nature ecology & evolution

Article

https://doi.org/10.1038/s41559-022-01967-w

Increases in intraspecific body size variation are common among North American mammals and birds between 1880 and 2020

Received: 28 August 2022

Accepted: 29 November 2022

Shilu Zheng [1], Juntao Hu [1], Zhijun Ma [1], David Lindenmayer [2] & Jiajia Liu [1,3]

Many studies have documented the average body size of animals declining over time. Compared to mean body size, less is known about long-term changes in intraspecific trait variation (ITV), which is also important to understanding species' ability to cope with environmental challenges. On the basis of 393,499 specimen records from 380 species collected in North America between 1880 and 2020, we found that body size ITV increased by 9.59% for mammals ($n = 302$) and 30.67% for birds ($n = 78$); human-harvested species had higher probability of ITV increase. The observed increasing ITV in many species suggests possible niche expansion and potential buffering effects against downsizing but it risks increased maladaptation to rapidly changing environments. The results demonstrate that trait mean and variance do not necessarily respond in similar ways to anthropogenic pressures and both should be considered.

Species morphological traits have been experiencing rapid shifts due to global environmental change in the past centuries[1,2]. This includes the general shrinkage of animal body size that has been widely reported in mammals, birds, fishes and invertebrates[2–4]. Theory predicts that smaller individuals have stronger ability to dissipate heat via a larger body surface area to volume ratio relative to larger individuals[5]. Thus, warming-induced selection is considered as one of the most prominent drivers of animal body size decline[6]. In addition, disproportionate harvesting of large individuals by humans is also driving a rapid decline in animal body size, especially in commercially exploited species[7]. Such downsizing trends have far-reaching consequences on individual fitness[8], which could disrupt trophic interactions[3] and further affect human welfare[2]. However, most studies to date focused on the long-term changing trends of average value of morphological traits[1,2,9], leaving trait variation within species unexplored.

The importance of intraspecific trait variation (ITV) has increasingly been acknowledged in ecological and evolutionary studies[10,11]. ITV is part of the raw material on which natural selection acts; higher ITV implies greater niche breadth and may provide a species with improved chances of persistence in variable environments[10]. For example, variability in life-history traits was found to be negatively associated with extinction risk in mammals[12]. Bird species with higher behavioural plasticity were at a lower risk of extinction than more conservative species[13]. Although beneficial for population sustainability in the face of uncertain and instable conditions, high ITV also implies inaccurate sensing of environmental cues (for example, bet-hedging strategies), which can jeopardize species mean fitness in the short term[14]. In summary, ITV is associated with species resilience under changing environmental conditions, providing complementary information in addition to species trait means. However, long-term ITV trends across species are unclear.

Directional shifts in ITV will be observed if there is disproportionate change in intraspecific trait distribution[11]. As predicted by the niche reduction hypothesis, species will either escape from, or have high mortality under, new environmental threats, leading to a reduction in realized niche breadth and associated decreases in ITV[15]. For

---

[1]Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, National Observations and Research Station for Wetland Ecosystems of the Yangtze Estuary, School of Life Sciences, Fudan University, Shanghai, China. [2]Fenner School of Environment and Society, The Australian National University, Canberra, Australian Capital Territory, Australia. [3]Institute of Eco-Chongming, Shanghai, China. ✉e-mail: liujiajia@fudan.edu.cn

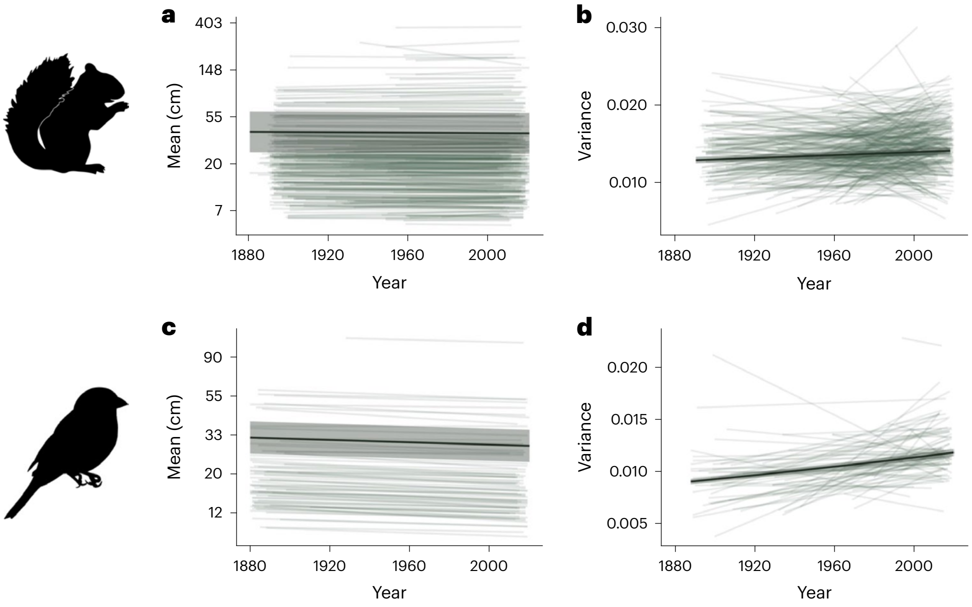

Fig. 1 | Changes in mean and intraspecific variation of body size over time. **a**–**d**, Fitted dark lines are the mean (± s.e.) of model predictions from LMMs (Supplementary Table 2) for mean (**a**,**c**) and ITV (**b**,**d**) of body size using 379,158 individuals representing 302 mammal species (**a**,**b**) and 14,341 individuals representing 78 bird species (**c**,**d**). Light green lines are predictions from species-specific linear models for each species. Credit: Silhouettes are from http://phylopic.org/ (xgirouxb[squirrel], Andy Wilson[bird]; https://creativecommons.org/licenses/by/3.0/).

example, ivory poaching has led to the rapid evolution of tusklessness in African savanna elephants (*Loxodonta africana*)[16]. Alternatively, species can cope with changing environmental conditions with adaptive or plastic responses, developing new trait values and increasing ITV. For example, in Australia, the shortest wing length has declined in the grey-crowned babbler (*Pomatostomus temporalis*) and jacky winter (*Microeca fascinans*) under climatic warming without the loss of long wing trait features[4]. Given adequate resources and an absence of natural predators, species adapted to urban environments may experience relaxed selection on body size, leading to an increase in ITV[17]. Moreover, in the face of unpredictable environmental changes or new threats, species may adopt a bet-hedging strategy, developing new trait values randomly to spread the risk of extinction under unpredictable conditions[18].

Importantly, species will differ in ITV temporal trends if the strength of selection varies among species with regard to human-related features and species inherent traits. For example, human-exploited species have been experiencing disproportional loss of trait values because of selective hunting, such as the preference for harvesting large-bodied fishes in fishery[19], which will have cascading effects on the dynamics of ITV[20]. In addition, as predicted by Bergmann's rule, larger-bodied species are more negatively affected by rising temperatures than are smaller-bodied species[21,22] and large body size extremes within larger-bodied species may experience stronger selection pressure than that in smaller-bodied species. Thus, larger-bodied species will be more likely to exhibit trait truncation and decreasing ITV. Because ITV is associated with species ability to persist in the face of new environmental challenges[12,13,23], non-random ITV changing trend across species will have far-reaching consequences on community restructuring and altering ecosystem functioning[3,24].

Here, we compiled individual-level body size data for mammal and bird specimens collected from 1880 to 2020 in North America, based on the VertNet database (http://vertnet.org). The compiled dataset included 302 mammal species and 78 bird species, representing 33.0% and 4.0% of the total number of known species in North America for each taxon, respectively (Supplementary Note). We chose these two groups because they had sufficient specimen records across a relatively long period, with species-level information available in multiple online databases. In this study, we first sought to determine long-term trend of body size ITV in mammals and birds and to assess the relationships between species ITV temporal changing trends and human activity as well as species inherent traits. Specifically, we evaluated six variables that have been suggested to be closely associated with intraspecific trait distributions and thus are possible covariates with ITV changing temporal trends: human harvest of the species, species ability to use artificial habitat, body mass, habitat breadth, generation length and litter/clutch size (Methods).

Results

We compiled head-to-tail length data from 379,158 mammal specimens representing 302 species and 14,341 bird specimens representing 78 species collected in North America between 1880 and 2020 (Supplementary Table 1). As predicted by linear mixed effects models (LMMs), we found that mammal body size decreased by an average of 3.13% ($n = 302$; slope (s.e.) = -2.27×10^{-4} (0.06×10^{-4}); $P < 0.001$; Fig. 1a and Supplementary Table 2) and bird species decreased by 10.11% over the past ~140 yrs ($n = 78$; slope (s.e.) = -7.62×10^{-4} (0.14×10^{-4}); $P < 0.001$; Fig. 1c and Supplementary Table 2). In contrast to downsizing, intraspecific variation in body size, as calculated using Bao's coefficient of variation[25], exhibited a significant increase in both groups (Figs. 1 and 2 and Supplementary Table 2), with no significant difference of ITV changing trend between females and males found in both mammals and birds ($P > 0.1$; Supplementary Table 3). Specifically, as predicted by LMMs, ITV increased by an average of 9.59% for mammals ($n = 302$; slope (s.e.) = 7.05×10^{-4} (0.87×10^{-4}); $P < 0.001$; Fig. 1b and Supplementary Table 2) and 30.67% for birds ($n = 78$; slope (s.e.) = 2.03×10^{-3} (0.04×10^{-3}); $P < 0.001$; Fig. 1d and Supplementary Table 2). In mammals, 62.9% of the species (190 out of the 302 species) showed increasing ITV, among which Aztex mouse (*Peromyscus aztecus*) and *Myotis nigricans* had the highest ITV increasing rate (Supplementary Table 1), while 75.6% of the bird species (59 out of the 78) showed increasing ITV, among which brown creepers (*Certhia americana*) and collared sand martin (*Riparia riparia*) had the highest body size ITV increasing rate (Supplementary Table 1).

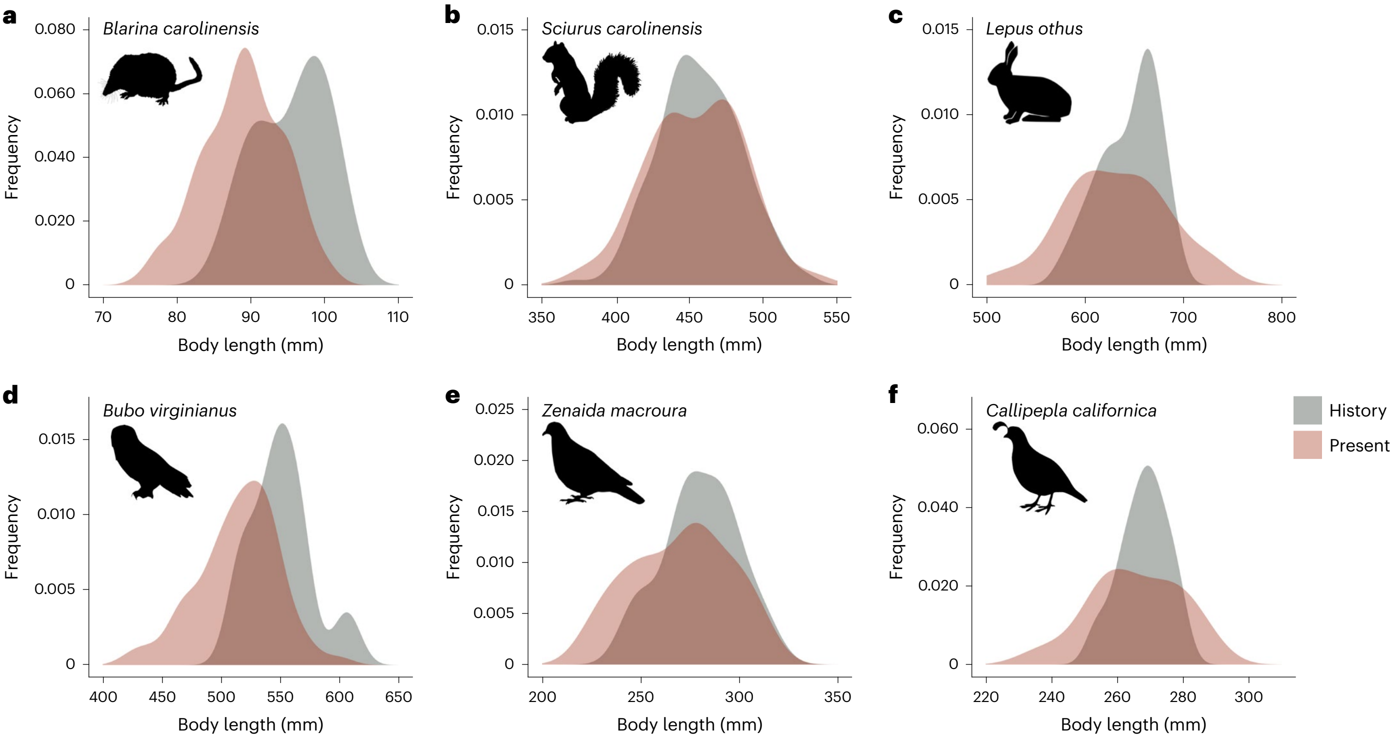

Fig. 2 | Examples of body size intraspecific distribution change from history to present. a–**f**, In downsizing species with increasing ITV, examples of three types of trait frequency distribution change are shown here, including the creation of new small extremes with the loss of large values (**a**,**d**); the creation of new small extremes without the loss of large values (**b**,**e**); and the creation of new trait extremes at both ends of trait distribution (**c**,**f**). Density plots show intraspecific trait distributions in history (grey areas) versus at present (red areas). Specifically, examples show trait distributions of *Blarina carolinensis* during 1947–1957 ($n = 15$) versus 2007–2017 ($n = 151$) (**a**); *Sciurus carolinensis* during 1893–1903 ($n = 148$) versus 2003–2013 ($n = 97$) (**b**); *Lepus othus* during 1969–1979 ($n = 58$) versus 2004–2014 ($n = 21$) (**c**); *Bubo virginianus* during 1960–1970 ($n = 10$) versus 2004–2014 ($n = 68$) (**d**); *Zenaida macroura* during 1973–1983 ($n = 13$) versus 2008–2018 ($n = 49$) (**e**); and *Callipepla californica* during 1895–1905 ($n = 23$) versus 1985–1995 ($n = 24$) (**f**). Credit: Silhouettes are from http://phylopic.org/ (Becky Barnes (**a**), Andy Wilson (**b**), xgirouxb (**c**,**d**), Ferran Sayol (**e**,**f**); https://creativecommons.org/licenses/by/3.0/).

As species differed in ITV changing trend in either direction (increasing versus decreasing ITV over time) and magnitude (how fast a species has increased in ITV over time or ITV increasing rate), we further assessed covariates associated with interspecific differences of ITV changing direction and magnitude. Using phylogenetic LMMs, we found that human activity was a main driver of increasing ITV. Relative to species not exploited by humans, mammal and bird species subject to human harvesting had a higher probability of increasing ITV (positive changing direction; $P = 0.059$ for mammals, $P = 0.068$ for birds; Fig. 3 and Supplementary Table 4). ITV of human-harvested bird species also increased faster than that of birds free from human exploitation (larger ITV changing magnitude; $P = 0.031$). In addition, mammal species that are capable of using artificial habitats had larger ITV increasing magnitude during the study period ($P = 0.058$). We also found that species inherent traits were associated with mammal ITV change patterns. Specifically, greater body mass was associated with higher probability of species experiencing decreasing ITV over time ($P = 0.035$; Fig. 3 and Supplementary Table 4); ITV of species with smaller litter size was more likely to increase ($P = 0.010$) and increased faster during the studied period ($P = 0.012$; Fig. 3 and Supplementary Table 4). For the 78 studied bird species, however, species inherent traits were not associated with ITV changing trend ($P > 0.1$).

Discussion

While body size shrinkage has been widely reported as a general pattern in response to recent environmental change[2,6], ITV trend and its relative contributions to animal responses remain elusive. By analysing ~400,000 mammal and bird specimen records from 302 mammal and 78 bird species in North America, we found that body size ITV increased by 9.59% for mammals and 30.67% for birds from 1880 to 2020. Moreover, human-harvested mammal and bird species had a higher probability of experiencing increasing ITV but larger-sized mammal species and species with larger litter size had a higher probability of experiencing decreasing ITV. Our results suggest that niche expansion could be a general trend across many mammals and birds in North America in the face of environmental change in the recent century, emphasizing the potential of species to cope with new environmental challenges. We suggest distinct but complementary roles between ITV and trait means and provide better understanding of the species ability to persist under rapid global change.

Increasing ITV is driven by the emergence of individuals with new body size extremes within species. Typical examples include the extension of trait distribution in the same direction as trait mean shifts, with (Fig. 2a,d) or without (Fig. 2b,e) the loss of trait extremes at the other end of trait distribution. Several studies have reported that directional trait shifts were accompanied by the creation of new trait extremes in the same direction of selection on trait means[4,8,26]. For example, the smallest body sizes were found to decrease (new body size values) within wild animal populations along with averaged body size decline, due to a warming-driven trophic mismatch[8] or hunting-driven early maturation[26]. In contrast, new trait extremes can be produced in the opposite direction of selection on trait means (Fig. 2c,f), such as in species adopting bet-hedging strategies in highly stressful or unpredictable environments[18]. For example, obligate avian brood parasites were found to choose more diverse hosts (increasing ITV in host selection behaviour) with increasing temperature variability[27], creating new trait values randomly.

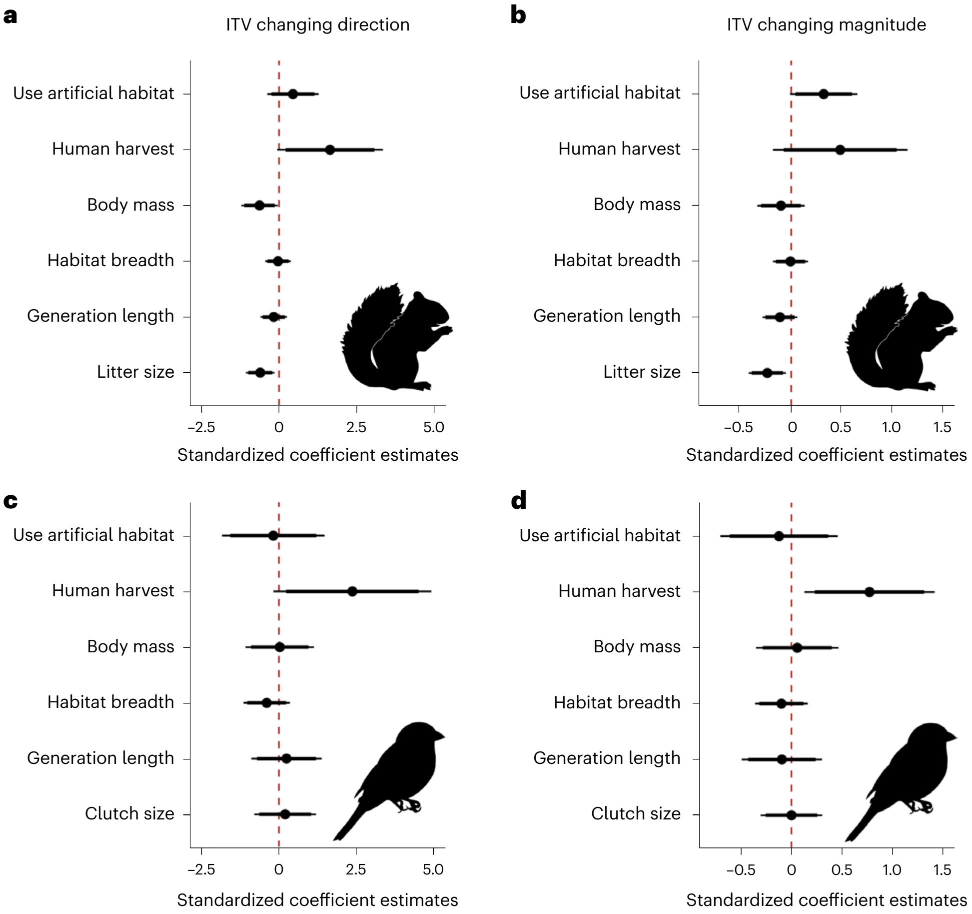

Fig. 3 | Drivers of interspecific differences in body size ITV changing trend. **a**–**d**, Relative effects of species-specific features on changing direction (**a**,**c**) and magnitude of body size ITV (**b**,**d**) over the recent 140 yr. Centres (dots) represent standardized coefficient estimates with 95% (thin segments) and 90% (thick segments) confidence intervals in phylogenetic LMMs (Supplementary Table 4) for mammals ($n = 302$) (**a**,**b**) and birds ($n = 78$) (**c**,**d**). Credit: Silhouettes are from http://phylopic.org/ (xgirouxb[squirrel], Andy Wilson[bird]; https://creativecommons.org/licenses/by/3.0/).

The creation of new trait extremes alone is not sufficient to explain the increasing ITV pattern we observed if there is rapid trait truncation at the other end of the trait distribution. This also suggests that individuals with old trait values still persist or at least the rate of trait loss is slower than that of new trait creation (Fig. 2a,d), such as in systems where the selection pressure was non-lethal for old trait values. For example, in polar bears (*Ursus maritimus*) with averaged body size shrinkage in response to warming, the smallest individuals were becoming smaller (the creation of new trait extremes) while large individuals survived (the retaining of old trait values)[28].

Although ITV has increased in many North American mammal and bird species, we found that species can differ in magnitude and direction of ITV changing trend, with human activity as a main driver of increasing ITV. These results add to the finding that human activity is not only a vital driving force in species-averaged trait shifts[7] but it is also influencing species trait distribution, in particular ITV[17,29]. For example, increasing body size ITV has been found in fishery systems because 'cautious' fishes can escape from size-selective harvesting and grow to a large size (thereby the retaining of old trait values), while more small-bodied fishes were produced under harvest pressure[26]. After being protected from human harvesting, loggerhead turtles (*Caretta caretta*) had more successful small-bodied first-time nesters producing individuals with small body size[30]. The increasing frequency of small-bodied turtles has driven declined ITV of the loggerhead turtle population.

Body size ITV trends were also associated with species inherent traits. We showed that large-bodied mammal species were more likely to have decreasing ITV and possibly a narrowing niche in the face of environmental change than were small-bodied species. Similarly, large-bodied species were found to be more affected by size-based selection such as climate warming and had a faster decline rate in body size than smaller species[3,21]. Moreover, litter size was negatively associated with ITV changing trend in mammals, implying that large litter size may accelerate trait truncation, resulting in increasing probability of declining ITV over time. As ITV is associated with species niche breadth and the ability to persist under new environments or threats[10,12,13], such non-random ITV changing trend across species will further affect winner–loser replacement in communities and alter ecosystem functioning[3,24].

Theory predicts that high trait variation can provide alternative strategies for species response to environment change. Increasing frequency of rare trait values can contribute to adaptive potential in new conditions and reduce extinction risk in rapidly changing environments[12]. Therefore, the observed increasing ITV pattern should be a positive signal, offering many species a higher chance of persistence in the face of new environmental challenges. For example, male Túngara frogs (*Physalaemus pustulosus*) from urban populations developed more sexually attractive calls made at higher rates and greater complexity than did forest frogs[31]. Increasing ITV in calls allowed Túngara frogs to expand their niche breadth from natural forests to urban habitats. In cases of adaptive responses, the retention of old trait values can secure the ability of shrinking species to rebound to the initial trait structure if selective forces are mitigated[29]. In addition, increasing ITV can indicate successful conservation efforts, such as those for European lobsters

(*Homarus gammarus*). For this species, individuals within protected areas and free from harvest pressure have increased in body size compared to individuals in unprotected locations which have undergone harvest-driven downsizing; ITV has therefore increased in European lobsters across protected and unprotected areas[32].

However, increasing ITV has costs. High ITV implies increasing probability of maladaptation, with increasing trait variance potentially driven by inaccurate sensing or prediction of environmental cues in unpredictable and fluctuating conditions or the disruption of developmental processes under new environmental stressors[33]; both of which will decrease species-averaged fitness in a short term[14,34]. In addition, new trait values may be maladapted and associated with reduced fitness. For example, warming-induced bill shortening in the red knot (*Calidris canutus*) compromised individual fitness due to diet change because birds with short bills had to feed on shallowly buried low-quality seagrass rhizomes instead of deeply buried high-quality bivalve prey[8]. Human-generated resources can be an important driver of new trait values in wild animals, with alternative food opportunities provided by people increasing diet variability[35,36]. However, a strong influence of human-generated resources on animal traits might be an 'evolutionary trap'. Both the quantity and quality of these resources are controlled by humans and can change quickly and unpredictably, raising extinction risk for species attempting to adapt to these new resources[37]. For example, during the COVID-19 outbreak and restricted tourism, animals that relied on food provided by tourists suffered from starvation[38].

Our study has some limitations. First, our work was based on specimen collections, with possible sampling bias due to geographical and seasonal preferences of specimen collectors[39]. Second, we analysed specimen records only at a continental level in North America but body size ITV changing trend may vary across biogeographic realms and scales. Third, due to limited trait data in the specimen dataset, we assessed only 302 mammal species and 78 bird species in North America. Relative to the total number of known species in North America (916 mammal species and 1,962 bird species[40]), our taxonomic coverage was limited (see the detailed risk of bias assessment according to the ROBITT procedure[41] in the Supplementary Note). Moreover, our conclusion was biased towards non-threatened species in North America and the increasing ITV pattern may not be universal among all species, especially among those at high risk of extinction and/or experiencing population decline[15]. Thus, it is critical for future studies to assess long-term ITV trends in a broader taxonomic and geographical coverage. Finally, mechanisms underlining intraspecific trait structure change and cascading effects on population dynamics remains unclear and elucidating them will require explicit and long-term monitoring of specific populations.

We have discovered an increased ITV pattern in many North American mammal and bird species between 1880 and 2020. Our results suggest that niche expansion could be a general trend across many species in the face of environmental change in the past century, emphasizing the potential for species to cope with environmental challenges. Increasing ITV and the retention of large-bodied individuals indicate possible buffering effects against average body size decline, which can potentially mitigate negative ecological impacts from downsizing on local ecological processes. With larger species having higher probability of showing a decreasing ITV, however, such buffering effects will be limited as larger species have been found to have faster downsizing rates[21]. Conversely, increasing ITV comes with a possibility of maladaptation and fitness decline. With increasing unpredictability of environmental change[42], it is reasonable to expect that a bet-hedging strategy and an increase in ITV will be increasingly common across species. During this process, some species may fail to switch between strategies and species extinction risk could be elevated[43]. Thus, it is critical to include trait variance in addition to trait means, to provide a clearer understanding of species responses to rapid environmental changes.

Methods

Data compilation

We used museum specimen datasets from the VertNet database to obtain individual-level body length (head-to-tail length) data of mammals and birds collected between 1880 and 2020. We used body length as the measure of body size because it is highly correlated with body mass[44], has implications for individual fitness[8] and has been measured for many specimens in VertNet datasets. We acknowledge that body mass is a more direct measure of body size. However, body mass measurements are highly variable in regard to the level of dehydration when the specimen is being weighed and the season when the specimen is being collected, yet such information was not available for most of the specimen records. Therefore, we considered that body length measurements were more reliable compared to VertNet body mass data. To control for data quality, we first removed records lacking species identification information or collection date and location (at continental level). Taxonomic information for each species was checked and modified following the taxonomy in VertLife (accessed in November 2021). As we focused on wild populations, records from laboratory or zoo animals were excluded. To minimize the influence of ontogenetic differences, records classified as non-adult were excluded. At this stage, the dataset included a total of 435,527 mammal specimens representing 367 species and 16,081 bird specimens representing 88 species. Second, we removed anomalous measurements differing by >20% from the median body size value in the dataset for each species (7.8% mammal specimen records and 2.4% bird specimen records were removed). We note that specimen records without life stage information were included in the data subset before removing anomalous measurements and suspected non-adult records were then removed as anomalous measurements. To obtain sufficient trait measurements and minimize bias in calculating ITV, we extracted species with more than ten valid measurements of total body length at every 5, 10 or 15 yr interval, depending on the number of records across the years (Supplementary Table 1). Only species with sufficient data spanning at least a 20 yr range were retained for further analysis, leaving a total of 400,234 mammal specimens representing 347 species and 15,178 bird specimens representing 81 species. Within this dataset, 95.7% of mammal specimens ($n = 382,849$) and 97.4% of bird specimens ($n = 14,791$) were collected from North America. To minimize bias in calculating ITV due to different sampling geographical scales, we excluded records from outside of North America. Finally, we re-evaluated data sufficiency for ITV calculation with above criteria, leaving a total of 379,158 mammal specimens representing 302 species and 14,341 bird specimens representing 78 species for subsequent analysis (Supplementary Table 1).

To assess drivers associated with ITV changing trend (direction and magnitude), we compiled two groups of variables: human-related features (human harvest of the species and species ability to use artificial habitats) and species inherent traits (body mass, habitat breadth, generation length and litter/clutch size). Specifically, hunter preference for large-sized individuals can either increase ITV if hunting was not lethal for all large individuals with more small individuals produced or decrease ITV due to directional selection and trait truncation under intensive harvest pressure[29]. Moreover, species that can use artificial habitats will have higher increasing rate of ITV than natural habitat specialists due to potential relaxation of selection with adequate food resources and an absence of natural predators[17].

As for species inherent traits, we considered body mass, habitat breadth (the number of suitable habitats), generation length and litter/clutch size as four variables possibly associated with ITV changing trends. As large-bodied species have been found to be more affected by changing selective pressure on body size compared to small-bodied species[21], we expected that large-bodied species would have a higher probability of experiencing a loss of large-bodied individuals and decreasing ITV. In addition, habitat breadth or the ability to use diverse habitat is strongly related to species niche breadth, which is expected to be positively correlated with ITV, as predicted in niche variation hypothesis[45]. In addition, species with shorter generation length may have higher ITV changing rate due to faster demographic rate[46]. As body size is a heritable trait[47], large litter/clutch size allows optimum trait values to be transmitted to a large number of individuals. The increasing frequency of optimum trait values will lead to trait convergence and decreasing ITV.

Due to the scarcity of long-term ITV data across traits across species, we obtained species-averaged traits to assess potential covariates associated with species ITV changing trend, while temporal changes in these covariates were out of the scope in this study. Specifically, human harvest of the species was assessed as whether the species has been harvested by human as food, medicine or sport hunting. This assessment was based on information in the International Union for Conservation of Nature (IUCN) Red List[40] (v.2021–2). Similarly, data on generation length, species ability to use artificial habitats, which was assessed as whether the species can use artificial habitats and habitat breadth for each species, which was calculated as the number of suitable habitats, was extracted from the IUCN Red List[40]. Body mass and clutch or litter size for birds and terrestrial mammals were extracted from ref. 24 and body mass of aquatic mammal species were extracted from PanTHERIA[48]. Missing values of clutch or litter size were further obtained from Animal Diversity Web (animaldiversity.org; accessed in November 2021). The compiled dataset used in this study can be found in Figshare (https://doi.org/10.6084/m9.figshare.21587145.v1).

Statistical analysis

To control the effects of varying sampling size on the value of coefficient of variation (CV), we randomly sampled ten specimen records without replacement within each year interval to calculate CV, using 'sample' function in R v.4.1.1 (ref. 49). To reduce the bias in calculating CV due to small sample size and non-normal distribution of trait values, we used Bao's coefficient of variation ($\mathrm{CV_b}$), which incorporated sample size, skewness and kurtosis of the trait sample distribution in calculating CV[25]. Specifically, $\mathrm{CV_b}$ was calculated with $\log_e$-transformed body length data within each year interval, as $\mathrm{CV_b} = \mathrm{CV} - \frac{\mathrm{CV}^3}{N} + \frac{\mathrm{CV}}{4N} + \frac{\mathrm{CV}^2\gamma_1}{2N} + \frac{\mathrm{CV}\gamma_2}{8N}$; where CV is the coefficient of variation calculated as the ratio of standard deviation to mean of the trait sample, N is the sample size and γ_1 and γ_2 are the skewness and kurtosis of the trait sample distribution[25]. The random-sampling procedure was repeated 999 times and ITV estimates were taken as the average of all $\mathrm{CV_b}$ values from 999 subsamples of each species during each year interval.

To assess the general trends of body size mean and ITV over time for mammal and bird species, we applied LMMs on $\log_e$-transformed body size with a Gaussian error distribution with an identity link and generalized linear mixed effects models (GLMMs) on $\mathrm{CV_b}$ with a Gaussian error distribution with a log link using the 'lme4' package v.1.1–27.1 (ref. 50) in R v.4.1.1 (ref. 49). Body size was $\log_e$-transformed before analyses because of high skewness of body size distribution among species (species with larger mean body size have much larger body size variance). In our model of mean body size, the fixed predictor effect was the year of a specimen being collected, and in the ITV model, the fixed predictor effect was the final year of each year interval used in calculating $\mathrm{CV_b}$. In both models, nested taxonomic information (species within family and family within order) was treated as a random intercept to account for phylogenetic relationships among species. For each species, ITV temporal changing magnitude was assessed by applying generalized linear models (GLMs) on $\mathrm{CV_b}$ with a Gaussian error distribution with a log link with year as the fixed predictor. The slopes of species-specific models were extracted as species ITV changing magnitude for further analysis.

To assess sex-based differences in ITV changing trend, we further extracted a subset of specimen records with information on gender. We re-evaluated data sufficiency of calculating ITV over time for each sex of each species, leaving 164,149 females of 270 species and 184,632 males of 266 species of mammals and 2,254 females of 37 species and 4,831 males of 50 species of birds for assessment. We calculated $\mathrm{CV_b}$ over time with $\log_e$-transformed body length using the same approach as described above. We applied GLMMs on $\mathrm{CV_b}$ with a Gaussian error distribution with a log link in the 'lme4' package v.1.1–27.1 (ref. 50) in R v.4.1.1 (ref. 49) to test sexual differences in $\mathrm{CV_b}$ changing trend. For mammals and birds separately, we treated $\mathrm{CV_b}$ as the response variable, the final year of each year interval used in calculating ITV, sex information and the interaction between these two variables as fixed predictors and nested taxonomic information (species within family and family within order) as a random intercept.

Covariates associated with species ITV temporal changing trends (changing magnitude and direction) were analysed using phylogenetic LMMs with the 'phyr' package 1.1.0 (ref. 51) in R v.4.1.1 (ref. 49), on mammals and birds separately. Specifically, ITV changing magnitude models were fitted with a Gaussian error distribution and ITV changing direction models were fitted with a binomial error distribution with logit link. In all models, fixed predictors included species-level averaged body mass ($\log_e$-transformed), habitat breadth, generation length ($\log_e$-transformed), litter/clutch size, the ability to use artificial habitat (no use as '0', use as '1') and human usage of the species (no use as '0', use as '1'). The variance inflation factor values for all predictors in the models were <3. Phylogenetic covariance matrix among species was included as a random effect to account for complete phylogenetic relationships among species. For mammals and birds, respectively, we downloaded 10,000 species-level pruned trees with species included in our analysis (302 mammal species and 78 bird species) from the posterior distributions of complete trees produced by refs. 52,53 from VertLife. The maximum clade credibility (MCC) tree was obtained from the 10,000 trees with common ancestor node heights using BEAST v.1.10.4 (ref. 54) for each group. The MCC trees were used to account for phylogenetic relationships among species in phylogenetic LMMs. In the models, variables with 90% confidence interval of the regression coefficient not overlapping zero are considered as important covariates associated with ITV changing trend. The 90% confidence interval was chosen as a conservative estimate of existing relationships following a neoFisherian approach[55]. Finally, both models were refitted with z-transformed variables (standardized to zero mean and unit standard deviation) to obtain the relative effects of each covariate on ITV changing trends (standardized regression coefficients).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Data from this work can be found in https://doi.org/10.6084/m9.figshare.21587145.v1 (Supplementary Data 1–3).

Code availability

Code from this work can be found in https://doi.org/10.6084/m9.figshare.21587145.v1 (Supplementary Software).

References

1. Bradshaw, W. E. & Holzapfel, C. M. Evolutionary response to rapid climate change. *Science* **312**, 1477–1478 (2006).
2. Sheridan, J. A. & Bickford, D. Shrinking body size as an ecological response to climate change. *Nat. Clim. Change* **1**, 401–406 (2011).
3. Audzijonyte, A. et al. Fish body sizes change with temperature but not all species shrink with warming. *Nat. Ecol. Evol.* **4**, 809–814 (2020).
4. Gardner, J. L., Heinsohn, R. & Joseph, L. Shifting latitudinal clines in avian body size correlate with global warming in Australian passerines. *Proc. R. Soc. B* **276**, 3845–3852 (2009).

5. Bergmann C. *Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse* (Göttinger Studien, 1847).
6. Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L. & Heinsohn, R. Declining body size: a third universal response to warming? *Trends Ecol. Evol.* **26**, 285–291 (2011).
7. Darimont, C. T. et al. Human predators outpace other agents of trait change in the wild. *Proc. Natl Acad. Sci. USA* **106**, 952–954 (2009).
8. van Gils, J. A. et al. Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. *Science* **352**, 819–821 (2016).
9. Ryding, S., Klaassen, M., Tattersall, G. J., Gardner, J. L. & Symonds, M. R. E. Shape-shifting: changing animal morphologies as a response to climatic warming. *Trends Ecol. Evol.* **36**, 1036–1048 (2021).
10. Des Roches, S. et al. The ecological importance of intraspecific variation. *Nat. Ecol. Evol.* **2**, 57–64 (2018).
11. Enquist, B. J. et al. Scaling from traits to ecosystems: developing a general trait driver theory via integrating trait-based and metabolic scaling theories. *Adv. Ecol. Res* **52**, 249–318 (2015).
12. González-Suárez, M. & Revilla, E. Variability in life-history and ecological traits is a buffer against extinction in mammals. *Ecol. Lett.* **16**, 242–251 (2013).
13. Ducatez, S., Sol, D., Sayol, F. & Lefebvre, L. Behavioural plasticity is associated with reduced extinction risk in birds. *Nat. Ecol. Evol.* **4**, 788–793 (2020).
14. Brady, S. P. et al. Causes of maladaptation. *Evol. Appl.* **12**, 1229–1242 (2019).
15. Scheele, B. C., Foster, C. N., Banks, S. C. & Lindenmayer, D. B. Niche contractions in declining species: mechanisms and consequences. *Trends Ecol. Evol.* **32**, 346–355 (2017).
16. Campbell-Staton, S. C. et al. Ivory poaching and the rapid evolution of tusklessness in African elephants. *Science* **374**, 483–487 (2021).
17. Thompson M. J., Capilla-Lasheras P., Dominoni D. M., Réale D. & Charmantier A. Phenotypic variation in urban environments: mechanisms and implications. *Trends Ecol. Evol.* **37**, 171–182 (2022).
18. Starrfelt, J. & Kokko, H. Bet-hedging—a triple trade-off between means, variances and correlations. *Biol. Rev.* **87**, 742–755 (2012).
19. Heino, M., Díaz Pauli, B. & Dieckmann, U. Fisheries-induced evolution. *Annu. Rev. Ecol. Evol. Syst.* **46**, 461–480 (2015).
20. Kindsvater, H. K. & Palkovacs, E. P. Predicting eco-evolutionary impacts of fishing on body size and trophic role of Atlantic cod. *Copeia* **105**, 475–482 (2017).
21. Hantak, M. M., McLean, B. S., Li, D. & Guralnick, R. P. Mammalian body size is determined by interactions between climate, urbanization, and ecological traits. *Commun. Biol.* **4**, 972 (2021).
22. Freckleton, R. P., Harvey, P. H. & Pagel, M. Bergmann's rule and body size in mammals. *Am. Nat.* **161**, 821–825 (2003).
23. Riddell, E. A., Odom, J. P., Damm, J. D. & Sears, M. W. Plasticity reveals hidden resistance to extinction under climate change in the global hotspot of salamander diversity. *Sci. Adv.* **4**, eaar5471 (2018).
24. Cooke, R. S. C., Eigenbrod, F. & Bates, A. E. Projected losses of global mammal and bird ecological strategies. *Nat. Commun.* **10**, 2279 (2019).
25. Yang, J. et al. Large underestimation of intraspecific trait variation and its improvements. *Front. Plant Sci.* **11**, 53 (2020).
26. Olsen, E. M. et al. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* **428**, 932–935 (2004).
27. Antonson, N. D., Rubenstein, D. R., Hauber, M. E. & Botero, C. A. Ecological uncertainty favours the diversification of host use in avian brood parasites. *Nat. Commun.* **11**, 4185 (2020).
28. Rode, K. D., Amstrup, S. C. & Regehr, E. V. Reduced body size and cub recruitment in polar bears associated with sea ice decline. *Ecol. Appl.* **20**, 768–782 (2010).
29. Edeline, E. et al. Harvest-induced disruptive selection increases variance in fitness-related traits. *Proc. R. Soc. B* **276**, 4163–4171 (2009).
30. Hays, G. C. et al. Changes in mean body size in an expanding population of a threatened species. *Proc. R Soc. B* https://doi.org/10.1098/rspb.2022.0696 (2022).
31. Halfwerk, W. et al. Adaptive changes in sexual signalling in response to urbanization. *Nat. Ecol. Evol.* **3**, 374–380 (2019).
32. Fernández-Chacón, A. et al. Protected areas buffer against harvest selection and rebuild phenotypic complexity. *Ecol. Appl.* **30**, e02108 (2020).
33. Sánchez-Tójar, A., Moran, N. P., O'Dea, R. E., Reinhold, K. & Nakagawa, S. Illustrating the importance of meta-analysing variances alongside means in ecology and evolution. *J. Evol. Biol.* **33**, 1216–1223 (2020).
34. Reed, T. E., Waples, R. S., Schindler, D. E., Hard, J. J. & Kinnison, M. T. Phenotypic plasticity and population viability: the importance of environmental predictability. *Proc. R. Soc. B* **277**, 3391–3400 (2010).
35. Klump, B. C. et al. Innovation and geographic spread of a complex foraging culture in an urban parrot. *Science* **373**, 456–460 (2021).
36. Bosse, M. et al. Recent natural selection causes adaptive evolution of an avian polygenic trait. *Science* **358**, 365–368 (2017).
37. Singer, M. C. & Parmesan, C. Lethal trap created by adaptive evolutionary response to an exotic resource. *Nature* **557**, 238–241 (2018).
38. Usui, R., Sheeran, L. K., Asbury, A. M. & Blackson, M. Impacts of the COVID-19 pandemic on mammals at tourism destinations: a systematic review. *Mamm. Rev.* **51**, 492–507 (2021).
39. Meineke, E. K. & Daru, B. H. Bias assessments to expand research harnessing biological collections. *Trends Ecol. Evol.* **36**, 1071–1082 (2021).
40. *The IUCN Red List of Threatened Species. Version 2021-2* (IUCN, accessed November 2021); https://www.iucnredlist.org
41. Boyd, R. J. et al. ROBITT: a tool for assessing the risk-of-bias in studies of temporal trends in ecology. *Methods Ecol. Evol.* **13**, 1497–1507 (2022).
42. Thornton, P. K., Ericksen, P. J., Herrero, M. & Challinor, A. J. Climate variability and vulnerability to climate change: a review. *Glob. Change Biol.* **20**, 3313–3328 (2014).
43. Botero, C. A., Weissing, F. J., Wright, J. & Rubenstein, D. R. Evolutionary tipping points in the capacity to adapt to environmental change. *Proc. Natl Acad. Sci. USA* **112**, 184–189 (2015).
44. Niklas, K. J. The scaling of plant and animal body mass, length, and diameter. *Evolution* **48**, 44–54 (1994).
45. Van Valen, L. Morphological variation and width of ecological niche. *Am. Nat.* **99**, 377–390 (1965).
46. Gaillard, J. M. et al. Generation time: a reliable metric to measure life-history variation among mammalian populations. *Am. Nat.* **166**, 119–123 (2005).
47. Postma, E. in *Quantitative Genetics in the Wild* (eds Charmantier, A. et al.) 16–33 (Oxford Univ. Press, 2014).
48. Jones, K. E. et al. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**, 2648–2648 (2009).
49. R Core Team. *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2022).
50. Bates D., Mächler M., Bolker B. & Walker S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).

51. Ives, A. R., Dinnage, R., Nell, L. A., Helmus, M. & Li, D. phyr: Model based phylogenetic analysis. R package version 1.1.0 https://CRAN.R-project.org/package=phyr (2020).
52. Upham, N. S., Esselstyn, J. A. & Jetz, W. Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biol.* **17**, e3000494 (2019).
53. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491**, 444–448 (2012).
54. Suchard, M. A. et al. Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evol.* **4**, vey016 (2018).
55. Hurlbert, S. H. & Lombardi, C. M. Final collapse of the Neyman–Pearson decision theoretic framework and rise of the neoFisherian. *Ann. Zool. Fenn.* **46**, 311–349 (2009).

Acknowledgements

We are grateful to data collectors and contributors to VertNet database. We thank H. Fan for assistance with data processing and thank R. Didham for advice on statistical analyses. We thank laboratory members for comments and discussions on the manuscript. This work was supported by the National Natural Science Foundation of China (32071646) to J.L. and the fellowship of China Postdoctoral Science Foundation (2022M710794) to S.Z.

Author contributions

S.Z. and J.L. conceived the project and developed the initial protocol for data collation. S.Z. cleaned the data and performed the analyses. S.Z., J.H., Z.M., D.L. and J.L. contributed to the first draft and the revisions.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41559-022-01967-w.

Correspondence and requests for materials should be addressed to Jiajia Liu.

Peer review information *Nature Ecology & Evolution* thanks Rob Cooke and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.

Reprints and permissions information is available at www.nature.com/reprints.

nature portfolio

Corresponding author(s): Jiajia Liu

Last updated by author(s): Nov 21, 2022

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Human harvest of the species was assessed as whether the species has been harvested by human as food, medicine or sport hunting. This assessment was based on information in International Union for Conservation of Nature (IUCN) Red List (version 2021-2). Similarly, data on generation length, species ability to use artificial habitats, which was assessed as whether the species can use artificial habitats, and habitat breadth for each species, which was calculated as the number of suitable habitats, was extracted from the IUCN Red List. Body mass and clutch or litter size for birds and terrestrial mammals were extracted from Cooke et al., and body mass of aquatic mammal species were extracted from PanTHERIA. Missing values of clutch or litter size were further obtained from Animal Diversity Web (animaldiversity.org; accessed in November 2021).
Data analysis	All analysis were performed in the R software v. 4.1.1 (2022).

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

Data from this work can be found in https://doi.org/10.6084/m9.figshare.21587145.v1 (Supplementary Data 1-3).

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	The study did not involve human research participants.
Population characteristics	n/a
Recruitment	n/a
Ethics oversight	n/a

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We investigated intraspecific body size variation changing trend in mammals and birds during the recent 140 years, using individual-level body size data from mammal and bird specimen collected in North America between 1880-2020
Research sample	Our dataset comprised a total of 379,158 mammal specimens representing 302 species, and 14,341 bird specimens representing 78 species for analysis.
Sampling strategy	From the VertNet database, we extracted all mammal and bird specimen records having species identification information, collection date and location information, and body length data.
Data collection	Individual-level specimen data were complied from VertNet database (http://vertnet.org).
Timing and spatial scale	Specimen included in our dataset were collected during 1880-2020 in North America.
Data exclusions	As we focused on wild populations, records from laboratory or zoo animals were excluded. To minimize the influence of ontogenetic differences, only adult individuals were included. Second, we removed anomalous measurements differing by more than 20% from the median body size value in the dataset for each species. We note that specimen records without life stage information were included in the data subset before removing anomalous measurements, and suspected non-adult records were then removed as anomalous measurements. To obtain sufficient trait measurements and minimize bias in calculating intraspecific trait variation (ITV), we extracted species with more than 10 valid measurements of total body length at every five-, ten-, or fifteen-year interval, depending on the number of records across years. Only species with sufficient data spanning at least a 20-year range were retained for further analysis, leaving a total of 400,234 mammal specimens representing 347 species, and 15,178 bird specimens representing 81 species. Within this dataset, 95.7% of mammal specimens (n=382,849) and 97.4% of bird specimens (n=14,791) were collected from North America. To minimize bias in calculating ITV due to different sampling geographical scales, we excluded records from outside of North America. Finally, we re-evaluated data sufficiency for ITV calculation with above criteria, leaving a total of 379,158 mammal specimens representing 302 species, and 14,341 bird specimens representing 78 species for subsequent analysis.
Reproducibility	Raw data are available at http://vertlife.org, Cooke et al. (https://doi.org/10.1038/s41467-019-10284-z), International Union for Conservation of Nature Red List and Animal Diversity Web.

Randomization	Specimen were assumed to be random samples in North America. We analyzed each class of terrestrial vertebrates (mammals and birds) separately given the uniqueness of their taxonomic history.
Blinding	Not applicable.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology and archaeology
☒	☐	Animals and other organisms
☒	☐	Clinical data
☒	☐	Dual use research of concern

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging