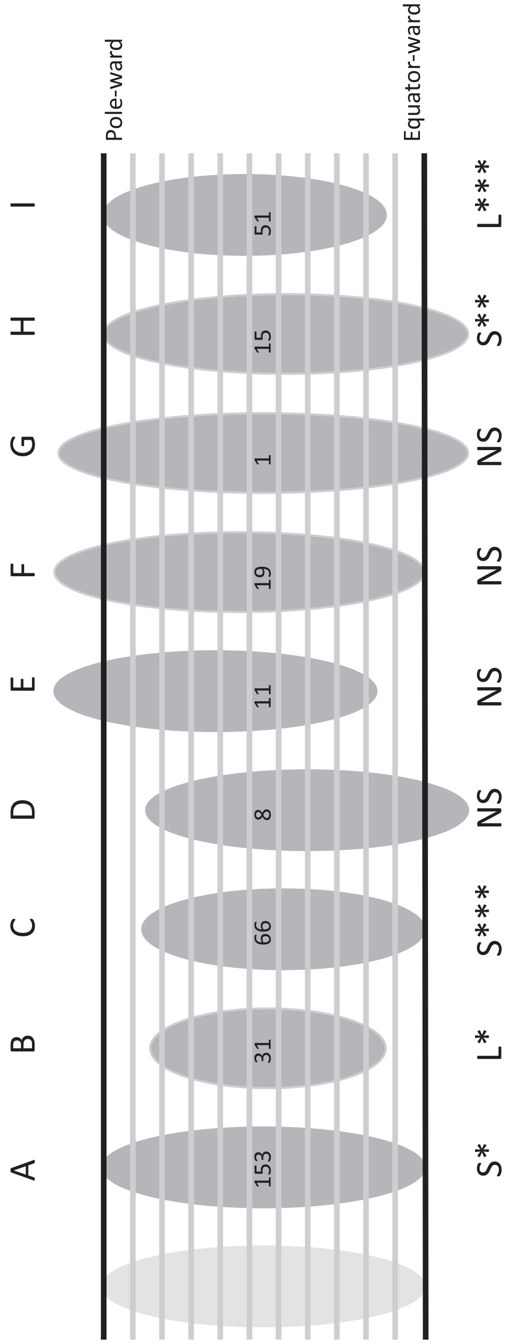

Figure 3. A cartoon depiction of the nine possible outcomes (dark grey ovals A–I) of latitudinal shifts of a species' established alien range relative to its introduced range. The lightest grey oval represents the introduced range of a species (n = 711), with the black horizontal lines indicating the highest (Pole-ward) and lowest (Equator-ward) limits of latitudinal bands to which the species was introduced. Grey horizontal lines delineate latitudinal bands. A species established range may occupy the same highest latitudinal band as its introduced range (outcomes A, H, I), may contract away from the highest latitudinal band (outcomes B, C, D) or may occupy a higher latitudinal band (outcomes E, F, G). Likewise, a species established range may occupy the same lowest latitudinal band as its introduced range (outcomes A, C, F), may contract away from the

Figure 3. (Continued)
lowest latitudinal band (outcomes B, E, I) or may occupy a lower latitudinal band (outcomes D, G, H). The numbers in each oval represent the number of established species with each outcome (total n = 355). Note that in reality, species' established alien ranges may be fragmented (i.e. they do not occupy all latitudinal bands between their Pole-ward and Equator-ward limits), and that Pole-ward and Equator-ward limits may lie in different hemispheres. S = the median mass of species in the group is smaller than expected from a randomisation test, L = the median mass of species in the group is larger than expected from a randomisation test, NS = the median mass of species in the group does not differ from random expectation; *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

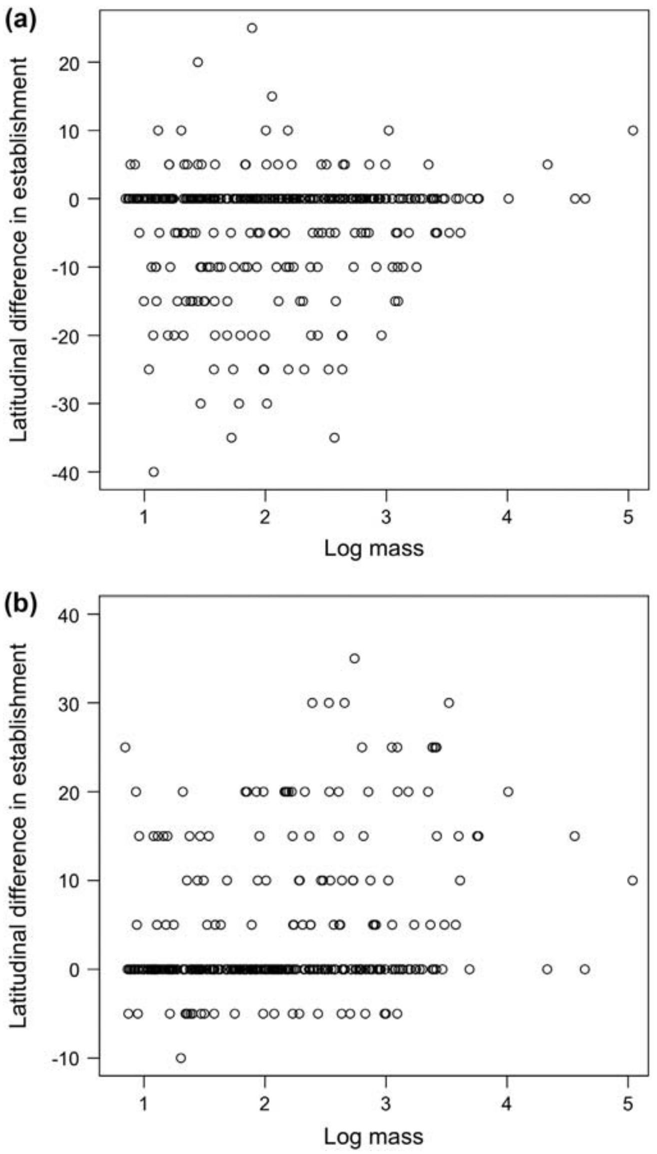

Figure 4. (a) The relationship between $\log_{10}$ body mass and the difference in the highest latitudes of establishment versus introductions. Negative differences imply that the highest absolute latitude of establishment is in a latitudinal band further away from the Pole than the highest absolute latitude of introduction. (b) The relationship between $\log_{10}$ body mass and the difference in the lowest latitudes of establishment versus introductions. Negative differences imply that the lowest absolute latitude of establishment is in a latitudinal band closer to the Equator than the lowest absolute latitude of introduction.

body size are due to variation in where species are introduced, or where they establish. Blanchet et al. (2010) argue that the latter is most likely, but it is not possible to be sure in the absence of data on failed fish introductions.

Humans have been introducing alien species for several thousand years (Grayson 2001), but most introductions have occurred in the last few decades (Seebens et al. 2017) – for example, more than three quarters of all dated bird introductions in the period 1500–2000 AD were from the twentieth century (Dyer et al. 2017a). These relatively short time scales may mean that alien species body masses may not have had time to respond to the ecological or evolutionary drivers hypothesised to have led to Bergmann's rule in native assemblages. In fact, a century or so of exposure to new conditions has been enough to produce body size clines within alien bird species (Johnston and Selander 1964, 1971, 1973, Baker and Moeed 1979, Baker 1980), and so to have modified body size gradients across species. For birds, though, this point is moot: alien bird species already exhibit Bergmann's rule as a result of where different species have been introduced. Exposure to the ecological or evolutionary drivers of Bergmann's rule in native species would not be expected to change that. Any study that aims to assess ecogeographic or biogeographic patterns in the distributions of alien species needs to incorporate information on the identities and numbers of introduced species if it is not to draw erroneous conclusions about the drivers of those patterns.

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Supplementary material (Appendix ECOG-03750 at <www.ecography.org/appendix/ecog-03750>). Appendix 1–3.