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The effect of insularity on avian growth rates and implications for insular body size evolution

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Island populations often differ in consistent ways from their mainland counterparts with respect to their ecology, behaviour, morphology, demography and life-history characteristics; a set of changes referred to as the 'island syndrome'. To understand the ecological and evolutionary drivers of the island syndrome requires characterization of suites of interacting traits. While patterns in some types of traits, e.g. body size, are well characterized across a range of taxa, key gaps remain. Growth rate is one such trait, being an important determinant of both increases and decreases in body size, and can vary with changes in predation pressure and food limitation; two factors that are known to differ between mainland and island environments. Using a phylogenetic meta-analytic approach, we characterize differences in growth rates among mainland and island altricial bird populations, controlling for environmental factors. We found a trend towards slower growth on islands in small-bodied (less than 1 kg) bird species. This is consistent with the idea that the pattern of body size increases in small-bodied island colonists is associated with the evolution of slower growth combined with shifts in age and size at maturity in relaxed predation regimes.

1. Introduction

Islands are excellent systems to study the factors that influence life-history variation, as island populations are exposed to a suite of environmental conditions that differ in predictable ways to their mainland counterparts [1]. These include lower predation pressure [2], and a shift in the balance of inter- versus intra-specific competition [3]. Indeed, these features of insular environments are often invoked to explain a series of repeated adaptations across a wide range of taxa, referred to as the 'island syndrome' [1,2,4]. In birds, changes in morphology (a tendency towards medium body size) [5] and decreased plumage dimorphism [6], behaviour (increased tameness, increased intraspecific aggression) [1,5,7], demography (increased population densities) [8–10] and life-history characteristics (a shift to a slower life-history strategy) [1,3,4,11,12] are features of the island syndrome. Slower life-history strategies are manifested in lower fecundity, increased adult survival [5], longer developmental period (the amount of time the offspring stay in the nest) and higher investment in offspring seen in island species compared to their mainland counterparts [11,13]. However, growth rate variation (i.e. the rate at which nestlings gain mass during development) has been a neglected component, despite being a key life-history descriptor in itself [14], with feedback links to other life-history variables e.g. survival [15,16]. Importantly, investigating insular growth rates may shed light on other features of the island syndrome, such as evolutionary shifts in body size [17].

Studies of continental bird species show that growth rates vary widely among species [18,19]. This variation has been attributed to a suite of biotic factors, such as nest predation risk, food limitation, clutch size, adult body size, nest type, phylogenetic relationships and biotic and abiotic factors associated with latitude [14,15,20–24]. Of these factors, nest predation risk is often considered the

predominant environmental driver of variation in growth rates across geographical regions, where selection favours faster growth rates in environments with high nest predation rates, thereby minimizing offspring mortality [21,24]. When food is limited and parental feeding rates drop, offspring growth rates may also decrease [25]. This effect can be compounded by high predation risk, as adults may make fewer provisioning trips to their offspring to reduce the chances of a predator discovering a nest [21]. However, even under such conditions, nestlings can increase growth rates, presumably through changes in resource allocation [21]. The effects of other factors include slower growth rate with smaller clutch sizes when adult survival is high [21,26]; slower growth in larger bodied species [19]; faster growth in species that have enclosed nests which decreases energy allocation needs for thermoregulation [27]; and faster growth rates in higher latitude populations with longer daylight hours [20,28].

The ‘island rule’ describes the trend for initially large-bodied species to evolve smaller body sizes on islands and initially small-bodied species to evolve larger body sizes [29], a biogeographic rule that has been of long-running interest [5,29–33]. Using a life-history approach, Palkovacs [17] theorized that the magnitude of shifts in the individual growth rate curve and the reaction norm describing age and size at maturity determine the direction and magnitude of body size shifts in island dwelling species. When release from extrinsic mortality (e.g. lower predation pressure) is the predominant driver of growth rate and age and size at maturity, body size increases are expected, as could be argued to be the case for initially small-bodied species (figure 1a). By contrast, when food limitation is the predominant driver, as may apply to initially large-bodied species, size decreases are expected (figure 1b). Central to this model, and a unified understanding of the ‘island rule’, is the prediction that growth rates on islands decrease. Slower insular growth rates in island versus mainland populations would be expected under the typical insular conditions of reduced (or absent) predation pressure in food limited environments (where intraspecific competition is high and area is limited), and where smaller clutch sizes are produced (where adult survival is high and parental investment is spread across a longer developmental period). However, this prediction hinges on the assumption that the developmental stage that nestlings achieve before fledging remains unchanged. If nestlings fledge at a later developmental stage, then growth rates themselves may be similar for island and mainland representatives [34].

Here, we examine growth rate variation across a wide range of bird species to investigate the effects of insularity on growth rates. We use a phylogenetic meta-analytic approach using data from published literature to determine the difference between growth rates of altricial birds from mainland areas and islands, controlling for the effects of latitude, clutch size, adult body size and nest type among species. We then compared variation in growth rates among islands including additional covariates of island area and isolation. Island area and isolation determine the equilibrium number of species present; small isolated islands are expected to be more depauperate than large islands close to mainlands [4]. Hence, these variables act as broad proxies for the potential for interspecific competition and predation. We ask the following questions: (i) are growth rates of insular altricial bird populations slower than mainland ones?; and (ii) are the variables that explain among-island variation in growth

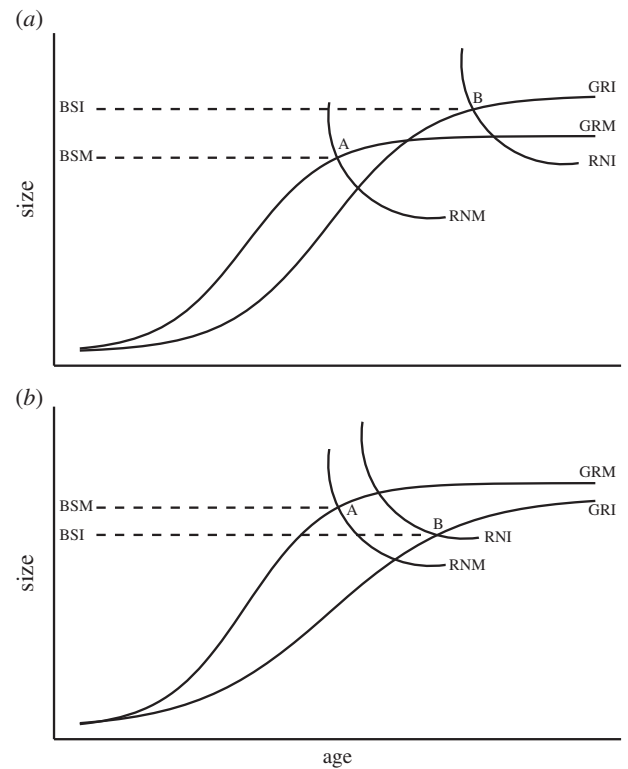


Figure 1. Theoretical prediction of avian body size changes from mainland to island environments as a product of shifts in growth rates and the reaction norm determining age and size at maturity. This is adapted from Palkovacs [17] general description of changes in adult body size on islands (BSI) compared to the mainland (BSM), but modified for avian growth rates specifically. (a) When predation release is the dominant ecological driver, the effect of reduced extrinsic mortality (shift from mainland to island reaction norm: RNM and RNI, respectively) is larger than that of lower growth rate (shift from mainland to island growth rate: GRM and GRI, respectively) resulting in increases in insular body size. (b) When food limitation is the dominant ecological driver, the effect of reduced growth rates is larger than that of reduced extrinsic mortality, resulting in smaller insular body sizes. Note that body size at maturity is determined by the intersection of the growth rate curve and the reaction norm of age and size at maturity (A and B).

rates similar in relative importance as those that explain mainland-island variation? We then discuss these findings with reference to insular body size evolution.

2. Methods

(a) Data collection

We conducted a literature search and compiled a database of nestling mass growth rates of terrestrial altricial birds covering studies published from 1910 to 2016. We first searched for publications from the Web of Science using combinations of the following keywords: ‘bird*’, ‘nestling*’, ‘offspring’, ‘growth rate*’, ‘develop*’, ‘rate*’, ‘growth’, ‘postnatal’ and ‘island’. From the resulting list of publications, we scanned the abstracts and selected all studies that mentioned descriptions of nestling growth or the species’ breeding biology. These studies were then read in more detail and growth rate estimates extracted. The bibliographies of these studies were then cross-checked for references to other studies that may contain estimates of nestling growth. Finally, we systematically searched through species accounts in three comprehensive bird handbooks that provided detailed information on growth rates (*The Birds of North America*, *Handbook of Australian, New Zealand and Antarctic Birds* and *The Birds of Africa*) [35–37].

We restricted the analyses to studies that reported growth rate values (k) estimated from a logistic model, as transformations of

these values are comparable among species [19]. k is the maximum relative growth rate (slope) at the point of inflection of a logistic curve, describing nestling weight over time, and is obtained from variations of the three-parameter Richards logistic equations (i.e. logistic, Gompertz and Von Bertalanffy) [38]. These equations describe the growth curve by estimating the asymptote (maximum weight during growth), k , and d (the age at inflection). Each of these equations fixes the inflection point at a specific percentage of the asymptote (50%, 37% and 30%, respectively), therefore to allow direct comparisons, we transformed all k constants for equivalence with the most widely used logistic equation using the method of Ricklefs [18]. We excluded studies that only reported growth in terms of grams per day, as interspecific variation in these rates is not directly comparable. Mean growth rate was averaged when reported for each sex separately. Bird Orders for which there were data of only mainland, or only island, populations were excluded from the analysis to avoid biasing the representation of growth rates among groups of species. Parasitic species were excluded from the analyses because the growth rates of their offspring vary widely depending on their host species [39]. Body size affects growth rate and the direction of insular body size evolution depends on the ancestral starting point; size reduction typically occurs if ancestral body sizes are greater than 1 kg, and size increases if less than 1 kg [29]. Hence, any trends in insular growth rate changes may be obscured if this directionality is not considered. As only 12 cases of growth rate estimation were available for birds greater than 1 kg, we restricted the analysis to birds with average adult body size of less than 1 kg.

Associated variables recorded for each growth rate were the sample size and the location, latitude of the study population, whether it was on an island or mainland, and for island populations, the distance to the nearest continent and the area of the island was log-transformed (taken from the Island Directory <http://islands.unep.ch/>) or using Google Earth if not stated in the study [40]). We excluded islands larger than 250 000 km², because of their similarity to mainland environments. For each species, mean adult body mass (grams) and modal clutch size were taken from the *Handbook of the Birds of the World Alive* (<http://www.hbw.com/>) [41], and log-transformed to conform to assumptions of normality. If mass was given for each sex, a mean was calculated. If modal clutch size was not given, average clutch size was used. Geographical coordinates were not reported in 13 cases, so were approximated from the known distribution of the species and general country or region descriptions provided in each study. We found multiple growth rates for 47 species, all of them mainland populations. When more than one growth rate was found for the same latitude, we averaged the k values and counted it as one data point in the analysis. The full dataset and code is accessible at <https://figshare.com/s/02ce3dbf88e1e3118925>. Publication bias was unlikely to affect the distribution of effect sizes of our meta-analysis because reporting growth rates is unlikely to depend on its magnitude and is not subject to statistical significance [42].

(b) Statistical analyses

We applied a Bayesian mixed effects phylogenetic meta-analytic approach [43], implemented in the package MCMCglmm [44] in R v. 3.4.0 [45] to analyse variation in growth rates (k). To test our hypothesis of the effect of insularity on growth rates, we fitted linear generalized mixed models, where we assume k to be normally distributed. First, we fitted a general model including fixed effects of insularity (i.e. mainland or island population), latitude, clutch size, body size and nest type (open or enclosed) using the entire dataset. Next, we restricted the dataset to include growth rates of island species only to investigate environmental influences on insular growth rates among island populations. We fitted a model including fixed effects of latitude, island area, distance to mainland, clutch size, body size and nest type. Both models included the random terms: study, species (to account for variation

introduced by having multiple measurements for 55 species), phylogeny (to account for similarity owing to shared evolutionary history) and measurement error (to account for variation introduced by sample size and to weight the effect sizes accordingly). The measurement errors were approximated using the inverse of the study sample size (i.e. $1/N$), following the recommendation of Hadfield *et al.* [43], as values of variance, or statistics from which it can be estimated, were reported in a very low proportion (9%) of studies. Using the taxonomy of Jetz *et al.* [46], we randomly sampled 100 phylogenetic trees from BirdTree.org (www.birdtree.org) for the 213 species included in the study using the 'Ericson All Trees' as the source. To account for phylogenetic uncertainty, we fitted the two statistical models tested over the 100 trees and extracted the mean density of the combined posterior distribution using the package mulTree [47]. We used an uninformative prior with variance, V , set to 1 and belief parameter, ν , to 0.002, for both fixed and random effects [44]. We ran two chains for 500 000 iterations, with a thinning value of 300 and a burn-in of 10 000. All models were required to have an effective sample size greater than 1000 and we checked for convergence between model chains using the Gelman-Rubin statistic, the potential scale reduction, where all models were required to be below 1.1 [48]. We considered fixed effects to be statistically significant when the 95% credible interval did not span zero. We estimated measures of goodness-of-fit by calculating marginal and conditional R^2 for each model (variance explained by the fixed effects only and that of combined fixed and random effects, respectively) according to [49].

3. Results

(a) General model

The general model assessing the effect of insularity on growth rates included 264 growth rates (231 mainland and 33 island populations) from 213 species across 198 different studies (marginal $R^2 = 0.32$, conditional $R^2 = 0.85$). There was a strong phylogenetic signal in the data (total variance explained = 35%) (figure 2). After accounting for phylogeny, significant effects were seen for latitude (faster growth at higher latitudes), nest type (faster in species with open cup nests) and adult body size (slower in larger species) (table 1). Growth rates in island species tended to be slower though the effect was marginally non-significant. Clutch size had a non-significant effect. An additional two models were tested (results not shown), one that included only mainland data and a second with a random subset of the mainland data to match the sample size of island data, to check for biases in the results owing to the larger amount of mainland data. The results of both models were qualitatively equivalent to the general model.

(b) Island model

The model included 33 growth rates from 30 species in 27 studies (marginal $R^2 = 0.52$, conditional $R^2 = 0.77$). A moderate phylogenetic signal was noted (total variance explained = 17%), and latitude had a significant positive effect (faster at higher latitudes) and adult body size a significant negative effect (slower in larger species) on insular growth rates. All other variables were not significant (table 2).

4. Discussion

Our comparative, phylogenetically controlled analysis of growth rates in altricial bird species found a trend towards slower growth rates in species that are predicted to increase

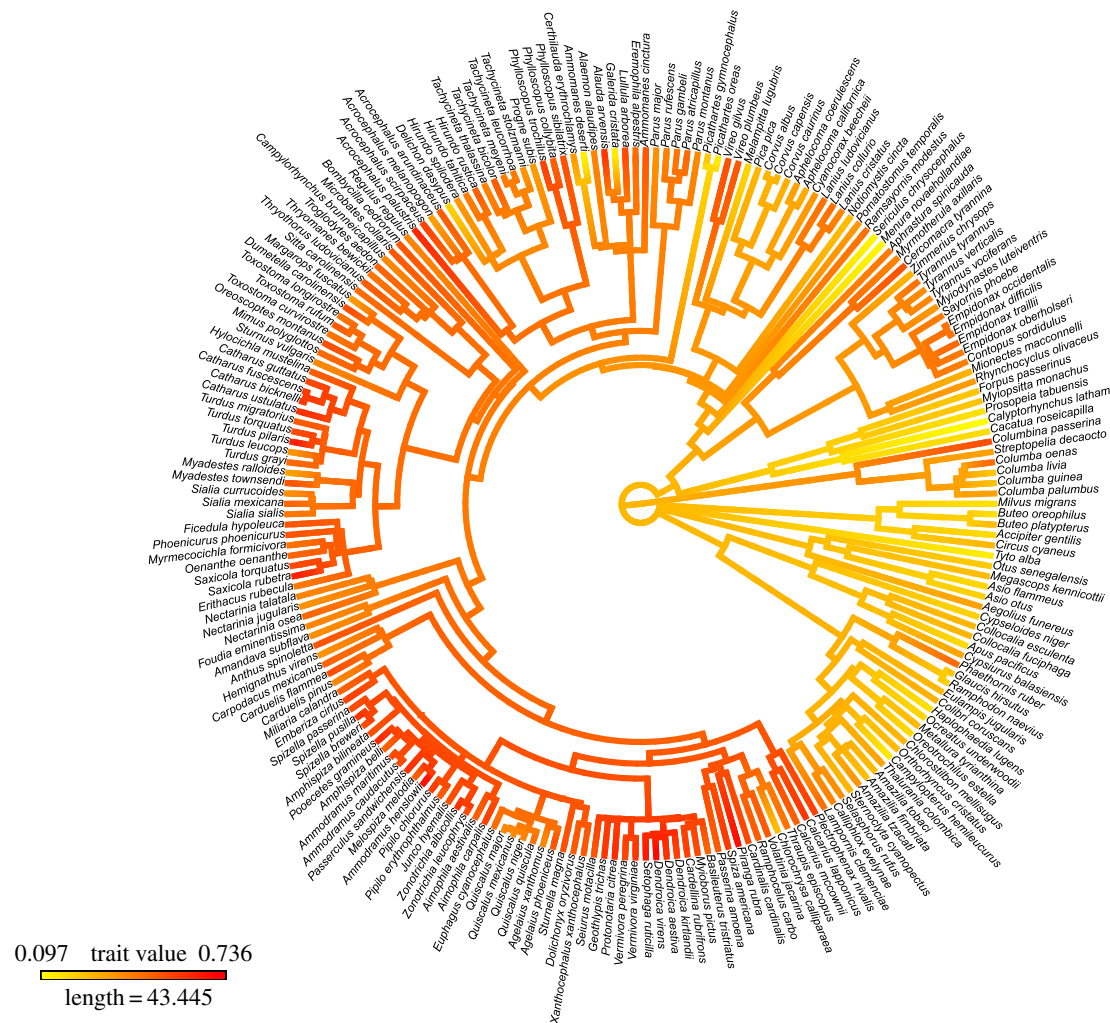


Figure 2. Growth rates (k) of 213 altricial bird species depicted on a phylogenetic tree (for methods of tree construction see [46]). Growth rates range from 0.097 to 0.736 (growth rates were averaged for species with multiple estimates) and show a strong phylogenetic signal (35% total variance explained). Dark red depicts fast growth rates and light yellow depicts slower growth rates.

Table 1. Potential predictors of growth rate variation in 213 species ($n = 264$) of altricial birds: population type (island or mainland), latitude, clutch size, adult body size, nest type (open or enclosed). (Estimates (black circles) are modal values from 100 models, and the error bars (grey shading) show the lower and upper 95% and 50% credible intervals (CI) from the 100 models.)

	estimate	lower CI	upper CI	posterior distribution
intercept	0.387	0.283	0.494	
island	-0.025	-0.055	0.007	
latitude	0.002	0.002	0.003	
log (clutch size)	0.017	-0.022	0.056	
log (body size)	-0.042	-0.054	-0.029	
nest type: open cup	0.038	0.008	0.068	
phylogenetic.var	0.005	0.002	0.014	
species.var	0.002	0.0001	0.003	
study.var	0.001	0.0001	0.002	
residual.var	0.002	0.002	0.004	

their body size in insular environments. In line with Palkovacs' [17] hypothesis, these empirical data support the idea that initially small birds achieve larger insular body sizes by

growing at a slower rate over a longer growth period, facilitated by a low predator environment. Growing at a slower rate and over a longer period allows for larger and higher

Table 2. Potential predictor of growth rate variation on islands in 30 species ($n = 33$) of altricial birds: island area, distance of the island to the mainland, latitude, clutch size, body size, nest type (open or enclosed). (Estimates (black circles) are modal values from 100 models, and the error bars (grey shading) show the lower and upper 95% and 50% credible intervals (CI) from the 100 models.)

	estimate	lower CI	upper CI	posterior distribution
intercept	0.254	0.033	0.474	
log (island area)	0.001	-0.009	0.011	
log (distance to mainland)	0.009	-0.013	0.032	
latitude	0.004	0.001	0.007	
log (clutch size)	0.074	-0.030	0.174	
log (body size)	-0.048	-0.078	-0.018	
nest type: open	-0.032	-0.086	0.0147	
phylogenetic.var	0.003	0.0002	0.018	
species.var	0.001	0.0002	0.006	
study.var	0.001	0.0002	0.005	
residual.var	0.004	0.002	0.010	

quality offspring to be produced by decreasing oxidative stress damage during development [50], decreasing the per nestling energy requirements on parents [51] and increasing the total amount of provisioning time [19]. This may translate to better survival and reproductive outcomes in high-density insular populations where intraspecific competition is likely to be elevated. Finally, assuming that the 35 island bird population growth rate estimates used in our study are a representative sample of insular altricial birds, then an increase in sample size would probably result in the significance of the insular trend to be noted.

Our finding of faster growth rates at higher latitudes, regardless of whether the dataset included all comparisons, or only comparisons among island populations, is in line with previous studies [52–54]. Increased resource availability at higher latitudes (Ashmole's hypothesis [55]), and increased daylight hours during the breeding season at higher latitudes (such that parents make greater total feeding trips to the nest) have been proposed as explanations of this pattern. More recently, Rose and Lyon [52] found that variation in daylight hours explained intraspecific latitudinal variation in growth rates and clutch size, while resource availability did not.

An inverse relationship between growth rates and adult body size has also been documented by other authors [20], however, as growth is indexed independently of body mass when calculating k [19], the cause of this relationship is difficult to determine. Remes and Martin [20] suggested this negative relationship may be because larger birds have higher survival rates [56,57] and, with increased adult survival under reduced extrinsic mortality, a lower energy expenditure on reproduction is expected [58]. Faster growth rate in open-cup nesters may be explained by higher nest predation risk selecting for faster growth to decrease nestling mortality in open- versus enclosed-nest types. However, recent findings argue that thermal benefits of enclosed nests are an important selective pressure favouring faster growth rates, and outweigh benefits of reduced nest predation risk [27]. We did not find a significant effect of clutch size, but this may be owing to the positive correlation between

clutch size and latitude, such that including both variables obscured the possible effect of clutch size on growth rate.

Comparison of growth rates among island populations showed that the effects of latitude and adult body size maintain their influence on growth rate variation in insular environments the same as on mainland populations. For body size, this suggests that particularities of insular environments which select for larger body size have also selected for slower growth rates. The lack of influence of other abiotic variables, distance to mainland or island area, on growth rates may reflect that these variables were not adequate proxies of variation in predator and competitor numbers as anticipated. A lack of support for the influence of nest type on insular growth rates may reflect the expected decrease in selective pressure from reduced nest predation risk. However, the lack of statistical significance for these variables should be interpreted with caution as it may be owing to the modest number of island growth rates rather than there being no effect.

It is important to mention that the high variability in the quality of reporting growth rates and associated data meant that close to half of the studies we found were excluded from this meta-analysis. Most studies published after Ricklefs' influential paper [59] report estimates of k , and thanks to the work done by Ricklefs [28], Oniki [60] and Starck and Ricklefs [14] calculating k from previously published raw growth data, many more species were able to be included in this study. However, a large number of studies that expressed growth in grams per day without enough detailed data to be reanalysed to estimate k still remain. Furthermore, an important aspect that led to excluding many studies that did report k was not reporting any type of variance statistic or sample size, when at least one is needed for weighting effect sizes in meta-analyses. To improve the comparability of growth rates in future studies, we encourage researchers to report all growth curve parameters together with a measure of their variance. Finally, Tjørve and Tjørve [61] have developed a 'Unified' family of models to describe growth patterns, improving upon the traditional logistic,

Gompertz and von Bertalanffy models, that the authors argue produce the most realistic estimate of growth parameters. The adoption of this new family of models would greatly improve the quality and comparability of growth rate statistics. Finally, a useful extension of this study would be to perform a pairwise comparison of growth rates of island species and their closest mainland relative when sufficient data become available.

Our study highlights the biogeographic and taxonomic gaps that limit our ability to form a more nuanced understanding of variation in altricial avian growth rates, particularly where it relates to the island rule. Growth rate estimates were predominantly from the Order Passeriformes, with only a moderate representation from five other Orders. Island population growth rate estimates were surprisingly under-represented in the literature. Hence, whether the tendency for slower growth in insular birds noted in the sample used in our study can be generalized to a wider range of bird Orders, and for bird species that evolve towards smaller insular sizes, remains to be established. Because of the significant negative relationship between adult body sizes and growth rate seen here and in other studies [19,20], one might predict that species which undergo size reductions on islands may have faster growth rates compared to their mainland counterparts. However, such a response may be countered by food limitation

imposed by space restriction and lower species diversity on islands [36]. Furthermore, as more growth rate data become available, our understanding of the effects of insularity on growth rates would benefit from additional analyses comprising intraspecific comparisons between mainland and island populations. Finally, more empirical information is needed to understand how reduced predation versus reduced resource availability on islands shapes variation of avian growth rates across species and hence how this will translate into body size changes across a broad range of species.

Data accessibility. The datasets used in the full and island mixed models, including references to the original studies, phylogenetic trees and the code to run the analysis are available in the electronic supplementary material.

Authors' contributions. E.M.S. performed data collection, data analysis and writing of the first draft of the manuscript. T.C. conceived the idea behind the study and edited the manuscript. S.M.C. contributed to the development of the ideas and methods behind the study and to the writing of this manuscript.

Competing interests. We declare we have no competing interests.

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