EVOLUTIONARY BIOLOGY

Convergent evolution toward a slow pace of life predisposes insular endotherms to anthropogenic extinctions

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Island vertebrates have evolved a number of morphological, physiological, and life history characteristics that set them apart from their mainland relatives. However, to date, the evolution of metabolism and its impact on the vulnerability to extinction of insular vertebrates remains poorly understood. This study used metabolic data from 2813 species of tetrapod vertebrates, including 695 ectothermic and 2118 endothermic species, to reveal that island mammals and birds evolved convergent metabolic strategies toward a slow pace of life. Insularity was associated with shifts toward slower metabolic rates and greater generation lengths in endotherms, while insularity just drove the evolution of longer generation lengths in ectotherms. Notably, a slow pace of life has exacerbated the extinction of insular endemic species in the face of anthropogenic threats. These findings have important implications for understanding physiological adaptations associated with the island syndrome and formulating conservation strategies across taxonomic groups with different metabolic modes.

INTRODUCTION

Many phenomena differentiate islands from mainland ecosystems, including the evolution of unique organisms, whose suites of distinctive features are commonly referred to as the island syndrome (*1*). This syndrome encompasses evolution toward intermediate body size (*2*, *3*) and many other distinctive adaptations in insular vertebrates, including a distinctive type of locomotion (*4*, *5*) and smaller brains (*6*–*9*) in large mammals and smaller flight muscles (*10*) and larger brains (*11*) in island birds relative to their continental counterparts. Many of these traits are related to energy costs and, consequently, are closely associated with the metabolic rate. For example, an enlarged brain requires an uninterrupted energy supply and thus has increased energy demand, whereas flightlessness and a decrease in muscle mass reduce metabolic expenditure (*10*–*13*). Ultimately, the metabolic rate reflects the energy cost of organisms undergoing phenotypic evolution as well as physiological adaptation when facing environmental change (*14*, *15*). Accordingly, along with changes in demography, behavior, morphology, and life history, predictable evolutionary shifts in the metabolic rate may occur in island species under convergent selective pressures.

Ecological strategies and the individual traits that define them, including life history, diet, and habitat breadth, show extraordinary diversity across vertebrates. Species can maximize their fitness using these strategies to adapt to changing environments and successfully sustain effective populations (*16*–*18*). Consequently, the ecological strategy adopted by a species may influence its vulnerability to extinction, as it dictates how well the species is able to withstand the threats to which it is exposed (*17*). Energy metabolism is usually thought to evolve in parallel with life history to determine the pace of life and predicts a taxon-specific optimal body mass in island mammals (*16*, *18*–*20*), potentially serving as an additional key component shaping the ecological strategy. However, the mechanisms by which the metabolic rate and life history traits can co-evolve likely differ between endotherms and ectotherms. While endotherms can maintain a stable internal body temperature despite fluctuations in the ambient temperature, ectotherms are markedly reliant on external temperatures and generally display a slower pace of life than endotherms (*21*, *22*).

On islands, vertebrates are expected to shift toward slower life history strategies and low energy expenditure in response to environmental stability and high intraspecific competition, such as low resource availability, low interspecific competition, and low predation (*23*–*25*). Of these, limited food resource decreases metabolic rates and population sizes, which increases the probability of population extinction in island endotherms, so endotherms are replaced by ectotherms in some small islands (*23*, *26*). However, the generality of evolutionary change toward a slow pace of life on islands remains a subject of debate, as it has only been verified in selected taxonomic groups (*27*, *28*) and in individual living or extinct taxa, such as black-tailed deer (*29*), the Balearian mouse goat (*30*), the Sicilian dwarf elephant (*31*), and the Ryukyu dwarf deer (*32*), sometimes with conflicting evidence (*33*, *34*). Furthermore, the relationship between metabolism and ecological strategies has not been investigated across insular species and different metabolic modes.

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In the present study, a large-scale dataset of metabolic rates from 2813 species of tetrapod vertebrates was used, including 695 ectotherms (38 island species; 5.47%) and 2118 endotherms (193 island species; 9.11%) (Fig. 1A), to determine whether there is a universal rule for the pace of life in island species across various metabolic modes. Notably, we compiled data on the ecology (body mass, generation time, litter/clutch size, environmental temperature, diet breadth, and insular endemism) and anthropogenic extinction risk of these species to quantify evolutionary relationships between their metabolism and life history strategies and to evaluate whether there was a substantial association between their metabolic rates and vulnerability.

RESULTS AND DISCUSSION
Universality of the slow pace of life in island endotherms
The scaling exponent of mass-metabolism allometric relationships ranges from 0.64 to 0.88 across vertebrate classes (Amphibia, Reptilia, Aves, and Mammalia) (*35*, *36*), which made it difficult to select a single value appropriate for controlling for allometry in the present analyses. Therefore, this study used relative metabolic rates (RMRs) scaled by body mass (residuals; see Materials and Methods). It was found that endemic island endotherms have lower RMRs than other endotherms (Fig. 1B and fig. S1). These results were robust and held when accounting for phylogenetic dependence [phylogenetic generalized least square (PGLS) analysis of variance (ANOVA), $P < 0.001$], although mammals exhibited a strong phylogenetic effect (fig. S1A and table S1). The trend toward a slow pace of life was not observed in island ectotherms (Fig. 1B and fig. S1). Using a Bayesian phylogenetic mixed model (BPMM) revealed a strong effect of insularity on the RMRs of endotherms after controlling for migratory behavior and locomotion mode [$\beta = -0.037$, credible interval (CI) = -0.057 to -0.016, and Particle Markov Chain Monte Carlo (pMCMC) < 0.001; $n = 2118$; table S2]. Conversely, the effect of insularity on the RMRs of ectotherms was not significant ($\beta = -0.026$, CI = -0.110 to 0.062, and pMCMC = 0.514; $n = 695$; table S2). Our approach based on RMRs allows to account for differences in mass-metabolism allometric relationships between ectotherms and endotherms and interclass. However, intraclass or other taxonomic differences may also occur. For instance, reptiles are characterized by steeper metabolic scaling than that of amphibians and scaling exponents vary across clades of each class (*35*, *37*), which might contribute to explain the absence of notable insularity effects on RMRs of ectotherms in our analyses.

Therefore, we further accounted for the effect of allometry by using the absolute metabolic rate as an alternative response variable and body mass as explanatory variable to produce qualitatively identical results ($\beta = -0.043$, CI = -0.063 to -0.020, and pMCMC < 0.001; $n = 2118$; Fig. 1C and table S2). We also compared the RMRs of island-mainland sister species and found that 75.65% of endemic island endotherms (146 species) reduced their RMRs relative to their closest mainland counterparts ($\beta = -0.062$, CI = -0.088 to -0.035, and pMCMC < 0.001; $n = 193$; Fig. 1D, fig. S3, and table S3), while less than half of the ectotherms exhibited this pattern. Moreover, we still found that island endotherms had lower absolute metabolic rates compared to mainland species when controlling for body mass and considering intraspecific variation by adding random effect specification in MCMCglmm based on a new dataset of intraspecies basal metabolic rates ($\beta = -0.077$, CI = -0.13 to -0.029, and pMCMC < 0.001; $n = 3328$ individuals from 391

endothermic species; table S4). These findings indicate that the lower RMRs observed in insular endotherms cannot be attributed to an increase in body size. Furthermore, these results corroborate those of PGLS ANOVA and BPMM across the complete dataset, suggesting a convergent shift toward low metabolic rates in endotherms, but not in ectotherms.

The evolution of distinct pace of life trajectories in island vertebrates with different metabolic modes is likely influenced by their different thermoregulation strategies, parental care strategies, phenotypic plasticity, and cognitive abilities. Island ectotherms not only do not converge toward a slow pace of life, as endotherms do, but they lack a general pattern altogether. This mirrors, at a larger scale, previous findings in island lizards with different reproductive strategies, encompassing a spectrum of taxa shifting either toward a slow or a fast pace of life (*38*). In some island endemics, such as fruit pigeons and pteropodid bats, a decrease in energy expenditure was observed relative to their continental relatives (*39*). Although the present study found a robust overall trend toward low metabolic rates across island endotherms, the effect of insularity on RMRs was still stronger in some clades (including Anseriformes, Columbiformes, Gruiformes, Trochilidae, Charadriiformes, Passeriformes, and Chiroptera) than in others (fig. S2). Furthermore, both evolutionary change and phenotypic plasticity resulting from ecological and physiological response might have had an effect on this shift, although we accounted for intraspecific variation of metabolism in our analyses. This variability in the effect of insularity on metabolism across endotherms parallels that observed in relation to other features of the island syndrome related to energy costs, such as changes in brain size (*11*, *40–42*).

Ecological mechanisms underlying the evolution of metabolic rates on islands
Many studies posit that the metabolic rate is a crucial physiological indicator affecting the diet, development, genome size, life history strategy, and environmental adaptation of an organism (*43–49*). In the present study, BPMMs were used to investigate correlations between metabolic rates and life history traits while evaluating the effect of insularity and accounting for other variables that define ecological strategies, such as diet and temperature (see Materials and Methods for descriptions of the predictor variables). Temperature, in particular, has long been recognized as a key driver influencing the evolution of metabolic rates (*50*, *51*). Although results of the multipredictor models used in this study showed a significant relationship between environmental temperature and metabolism across vertebrates with different metabolic modes (pMCMCs < 0.001; Fig. 2A and table S5), the overall effect of temperature on RMRs was negligible (Fig. 2A).

These models also indicate that generation length has a significant negative effect on RMRs in all tetrapod vertebrates, and that body mass negatively affects the RMRs of birds, but not those of ectotherms (pMCMCs < 0.05; Fig. 2A and table S5). The RMRs appear to be decoupled from generation length variation in insular mammals and ectotherms (Fig. 2B). This was in contrast to the observations of mainland mammals and ectotherms, and mainland and insular birds, for which the RMR typically showed a negative relationship with this life history trait and might reflect variation in the mechanisms underpinning the island syndrome in different clades of vertebrates. In accordance with the broader results on endotherms (*39*), this study found that insular birds evolved a slower
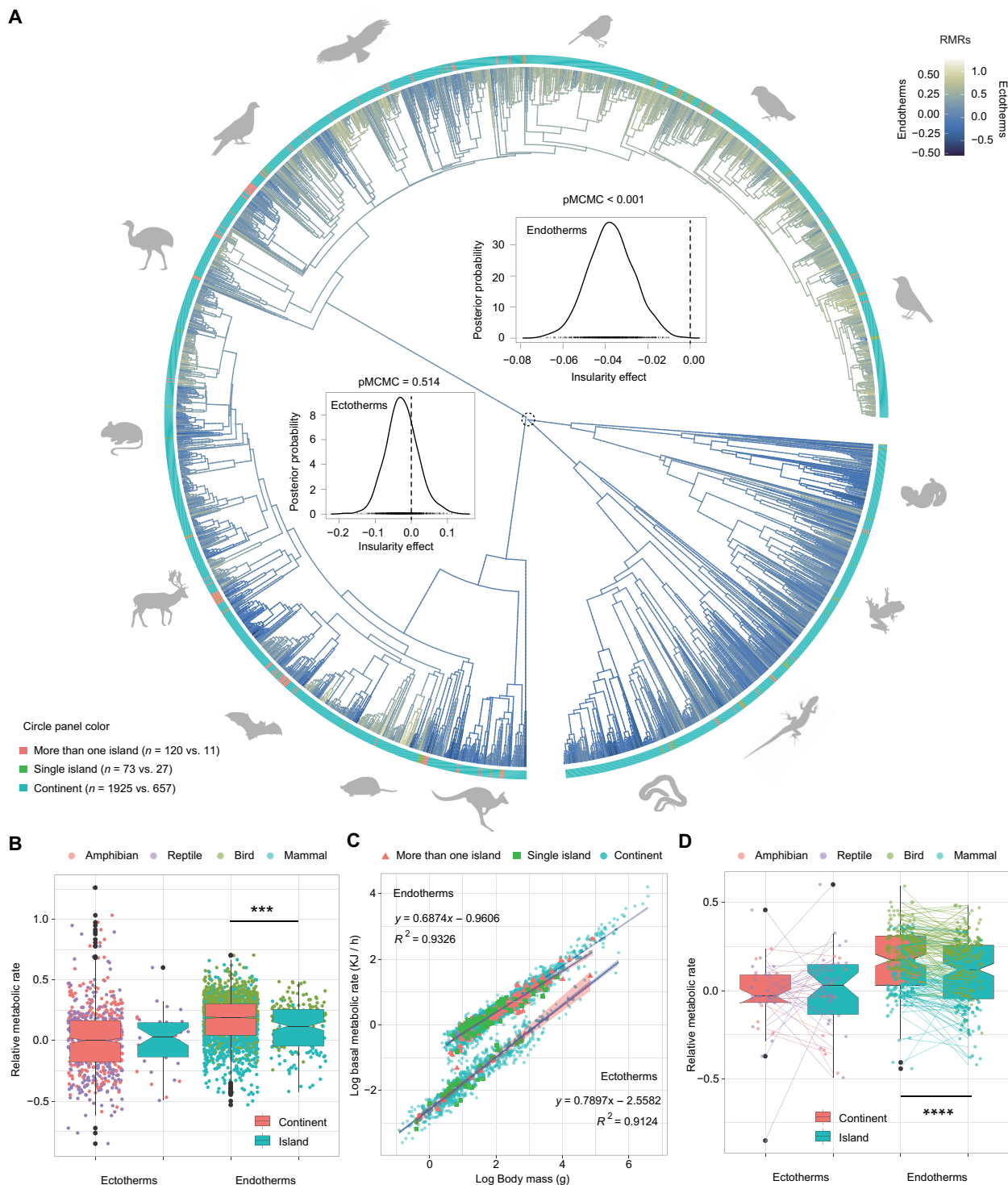
Fig. 1. Mapping of RMRs across the vertebrate tree of life and metabolic differences between mainland and island species. (**A**) Ancestral reconstruction of RMRs and phylogenetic distribution of island and mainland species. Histograms represent the posterior samples of the BPMM models, showing a strong effect of insularity on RMRs across endotherms, but not across ectotherms. The colors in the circular panel represent species from multiple islands, a single island, or the mainland. (**B**) Island endotherms, but not ectotherms, have relatively lower metabolic rates than their mainland counterparts. (**C**) The effect of allometry on metabolism. A clear regression of body mass-metabolism for insular endotherms plots below that of continental species. (**D**) A sister-taxa analysis confirms the trend of slow metabolic rate in island endotherms. Boxes denote the 95% lower and upper confidence limits. The black solid circles indicate outliers in (B) and (D). Black asterisks represent statistically significant differences under PGLS ANOVA. Symbols: ***$P < 0.005$ and ****$P < 0.001$. Silhouettes have been adapted from PhyloPic images (http://phylopic.org/) and are available under a CC-BY 4.0 license (https://creativecommons.org/licenses/by/4.0/).
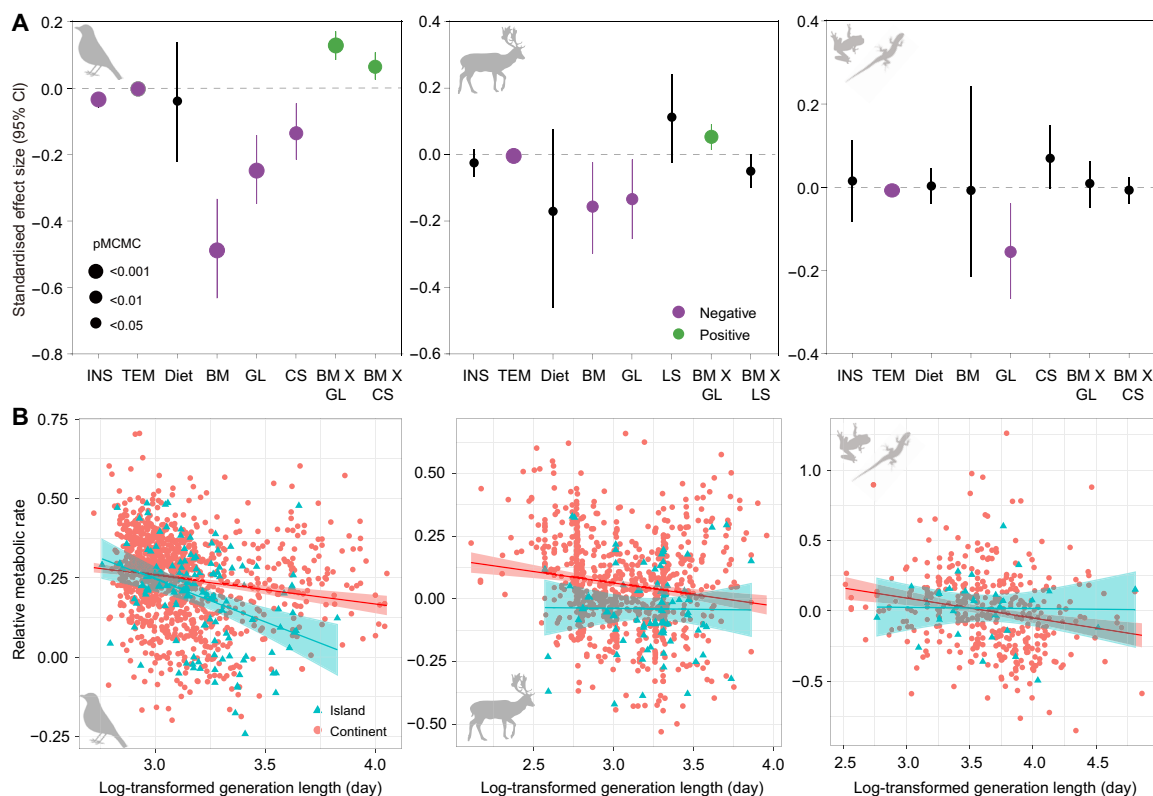
Fig. 2. Predictors of RMRs in endotherms. (**A**) Coefficient estimates from a multipredictor BPMM predicting variation in RMRs among bird ($n = 1227$), mammal ($n = 871$), and ectothermic ($n = 437$) species. Color-filled circles indicate mean standardized effect sizes and lines denote 95% CI. Purple-filled and green-filled circles show predictors with significant (pMCMC <0.05) negative and positive effects, respectively. INS, insularity; TEM, annual mean temperature; BM, body mass; GL, generation length; CS, clutch size; LS, litter size. (**B**) Relationships between selected predictor variables and RMRs in insular and continental endotherms. Solid lines indicate linear trend estimates, and color shading indicates SE bands. Silhouettes have been adapted from PhyloPic images (http://phylopic.org/) and are available under a CC-BY 4.0 license (https://creativecommons.org/licenses/by/4.0/).

metabolism than their continental counterparts independent of other predictors ($\beta = -0.034$, CI $= -0.058$ to -0.011, and pMCMC < 0.001; Fig. 2A and table S5). In particular, birds with longer generation length were found to be characterized by lower RMRs on islands than on continents (Fig. 2B and table S5).

Together, the results of BPMMs suggest that ecology and life history traits interact in complex ways to influence the evolution of metabolism on islands. Notably, allometric relationships are an important component of these dynamics. Specifically, this study found that the effect of clutch size on the RMRs of birds and the impact of generation length on the RMRs of birds and mammals were size-dependent (pMCMC < 0.05; Fig. 2A). To disentangle the cause-and-effect relationships between the selected predictor variables and how these variables affect the pace of life of insular species, phylogenetically controlled path analysis was then performed (*52*).

This study compared nine candidate path models (fig. S4) and found the best-supported causal scenarios [models with the lowest *C* statistic information criterion with a correction for small sample sizes (CICc); see Materials and Methods] for birds, mammals, and ectotherms (Fig. 3). In the best model obtained for birds (CICc = 37.6 and $P = 0.883$), insularity directly and negatively affected the RMRs (path coefficient $= -0.27$; Fig. 3A). Island living also indirectly affected the RMRs through decreases in the annual mean temperature

(path coefficient $= -0.16$; Fig. 3A). A negative correlation was identified between the body mass and the RMR (path coefficient $= -0.17$; Fig. 3A), indicating an alternative pathway to insularity. According to the model, bird insularity influences dietary strategies, possibly via resource limitation, and drives the evolution of longer generation lengths, indicating a shift toward a slow pace of life (path coefficients $= 0.25$ and 0.17 for diet and generation length, respectively; Fig. 3A). Although dietary items had no direct effect on RMRs, limited food resources likely directly affected RMRs in island birds, as reported (*23–25*).

The best supported causal scenario for mammals (CICc = 48.5 and $P = 0.104$) showed that island living had a direct negative effect on RMRs (path coefficient $= -0.14$; Fig. 3B). Moreover, it was found that the effect of insularity on the RMR was indirectly mediated by temperature (path coefficient $= -0.19$; Fig. 3B). Living on islands is linked to greater generation lengths in mammals (path coefficient $= 0.09$; Fig. 3B), as in birds. These results suggest that low metabolic rates associated with island living influence the evolution of long generation length or lead to longer generation length through affecting physiological responses (e.g., low free radical–induced damage to cells) in endotherms (*53*). In addition, results of path analysis, in accordance with those of BPMMs, confirm the important role of body mass in modulating the relationship between metabolism and life history,
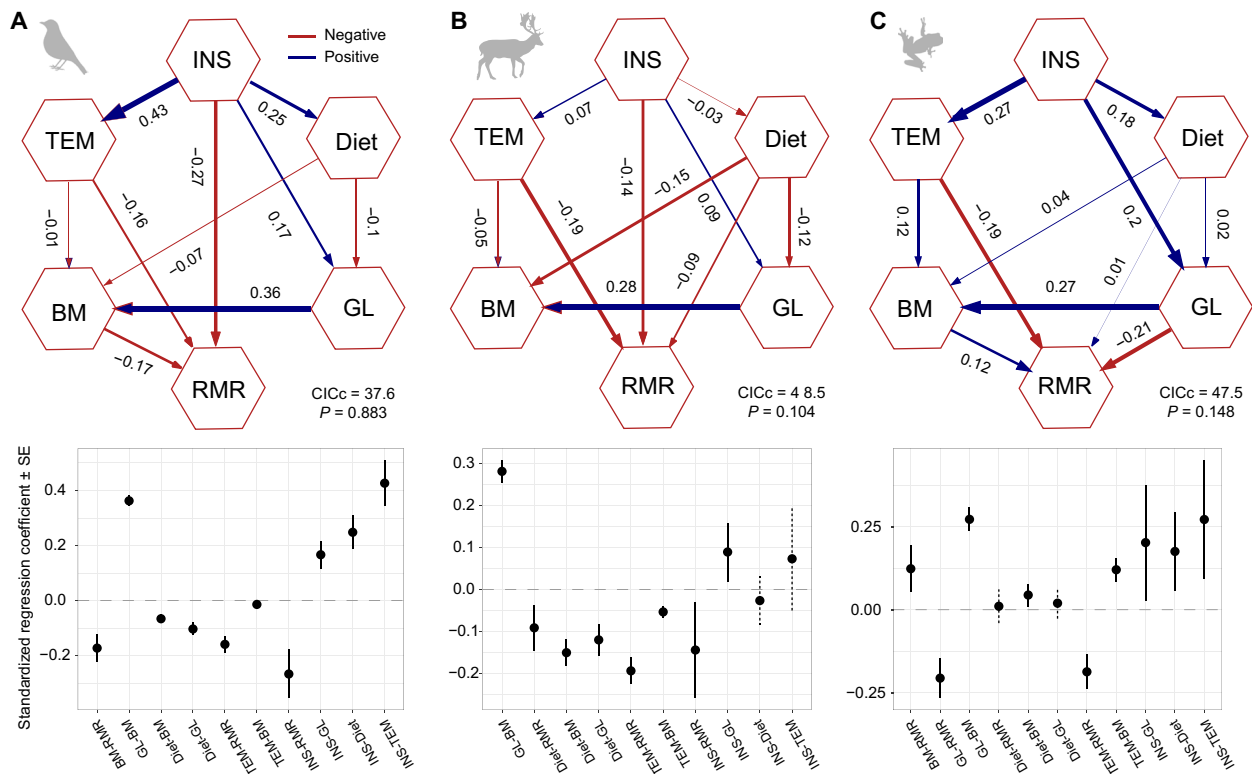
Fig. 3. Causal mechanisms behind changes in RMR on islands. (**A**) Birds ($n = 1227$). (**B**) Mammals ($n = 871$). (**C**) Ectotherms ($n = 437$). Arrows point to the response variables of the underlying regression models and their widths are proportional to the log-transformed standardized regression coefficients, with significant coefficients (95% confidence intervals significantly different from 0) represented by full lines. Decimal values representing untransformed coefficients are displayed above the arrows. Panels below show standardized regression coefficients with SEs for each path model. BM, body mass; GL, generation length; INS, insularity; TEM, annual mean temperature. $P > 0.05$ indicates that the model fits the data. Silhouettes have been adapted from PhyloPic images (http://phylopic.org/) and are available under a CC-BY 4.0 license (https://creativecommons.org/licenses/by/4.0/).

following the metabolic theory of ecology (*44*), but their causal effects on each other need further testing.

Notably, the path analysis showed no association between RMRs and insularity in ectotherms, in contrast to the findings in endotherms (Fig. 3C). Nevertheless, there was an alternative pathway mediating the negative effect of insularity on RMRs due to the annual mean temperature and generation length (path coefficients = −0.19 and −0.21 for temperature and generation length, respectively; Fig. 3C). In addition, insularity was found to positively affect diet breadth and influence the evolution of generation length (path coefficients = 0.18 and 0.2 for diet and generation length, respectively; Fig. 3C). Cold climate is connected with increased body sizes and high metabolic rates of vertebrates, following Bergmann's rule and metabolic theory (*44*, *54*). Islands usually have stable environmental climates, which causes a generally indirect effect on the low RMRs through environmental temperature across ectotherms and endotherms.

The island rule predicts small-species gigantism and large-species dwarfism on islands and is universal across vertebrates, although less evident in amphibians (*3*, *55*). Metabolism has long been linked to body mass (*44*), and thus, it would be anticipated that changes in metabolic rates on islands would mirror the island rule pattern. Conversely, this study found different effects of insularity on the metabolic rates of endotherms and ectotherms and marked differences in the relationships between metabolism and life history in these two groups.

Therefore, different metabolic processes might underlie convergent body mass evolution in island vertebrates with different thermal characteristics. The results emphasize the contextual nature of insular changes in metabolic rate, which are an integral part of a comprehensive set of adaptations associated with the island syndrome.

High anthropogenic extinction risk associated with low metabolism on islands

Irrespective of the generality of a slow pace of life syndrome in island vertebrates, low metabolic rates might influence the vulnerability to extinctions of these taxa. This study tested this hypothesis using data from the International Union for Conservation of Nature (IUCN) Red List (*56*) in addition to PGLS and phylogenetic logistic regressions. Two binary extinction variables were defined by classifying species as nonthreatened and threatened. It was found that threatened endotherms were characterized by lower RMRs on islands and on the mainland (Fig. 4A). Conversely, threatened ectotherms exhibited significantly lower RMRs only on islands (PGLS, $P = 0.028$ and $n = 34$; Fig. 4A and table S7). The RMR was significantly and negatively associated with the probability of being threatened in endotherms and ectotherms, and insular species were generally more vulnerable to extinction compared to mainland species with the same RMRs ($P = 0.007$ and 0.042 for island endotherms and ectotherms, respectively; Fig. 4B and table S8).
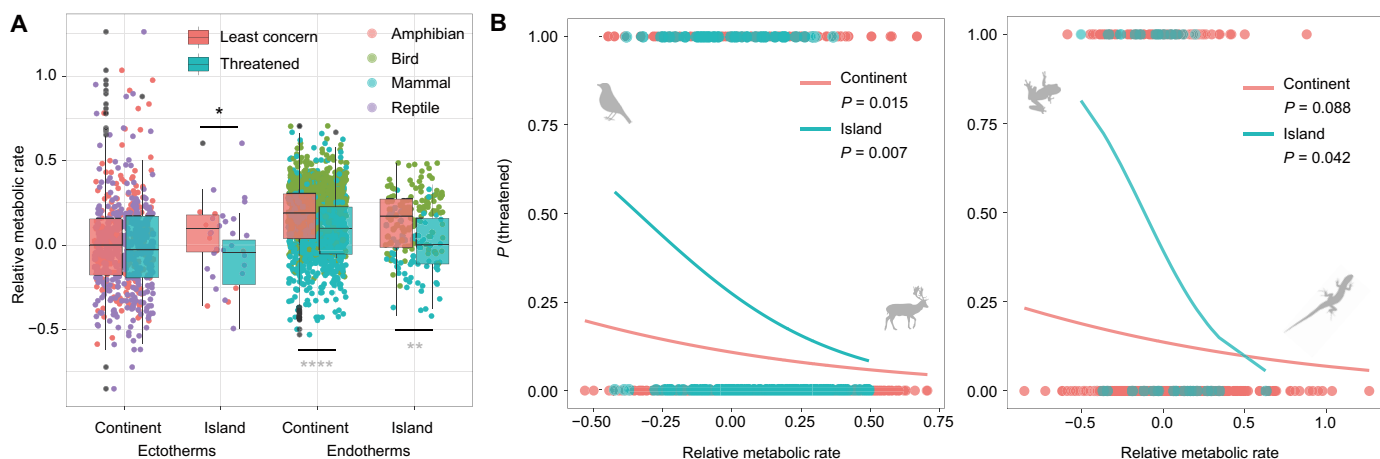
Fig. 4. Anthropogenic extinctions risk and RMR. (**A**) Island species with slower metabolic rates face higher extinction risk. Gray and black asterisks represent statistically significant differences under PGLS ANOVA and ordinary *t* test, respectively. (**B**) Relationships between RMR and probability of being threatened in endotherms and ectotherms. Symbols: *$P < 0.05$, **$P < 0.01$, ***$P < 0.005$, and ****$P < 0.001$. Silhouettes have been adapted from PhyloPic images (http://phylopic.org/) and are available under a CC-BY 4.0 license (https://creativecommons.org/licenses/by/4.0/).

Island endemic species have faced widespread extinctions since the Late Pleistocene (*3, 57*). The primary causes of these extinctions are directly or indirectly related to human activities and include the introduction of invasive species, habitat loss, resource overexploitation, and climate change (*58*). Large-bodied, flightless, ground-nesting species and species that have experienced more extreme body size shifts relative to their mainland counterparts have been disproportionally affected by these extinctions (*26, 59–62*). The results of the present study indicate that a slow pace of life is another factor predisposing island vertebrates to anthropogenic extinctions. This is in agreement with previous studies highlighting the important role of life histories in prehistoric extinctions of continental and insular mammals (*63*) and the association between a slower reproductive rate and a higher extinction risk in extant large mammals (*64*). While morphological changes such as dwarfism and gigantism have likely driven island extinctions via facilitating direct overexploitation and predation by introduced species (*62*), shifts toward a slow metabolic strategy and life history may, in parallel, negatively affect species resilience through slowing down recovery following disturbance. Furthermore, low mass-specific metabolic rate and long generation time are related with reduced population growth rates, which have been reported to contribute to high extinction probabilities (*65*).

In summary, the present study shows that island endotherms tend to have a slower pace of life than their continental close relatives across a comprehensive group of 2813 vertebrate species. The findings support the hypothesis, derived from empirical evidence and evolutionary theory, which suggests that the pace of life in vertebrates with different metabolic modes is influenced by trade-offs between the energy costs of living on islands, generation length, and environmental variation. Although physiological adaptations toward a slow pace of life, along with other evolutionary innovations, may increase the fitness of insular species in response to ecological release and resource limitation in pristine island environments, these adaptations may also increase vulnerability to extinction after human colonization. This research advocates for the potential application of traits associated with the island syndrome to enhance the conservation of remaining island species. In particular, it is suggested that conservation prioritization of insular species should consider metrics of physiological divergence relative to mainland forms, alongside metrics of evolutionary history and morphological change.

MATERIALS AND METHODS
Insular terrestrial vertebrates
The geographical occurrences of species were extracted from the spatial data provided on the IUCN red list website (http://iucnredlist.org) for amphibians, reptiles, and mammals and from BirdLife International for birds (http://datazone.birdlife.org/home). It was then determined whether each species in the dataset was continental or an island dweller. Species that occurred only on islands and not on continents were classified as endemic insular tetrapods. Islands were defined as land masses disconnected from continent and surrounded by water, larger than 1 km^2 in area and smaller than Greenland (*66*).

Metabolic data
Basal metabolic rates were compiled from the literature (see data S1) and were converted to kilojoule per hour from the oxygen consumption rates by using 1-ml O_2 = 20.083 J. The metabolic rates of ectotherms depend on the ambient temperature, which usually does not reach the vicinity of 40°C, near the body temperature of endothermic species. Therefore, the metabolic rates measured at different ambient temperatures were converted to the metabolic rates at 25°C according to the equation reported by White *et al.* (*35*)

$$q_{25} = q \times Q_{10}^{\frac{25-TC}{10}}$$

where q is the standard metabolic rate at the ambient temperature (kilojoule per hour), *TC* is the environmental temperature (°C) at which measurements were taken, and Q_{10} is a constant used for temperature normalization, where $Q_{10} = 2.21$ and 2.44 for amphibians and reptiles, respectively. We normalized the metabolic rate to 25°C according to the Boltzmann-Arrhenius principle (*67*). Although the Boltzmann factor correction for temperature between the body mass and the metabolic rate is more appropriate than the

Q_{10} factor in ectotherms (*35*), there is an extremely close correlation between the metabolic rates obtained using the van't Hoff and Boltzmann-Arrhenius principles (fig. S5). Therefore, the results obtained using the van't Hoff principle were used to perform the following analyses.

The temperature of 25°C was selected for two reasons. First, this temperature represents tropical forest habitats, where the diversity of life forms is the greatest, especially for ectotherms (*68*). Second, the temperature of 25°C is often in the thermoneutral zone, where basal metabolic rates are measured in endotherms (*35*). Birds and mammals have a stable body temperature and reach a lowest oxygen consumption at thermoneutral zone that is basal metabolic rates. Therefore, no temperature adjustments of metabolic rates were performed for endotherms. Last, a large dataset of metabolic rates was obtained from 2813 species of tetrapod vertebrates, comprising data on 1239 birds, 879 mammals, 401 non-avian reptiles, and 294 amphibians.

There are general allometric relationships between body mass and many traits, such as brain size, metabolic rate and egg mass (*11, 47, 69*). Here, two methods were used to control for the effect of body mass in our analyses, in agreement with previous studies (*11, 47, 69*). First, the absolute metabolic rate was retained as an alternative response variable and body mass was used as an explanatory variable in the models. Second, we obtained RMRs (residual basal metabolic rates) by regressing the log-transformed basal metabolic rates against the log-transformed body masses using PGLS. RMRs were extracted to conduct all downstream analyses. In particular, to account for the effects of body mass on metabolic rate separately in endotherms and ectotherms, we defined RMRs using the respective residuals from log-log PGLS regressions of the absolute metabolic rate against body mass in the two groups. We performed the residual analyses for ectotherms and endotherms separately because endotherms with the same body mass exhibit higher metabolic rates than ectotherms. We also obtained RMRs (=residuals) from four different log-log PGLS regressions (one for each class) to evaluate the potential effect of inter-class differences in mass-metabolism allometry on our analyses (see table S9). In addition, to account for further taxonomic heterogeneity in mass-metabolism relationships, we conducted comparisons between island-mainland sister species. As mentioned previously, we obtained similar results using these different methods. Nevertheless, we acknowledge that differences in metabolic scaling may exist not only between endotherms and ectotherms and interclass but also intraclass, and we discussed their potential effect on our results (see Results and Discussion).

Phylogenetic analyses

A comprehensive time-calibrated species-level phylogenetic tree was used for each extant vertebrate clade. For birds, this study used a fully resolved tree overlaid on the Hackett backbone from the Bird Tree projects (*70*) for the 1239 species in the dataset. For all species of mammals in the dataset (*n* = 879), this study used a phylogenetic tree from Upham *et al.* (*71*) that consisted of a robust evolutionary timescale comprising approximately 6000 living species. For squamates, a fully sampled phylogenetic tree from Tonini *et al.* (*72*) was used for 359 species. For amphibians, a phylogenetic tree from Jetz and Pyron (*73*) was used for the 294 species in the dataset. We randomly extracted 1000 fully resolved trees for each clade from these supertrees, and TreeAnnotator (*74*) was applied to construct a maximum clade credibility tree with a burn-in of 10% of the sampled trees. Trees for turtles and crocodiles were obtained from Thomson

et al. (*75*) and Oaks (*76*), respectively. A combined tree for endothermic and ectothermic taxa was constructed using the divergence dates of each clade according to the Time Tree of Life (http://www.timetree.org) (*77*). PGLS ANOVAs were used to assess differences in RMRs between insular and mainland species.

Ancestral state reconstruction

To determine the nodes where transitions between metabolic modes occurred on the tree, we performed the maximum likelihood reconstruction of continuous traits to RMRs across endothermic and ectothermic trees. Ancestral states were reconstructed using the fastAnc function, and the results were mapped using "phytools" and "ggtree" (*78, 79*).

Bayesian phylogenetic mixed model

BPMMs were applied to test whether island species had slower metabolic rates than mainland species, as implemented in the MCMCglmm R package (*80*). In all cases, an inverse-Wishart prior ($V = 1$ and $v = 0.002$) was used. Each model was run for 1,010,000 iterations with a burn-in of 100,000, and chains were sampled every 1000 iterations. After running the models, the autocorrelation between samples and the model was tested to ensure that it was <0.1; otherwise, the thinning intervals and the final number of iterations were increased to obtain 1000 samples. The parameter estimates obtained from models were presented as the posterior mode and the 95% lower and upper CIs of the posterior samples. The model specifications are detailed in the supplementary tables.

To verify whether RMRs were lower in island species compared with their closest continental species, BPMMs were used between sister-species comparisons. Three models were set for endotherms and ectotherms. First, the RMR was set as a function of insularity. Second, the RMR was the response variable, and the body mass category (above or below the median) and insularity were explanatory variables. Third, the body mass category was included as a response variable with insularity. In addition, BPMMs of the log-transformed body mass as a function of island species were performed to test whether there were body mass differences between island species and their closest continental taxa.

In addition, although basal metabolic rate represents the baseline energy expenditure to maintain basic physiological functions, it still exhibits phenotypic plasticity. We compiled a new dataset of intraspecies basal metabolic rates to investigate phenotypic plasticity and evolutionary change. This dataset included 3328 individuals from 391 endothermic species (2093 samples from 74 bird species and 1235 individuals from 317 mammal species) and 1732 samples from 238 ectothermic species (773 individuals from 111 amphibians and 959 individuals from 126 reptiles) (see data S1). Of these, there were 156 samples from 24 island endothermic species and 205 individuals from 16 island ectothermic species. We performed phylogenetic generalized linear mixed models through adding random effect specification in MCMCglmm to account for intraspecific variation.

The relationships between RMRs and predictors across species were assessed by using BPMMs in MCMCglmm to fit RMRs as the response variable, with six variables (insularity, annual mean temperature, diet, body mass, generation length, and clutch/litter size in birds and mammals) and the interaction between life history traits and body mass as predictors.

Life history, environmental factors, dietary items, and locomotion modes

We separately obtained data for three life history traits (body mass, litter or clutch size, and generation length) from endotherms and ectotherms using the amniotes database (81), AmphiBIO (82), and other literature (see data S1). These traits reflected the life history components and maximized the number of species with a complete set for endotherms and ectotherms. To obtain nuanced information, analyses of individual life history traits in phylogenetically controlled mixed models were performed separately (table S5). The models suggested that the individual traits (body mass and generation length, but not litter or clutch size in mammals and ectotherms) had a stronger effect size on RMRs. Therefore, this study used the body mass and generation length related to RMRs to perform phylogenetically controlled path analysis.

The present-day geographical occurrences of tetrapod species were obtained at a resolution of 0.5° from the IUCN red list website for amphibians, reptiles, and mammals and from BirdLife International for birds. These two websites contain polygons with precise information on the distribution of the species. Some species had no range polygons in the IUCN red list, and the annual mean temperature was extracted according to each occurrence from the Global Biodiversity Information Facility (http://www.gbif.org) after removing outlier data. Last, these data were combined, and each occurrence was overlapped with layers of climate factors from WorldClim (http://worldclim.org) at a 2.5–arc min resolution to calculate the mean values (83). Some marine mammals that live and reproduce entirely in marine environments were excluded, such as dolphins and whales. For marine species that breed on land, including turtles and seals, this study obtained the mean temperatures of breeding sites.

For birds and mammals, dietary items were classified into 10 types and percentage of each type ranged from 0 to 100 (84). The first component was captured from dietary principal component analysis (84). For amphibians and reptiles, food items were obtained from published data (82, 85). Locomotion modes were classified as flying (e.g., most birds and Chiroptera), swimming (e.g., penguins, whales, seals, sea turtles, and Urodela), bipedal/jumping (e.g., bipedal: flightless birds and kangaroos; jumping: frogs), quadrupedal (e.g., most mammals, reptiles, and amphibians), and legless (e.g., snakes and caecilians). To run the BPMM models in table S2, we classified the locomotor modes of ectotherms into 1 (quadrupedality in mammals), 2 (bipedality in birds and mammals), and 3 (flight/swimming in birds and mammals). In ectotherms, locomotor modes were defined as 1 (swimming in turtles), 2 (jumping in frogs), 3 (legless in snakes and caecilians), and 4 (quadrupedality in reptiles and amphibians).

Phylogenetic path analysis

This study examined hypothesized causal effects in the connections among insularity, RMRs, life history, temperature, and dietary niches using phylogenetic path analyses implemented in the phylopath package (86). Phylogenetic path analyses can estimate the most likely evolutionary pathways through assessing the direct and indirect effects among candidate variables and allow the testing of alternative models of presumed relationships by estimating the magnitude of these effects, such as the path coefficients and overall model fit (87). This method can combine PGLS with the d-separation method (52) to test for the most likely relationships in the data.

We constructed nine relevant models of the relationships among these variables by assuming that each variable has only one path to each of the other variables (fig. S4). We then tested a set of conditional independencies by calculating Fisher's C statistic (88) for each path model based on the d-separation method combining P values of underlying PGLS models. We further calculated CICc and CICc weight to rank the path models and assess their probability. On all plausible models, the proposed causal model fits our data, then P value is more than 0.05 for the C statistic and the model has the lowest CICc value, which represents the final best supported path model (table S6).

In our models, we assumed that changes on BM, RMR, and GL are the results of adaptation to island living and we mainly explored relationships among insularity, RMR, other life history traits and ecological factors. Of these, RMR is a central result from island living and is affected by other life history traits and ecological characteristics, although in turn, RMR can influence them through altering some physiological processes (such as cell oxidative damage) and adaptive plasticity.

Phylogenetic logistic regressions

The extinction analysis by its very nature (due to being in the Anthropocene) mostly looks at the vulnerability of species to human-caused extinction. To assess connection between RMRs and anthropogenic extinctions, we estimated the proportion of threatened species using two binary response variables. In particular, we obtained the threatened levels from IUCN Red List (56), which provides the category of anthropogenic extinctions for each species including least concerned (LC), near threatened (NT), vulnerable (VU), endangered (EN), critically endangered (CR), extinct (EX), extinct in the wild (EW), and data deficient (DD). Anthropogenic extinction risk was evaluated according to the percentage of species threatened with categories critically endangered, endangered, and vulnerable. We grouped species as nonthreatened including LC and NT or threatened including CR, EN, and VU in our database. Phylogenetic logistic regressions were fitted to investigate the anthropogenic extinction risk of tetrapod vertebrates from their RMRs using the package sensiPhy (89).

Supplementary Materials

This PDF file includes:
Figs. S1 to S5
Tables S1 to S9
Legend for data S1

Other Supplementary Material for this manuscript includes the following:
Data S1

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