Increasing environmental variability inhibits evolutionary rescue in a long-lived vertebrate

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Evolutionary rescue, whereby adaptive evolutionary change rescues populations from extinction, is theorized to enable imperiled animal populations to persist under increasing anthropogenic change. Despite a large body of evidence in theoretical and laboratory settings, the potential for evolutionary rescue to be a viable adaptation process for free-ranging animals remains unknown. Here, we leverage a 38-year dataset following the fates of 53,959 Magellanic penguins (*Spheniscus magellanicus*) to investigate whether a free-ranging vertebrate species can morphologically adapt to long-term environmental change sufficiently to promote population persistence. Despite strong selective pressures, we found that penguins did not adapt morphologically to long-term environmental changes, leading to projected population extirpation. Fluctuating selection benefited larger penguins in some environmental contexts, and smaller penguins in others, ultimately mitigating their ability to adapt under increasing environmental variability. Under future climate projections, we found that the species cannot be rescued by adaptation, suggesting similar constraints for other long-lived species. Such results reveal how fluctuating selection driven by environmental variability can inhibit adaptation under long-term environmental change. Our eco-evolutionary approach helps explain the lack of adaptation and evolutionary rescue in response to environmental change observed in many animal species.

animal conservation | climate change | evolutionary rescue | Magellanic penguins

Significance

Animals may be able to adapt to human-induced environmental change, thereby rescuing their populations from extinction. Yet it is unclear whether long-term adaptive change in genotypes, known as evolutionary rescue, is possible for free-living animals. Using a multidecadal dataset on Magellanic penguins, we show that despite strong selection on body size, some environmental conditions favored larger bodies, and others favored smaller bodies, thus preventing consistent evolution in one direction or the other. This ultimately led to a lack of adaptive evolutionary change and predicted population extirpation for this penguin species. Such findings highlight that fluctuating selection can be driven by environmental variability, and these processes could eliminate the possibility of evolutionary rescue for many long-lived animal species.

Under the increasing threat of environmental change, animal populations have persisted by adapting in a variety of ways (1–3), yet many species are still predicted to go extinct under ensuing change (4). One way in which animal populations can persist in response to unprecedented environmental change is through evolution (5–8). Evolutionary rescue, which is an adaptive change in genotypes that allows for population recovery (i.e., U-shaped population trajectory), is a hypothesized mechanism for enabling species to survive rapid environmental transformation in the Anthropocene (9–11). Indeed, evolutionary rescue may have allowed animals to exist through past environmental changes throughout evolutionary history (12). Moreover, a large body of theoretical and laboratory evidence has shown that evolutionary rescue is a viable mechanism of population recovery in controlled settings (9, 10), driven by a variety of factors including density dependence, demographic stochasticity, genetic variation, hybridization, and environmental change (11, 13). Limited evidence from rodents and rabbits suggests that evolutionary rescue may also occur in natural environments undergoing human-induced environmental change (9), although this evidence has been constrained to rapidly reproducing, abundant species subject to acute anthropogenic pressures (pesticides and disease). Thus, despite it being hailed as a possible way for species to persist in the face of change, the potential for evolutionary rescue in long-lived, free-ranging animal populations that are among the most at-risk of extinction (14, 15) remains untested.

Using a 38-year dataset of free-ranging Magellanic penguins (*Spheniscus magellanicus*) (Fig. 1A), we provide empirical investigation of evolutionary rescue in a long-lived vertebrate species. To do so, we collected demographic data from 53,959 Magellanic penguins and morphological data from 1,920 parent–offspring pairs from 1982 to 2019 at Punta Tombo, southern Argentina (Fig. 1 A and B)—a region undergoing long-term environmental change (Fig. 1 C and D). The colony was once the largest of the species (16), but has declined by ~50% since the 1980s, and is projected to approach local extinction within the next century due to documented impacts of changing oceanographic conditions in their summer breeding and northern wintering grounds on demographic rates (17) (Fig. 1 C–E). A key trait on which selection may act, potentially supporting evolutionary rescue in this species, is body size. Larger body sizes significantly increase prey capture (18, 19), juvenile and adult survival (20) (Fig. 2A), and reproduction (21) in this species. Penguin body sizes are also significantly heritable year-to-year (h^2= 0.123 to 0.568 using animal
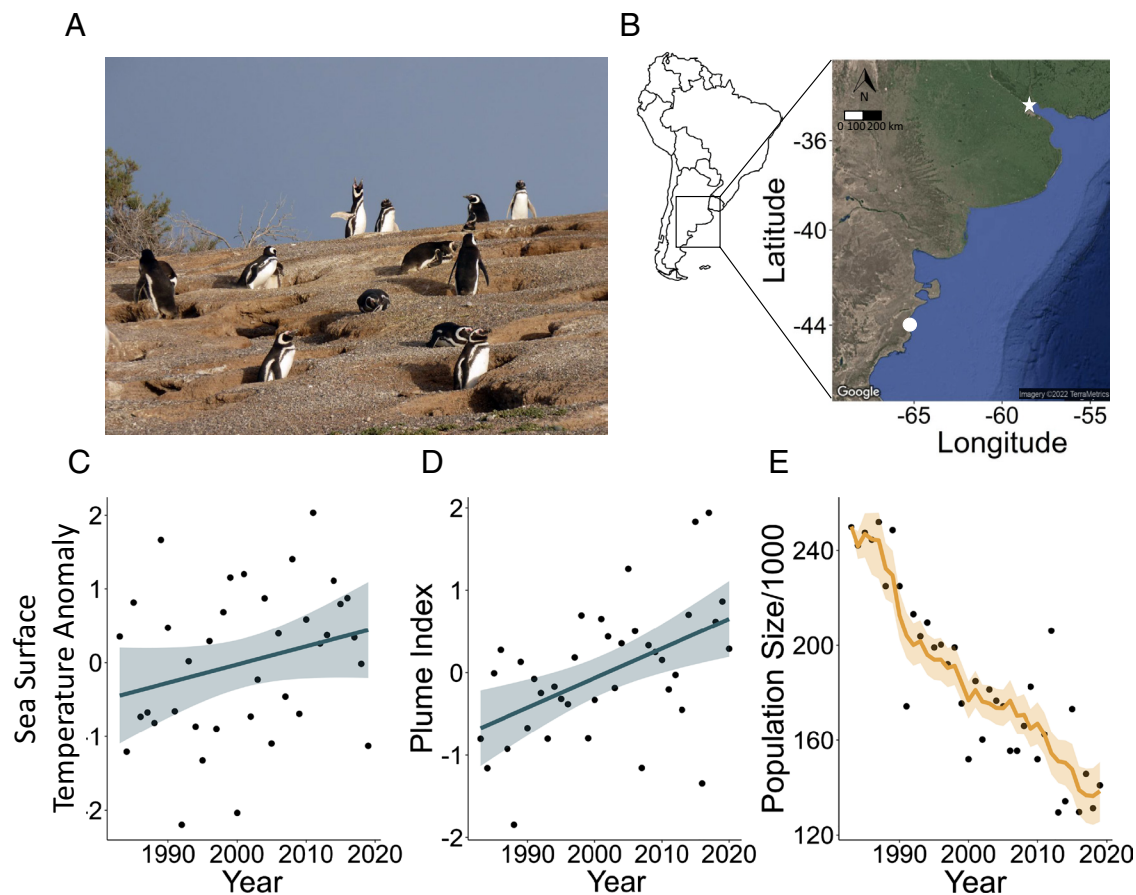
Fig. 1. Trends in oceanographic variables, population size, and body size traits for Magellanic penguins at Punta Tombo, Argentina. (*A*) Breeding penguins at Punta Tombo, Argentina. (*B*) The location of the breeding colony at Punta Tombo (circle) and the Rio de la Plata plume source (star), which provides key foraging habitat in the penguin's oceanic wintering area. (*C*) Sea surface temperature anomalies in breeding season foraging grounds over years. (*D*) Rio de la Plata plume indices in wintering grounds over years. Blue lines and shading indicate means and 95% CIs of a linear model fit to the increasing trend of these variables. (*E*) Population size over years at Punta Tombo. Orange lines and shading indicate the means and 95% CRIs of the eco-evolutionary model fit to these data.

models and parent–offspring regressions (21); mean biometric heritability (22) (hereafter, heritability) = 0.16, 95% CI = 0.08 to 0.24, see *Materials and Methods*), which is within the range found in Darwin's finches (*Geospizinae*) (23). Given apparently strong selection for larger bodies and high heritability, adaptive change in body size should be possible. We built an eco-evolutionary model to evaluate whether penguin body size is evolving in ways that reduce risk of extinction. Specifically, we aimed to 1) assess the effects of changes in environmental conditions on morphological adaptation; 2) understand whether and how evolutionary adaptation may allow the population to persist under long-term environmental change; and 3) examine hypothetical scenarios to understand the environmental scenarios and eco-evolutionary mechanisms by which evolutionary rescue may occur in long-lived species. Given the dire conservation threats facing many long-lived species, it is critical to understand how environmental change affects the likelihood of evolutionary rescue occurring in free-ranging, declining populations, and to identify the biological contexts in which evolutionary rescue may or may not occur.

Results

Body Size Adaptation in Response to Environmental Conditions.
Given our previous research demonstrating strong relationships between environmental conditions and demographic rates (17) and body sizes and demographic rates (20, 21) (Fig. 2*A*), we assessed the effects of changes in environmental conditions on

morphological adaptation (Aim 1). We hypothesized that body size would increase as penguins adapted to long-term shifts in the environment over the 38-year study period (~5 to 8 penguin generations). This time scale is similar to other studies showing phenotypic change in response to the environment in longer-lived vertebrate populations (24–26). Over the study period, we found that body size weakly increased over time (mean standardized trait change = 0.484 out of scale –5 to 5; 95% CI = 0.220 to 0.660; 0.0535 haldanes) (Fig. 2*B*). However, this trait change only led to very minor increases in juvenile, prebreeding, and adult survival (0.014, 0.004, and 0.009, respectively), despite strong selective pressure (Fig. 2*A*), ultimately leading to the population being unable to recover from long-term decline (population growth rate = 0.98; 95% CI: 0.977 to 0.985) (Fig. 1*E*). Given the lack of a strong evolutionary response to long-term environmental change, we hypothesized that strong interannual environmental variability decreased penguins' likelihood of trait adaptation, and therefore evolutionary rescue.

To understand whether and how evolutionary adaptation may allow the population to persist under long-term environmental change (Aim 2), we first determined the relationships between oceanographic variables and eco-evolutionary characteristics for the species. We used a recently developed method, IPM^2, which allows for interactions between the environment and individual trait effects on demographic rates, and can thereby forecast changes in population size and individual trait distributions in response to environmental change (27). IPM^{2}s combine integrated population models,
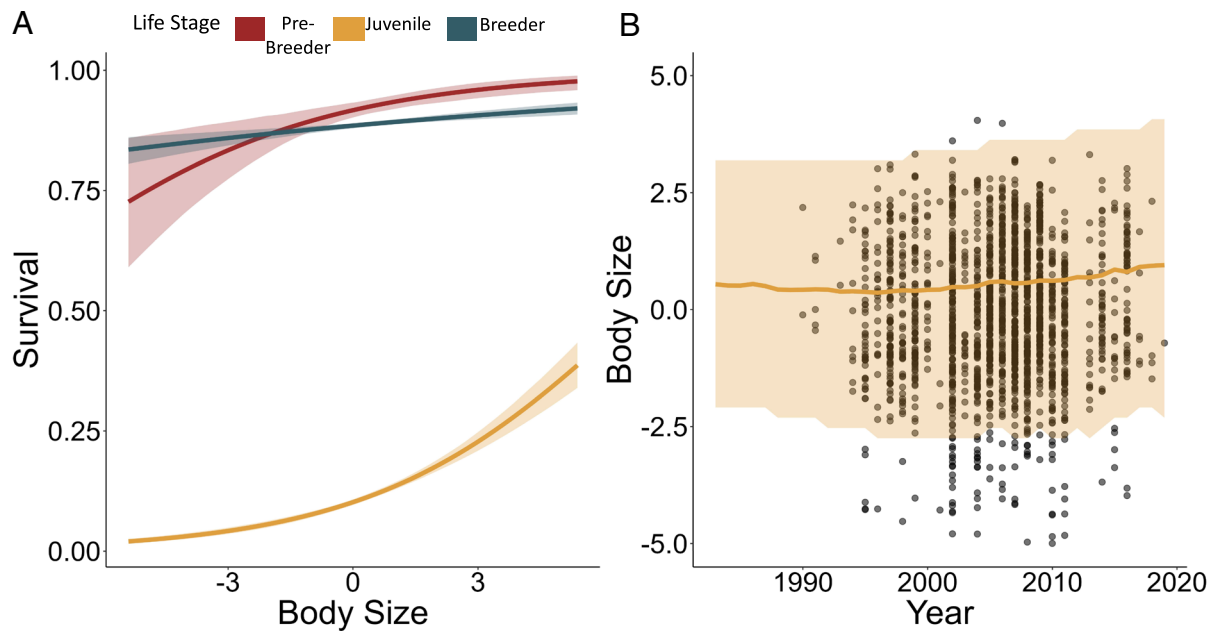
Fig. 2. Trend in body size traits and relationship to life stage and penguin survival. (*A*) The effect of body size on penguin survival, sorted by life stage of the penguin. (*B*) Standardized individual body sizes over years at Punta Tombo. Lines and shading in indicate the means and 95% CRIs of the eco-evolutionary model fit to these data.

which allow for joint analysis of population and demographic data, with integral projection models, which link individual traits and demography (28, 29). IPM^{2}s have been shown to produce accurate predictions of changes in individual traits and population size while also providing novel mechanistic insights into eco-evolutionary dynamics (27). Using the interactive effect of oceanographic variables and body size on survival, we parameterized an IPM^2 model using data on oceanographic conditions, individual traits, demography, and population size. The resulting eco-evolutionary model closely matched our observations of shifts in population size and body size over time (Figs. 1*E* and 2*B*).

We then quantified how two demographically important and rapidly changing oceanographic variables—sea surface temperature and the Rio de la Plata plume—interacted with body size to influence survival. Warming sea surface temperatures near the breeding grounds correlate with reduced reproductive success and survival (17, 30, 31). These ocean temperatures, which are becoming significantly warmer and less variable over time (linear model fit to rolling 5-y average, $\beta = 0.035$, $P < 0.001$; variance, $\beta = -0.0237$, $P = 0.0184$), decreased survival for all juvenile and adult individuals, but individuals with larger body sizes were least negatively impacted (Fig. 3 *A* and *C*). During annual migrations, penguins are also influenced by the strength of the Rio de la Plata in northern Argentina (Fig. 1*B*), which provides important habitat for key forage fish (32), whereby stronger plumes increase turbidity in oceanic foraging areas, causing decreased prey encounter rates for penguins (32). Higher Rio de la Plata plume indices (i.e., weaker plume strength, see *Materials and Methods*) correlate with increased penguin body condition, fledging success, and survival (17, 20, 32). These plume indices, which are becoming significantly higher but more variable over time (linear model fit to rolling 5-year average, $\beta = 0.0370$, $P < 0.001$; variance, $\beta = 0.0266$, $P = 0.0025$), increased survival for all juvenile individuals (Fig. 3*B*). Both juvenile and adult individuals with larger body sizes were the most positively impacted by high plume indices, potentially because they can dive deeper and longer than their smaller

counterparts to take advantage of more concentrated prey under these plume conditions (19, 32). Importantly, however, lower plume indices reversed this pattern of selection for adults, with smaller individuals surviving better than larger ones under these conditions (Fig. 3*D*). This is plausibly because as lower plume indices reduce prey densities and prey encounter rates (32), larger individuals are more limited by higher metabolic constraints than smaller individuals (18), so smaller individuals survive better under these limiting prey conditions. Smaller juvenile individuals might do more poorly in poor plume conditions compared to adults of similar size due to the importance of gaining prey finding and hunting experience on how to forage effectively in certain prey conditions (33). We further found that the plume index had a significant but opposing effect on mean body size in the population depending on high versus low plume index conditions, driven by fluctuating patterns of selection in which years with higher plume indices selected for larger penguins, whereas years with lower indices selected for smaller penguins (Fig. 4*A* and *SI Appendix*, Fig. S2 as a consequence of the relationships shown in Fig. 3 *B* and *D*). Thus, we show that selection pressure and body size change fluctuate depending on oceanographic conditions.

Evolutionary Rescue Under Long-Term Environmental Change. Global climate change is altering the variability of climate conditions and increasing the likelihood of extreme events (34), which could amplify the impact of fluctuating selection on this species. We hypothesized that environmental variability, coupled with fluctuating selection pressure on body size, may reduce the ability of Magellanic penguins to adaptively track long-term environmental changes, and thereby reduce the likelihood of evolutionary rescue (9, 10). Indeed, theoretical simulations and laboratory experiments in bacteria and yeast indicate that the rate and variability of environmental change can impede evolutionary rescue (9, 10, 35–38). To investigate this, we simulated projections over 100 years using our parameterized IPM^{2}s under different environmental scenarios to determine the effects of interannual
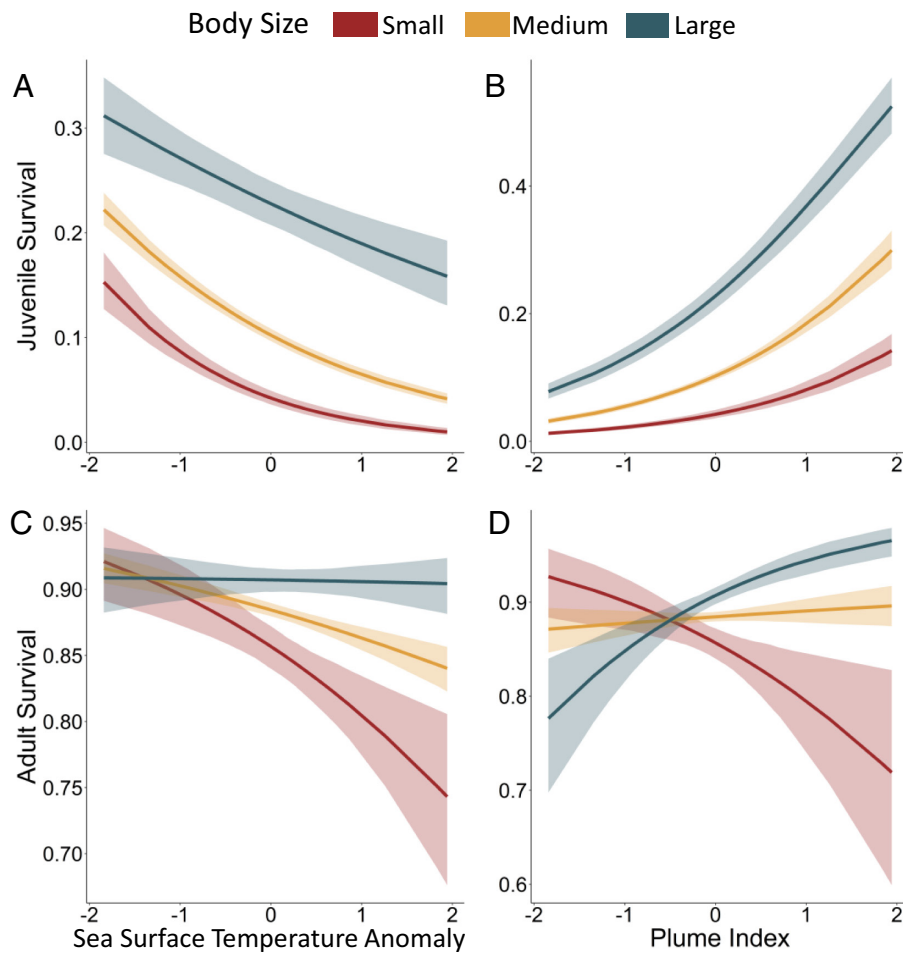
Fig. 3. The relationship between oceanographic conditions, body size, and penguin survival. (*A–D*) Effect of sea surface temperature anomalies and Rio de la Plata plume index on juvenile survival (*A* and *B*) and adult survival (*C* and *D*) by body size. Colored lines indicate the mean and shading indicates the 95% CRIs.

environmental variability, as measured by the interannual SD in SSTA and plume index, on body size change. Increasing the interannual variability of SSTA had a positive effect on the long-term change in mean body size in the population (20.2% change moving from low (0.5) to high (1.5) long-term variability) (Fig. 4*D*). In strong contrast, increasing the interannual variability of the plume index had a very large negative effect on the long-term change in mean body size (–85.4% change moving from low (0.5) to high (1.5) long-term variability) (Fig. 4*C*), indicating that high variability in plume conditions inhibits long-term adaptation in body size. In sum, we found that opposing patterns of selection in concert with increasingly variable plume conditions reduced the ability of the species to adapt to its rapidly changing environment.

Finally, to estimate the likelihood of evolutionary rescue for the species and those with similar eco-evolutionary traits under future scenarios of environmental conditions, we used our parameterized IPM^{2}s to project populations 100 years into the future under different conditions (Fig. 5). Here, we formally define evolutionary rescue as significant trait change in concert with population recovery with a geometric lambda $\gtrsim 1$ (9, 10). Under current conditions of environmental change, we estimate that the penguin population will continue to decline, with a geometric lambda of 0.989 (95% CI: 0.984 to 0.990), in accord with previous estimates in nonevolutionary models (17), with a weak mean body size change of 0.523 (95% CI: 0.275 to 0.749) over 100 years. If we extend the current rate of increase in the interannual variability of the plume index, the penguin population is

projected to decline even further and display a lack of any adaptation (geometric lambda = 0.980, 95% CI: 0.971 to 0.989; mean body size change = –0.088, 95% CI: –0.420 to 0.288).

Given the dependence of evolutionary rescue on environmental conditions, we also explored the importance of demographic and genetic factors that have been shown to modulate evolutionary rescue in theoretical and laboratory studies (10, 13). To understand the environmental scenarios and eco-evolutionary mechanisms by which evolutionary rescue may occur in long-lived species (Aim 3), we additionally examined the mediating effects of age to maturity (demographic factor) and heritability (genetic factors) as examples of traits which could promote evolutionary rescue (10). Life history traits such as age to maturity help animals respond faster to climate change (39, 40), which can allow for animals to better track their environments (9, 10). Magellanic penguins can begin breeding after age four, but when age to maturity was set to occur after the first year, simulated populations were more likely to recover, with a geometric lambda of 1.007 (95% CI: 0.992 to 1.010). However, this rescue was solely due to demographic factors (i.e., increased recruitment) rather than body size adaptation, as body size did not change appreciably under this scenario (0.314, 95% CI: –0.013 to 0.591). Similarly, setting age to maturity to age two allowed populations to stabilize, while maturity set more realistically to age three caused populations to decline (*SI Appendix*, Fig. S3). High heritability may also bolster adaptation (41), so we also considered the level of trait heritability necessary for evolutionary rescue. Only under high levels of inheritance (e.g., $\alpha_1 = 0.8$) did simulated
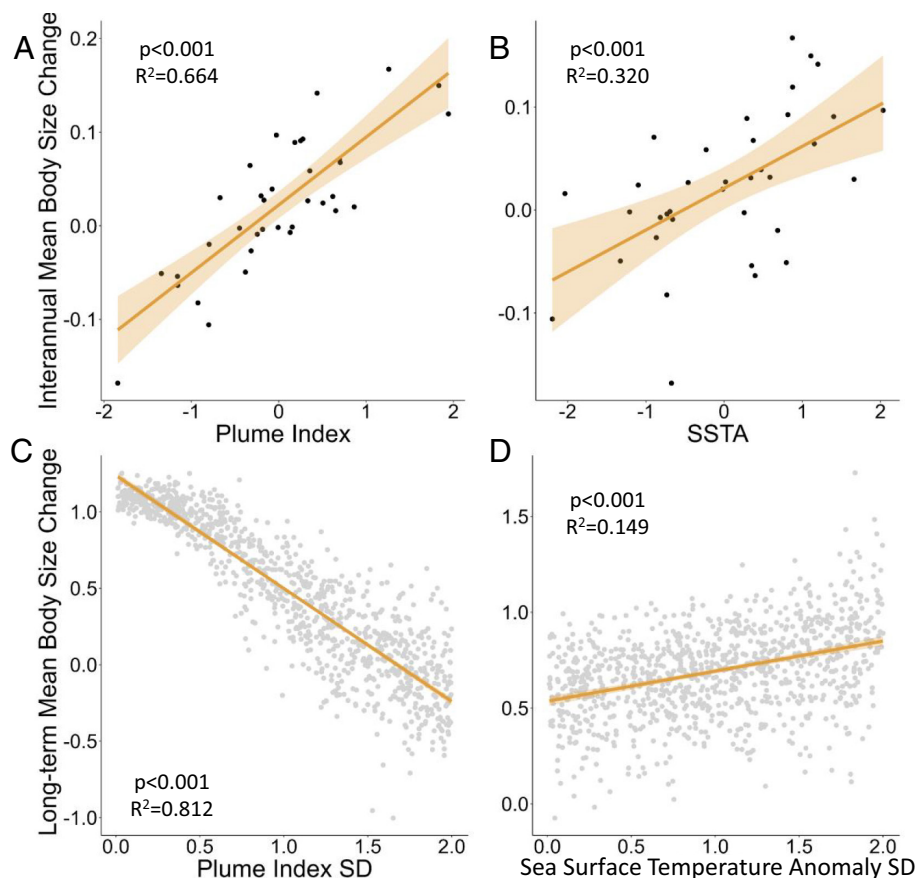
Fig. 4. The relationship between oceanographic variability and short- vs. long-term changes in body size. (*A* and *B*), Effect of Rio de la Plata plume index (*A*) and sea surface temperature anomalies (*B*) on observed interannual mean body size change. (*C* and *D*), Results of a sensitivity analysis using population projections over 100 years showing the effects of long-term changes in plume index interannual SD (*C*) and sea surface temperature anomalies' interannual SD (*D*) on long-term mean body size change. Orange lines and shading indicate mean and 95% CIs of a linear model fit to the trend of this relationship.

populations experience evolutionary rescue (geometric lambda = 0.998, 95% CI: 0.992 to 1.010; mean body size change = 1.60, 95% CI: 1.267 to 1.891). This exercise illustrates that the path to evolutionary rescue may be unrealistic for similar long-lived vertebrate species in rapidly changing environments. However, such results indicate that environmental variability may be overcome by long-term adaptation in other species or contexts with earlier ages to maturity or greater trait heritability, thus shedding light on the biological contexts in which evolutionary rescue may occur in natural settings.
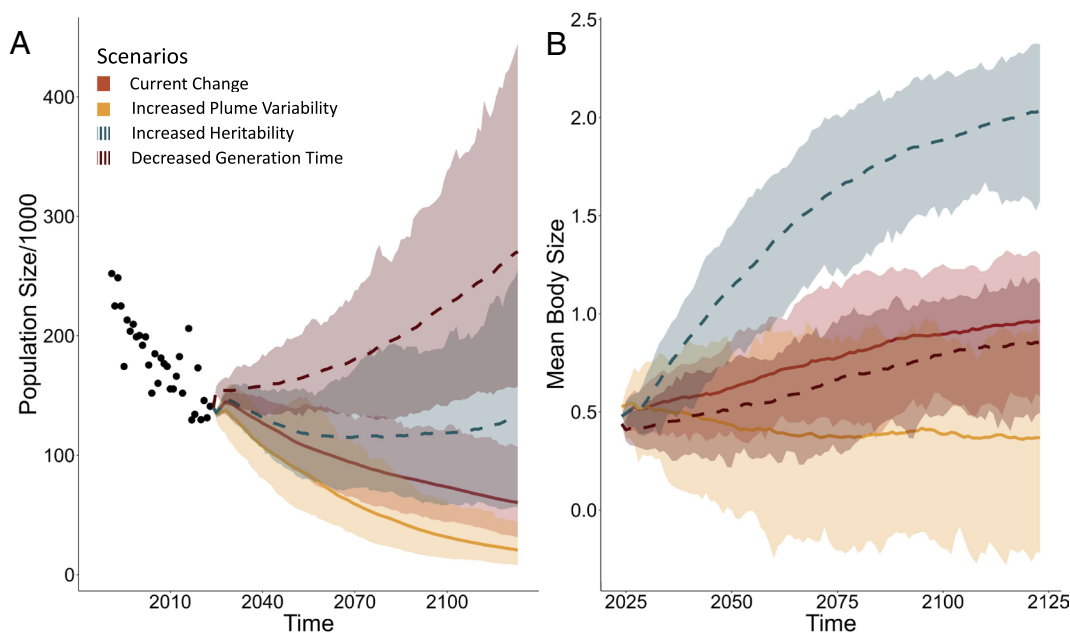

Fig. 5. Population size and body size distribution projections over time under different scenarios. (*A*) Population size, where black circles represent observed population counts and lines indicate future projections. (*B*) Projected body size distributions. Scenarios are as follows: The red solid line shows projections under current climate conditions. The orange solid line shows projections under increasing plume index SD. The blue dashed line shows projections under increased heritability. The purple dashed line shows projections under decreased age to maturity. Colored lines indicate the means and shading indicates the 95% CRIs.

Discussion

In summary, our work found that increasing variability of key environmental conditions (here, the plume index) underlies the lack of observed changes in penguin body size, and ultimately, the absence of evolutionary rescue. The relatively small rate of change in penguin body size that we found is comparable in magnitude to other meta-analyses of phenotypic selection which indicate that weak, nonsignificant selection is common in nature (42–44). The evidence shown here (Fig. 4 and *SI Appendix*, Fig. S2) and elsewhere (21) for fluctuating selection in this species mirrors observations of Darwin's finches and other species, where selection reversed between climatically different years, leading to stability in phenotypic traits over time (45–48). We demonstrate in a free-ranging, long-lived animal how fluctuating selection can act in concert with environmental variability to inhibit adaptation and rescue under long-term directional environmental change. Thus, evolutionary stasis can be maintained by fluctuating selection over time (42, 49), which when coupled with the advent of rapid environmental change in the Anthropocene (34), may slow down adaptive directional trajectories of these traits. These results foreshadow that as global environmental change accelerates, increasing climate variability and frequency of extreme events could slow down or preclude adaptation in animals (3), despite high levels of additive genetic variance (41). We do note, however, that intense periods of extreme events could reverse this stasis due to rapid trait change (45, 50), though this was not observed in our study system despite increasing occurrence of extreme events (17, 51). Populations may also persist by nonevolutionary means in response to environmental change—such as via behavioral plasticity or metapopulation dynamics. Our results point to the need to investigate which characteristics of environmental change (e.g., extreme events, autocorrelation, amelioration) eliminate the possibility of evolutionary rescue (10) as a means for species persistence.

There is a diverse array of nonenvironmental factors which have been shown in theoretical and laboratory studies to influence the probability of evolutionary rescue, including demographic factors like density dependence and immigration/emigration, and genetic factors like standing genetic variation and mutation rates (10, 13). For example, studies with yeast and bacteria have shown that dispersal and metapopulation dynamics can improve the likelihood of evolutionary rescue as immigrants introduce phenotypic variants upon which selection can act (38, 52). Future research, including more in-depth examination of other penguin colonies which may disperse to Punta Tombo (17, 53) may elucidate the importance of metapopulation dynamics to evolutionary rescue in this system. In addition, here we focused on body size as an evolutionary trait because of its strong ties to fitness. However, other fitness-related traits may be important to examine in the future. For example, phenological traits such as laying and hatching date are shifting earlier in this species in response to oceanographic conditions, but these traits are only indirectly tied to fitness (20). Extending our IPM^2 to incorporate these phenological shifts (54) and quantitative genetics (25, 55) and their effects on body size and fitness represent an important extension of the approach we illustrate here.

Evolutionary adaptation can be swift in animals (45, 56, 57), and adaptive tracking of environmental change has been observed in long-term studies (45, 58, 59), yet there is little to no evidence for evolutionary rescue in wild and/or long-lived vertebrates (9, 10). This may be due to data limitations for long-lived species, or as shown here, because rapid environmental change can exacerbate fluctuating selection pressures or other biological constraints. Despite this, it is crucial to understand the environmental and eco-evolutionary contexts in which biologists and conservationists can and cannot expect evolutionary rescue to occur. Doing so may help identify species most vulnerable to environmental change, prioritize interventions such as protecting climate refugia (60), and highlight potential hotspots for evolutionary rescue (61). We suggest that applying what is known from theoretical and experimental settings (10, 36, 37, 49) to empirical studies of long-lived vertebrates of conservation concern using these eco-evolutionary models is an important next step in understanding evolutionary rescue. Our work illustrates the importance of leveraging long-term studies of animals (62) with eco-evolutionary models (28) to understand how populations are affected by eco-evolutionary change spurred by rapidly changing environments.

Materials and Methods

Study System. Magellanic penguins in the south Atlantic are long-lived, migratory predators that track the seasonal migration of Argentina anchovy (*Engraulis anchoita*) to northern Argentina up to southern Brazil from April to August (63). The Magellanic penguin colony at Punta Tombo, Argentina (44°03′S, 65°13′W) was established in the 1920s and was once the largest colony of its species, reaching approximately 400,000 breeding pairs in the 1960s to 1980s (16). The population has declined by ~50% since then in response to climate change, among other anthropogenic pressures like oiling and bycatch (17, 64, 65). Breeding penguins at Punta Tombo arrive in September to early October, and lay eggs in mid-October to November. Chicks hatch in mid-November to early December and fledge in mid-January to mid-February (20, 64).

To measure annual survival, we banded 45,359 fledglings and 8,600 adults at the Punta Tombo colony from 1982 to 2019. We banded individuals with stainless-steel flipper bands or small metal tags attached to the foot webbing (66). We did daily searches for banded individuals throughout the breeding season (67). To measure reproduction, we monitored nests from 1983 to 2019 in an area of ~7,200 km^2 from mid-September to late February and marked chicks to follow them until they fledged or died. Chicks were considered fledged if they were last seen after January 10, weighed ≥1,800 g, and had not lost weight in the last few measurements (68). Reproductive success was estimated as the number of fledged chicks divided by the number of nests with eggs (max. eggs per nest = 2).

To measure breeding population density at the colony, we established a grid survey with transects running 1.5 km north to south and 2 km east to west and counted the number of nests, eggs, chicks, and penguins within a 100 m^2 circle every 100 m along the transects from 1987 to 2019 (65). We multiplied the estimated breeding pair density by 3.524 km^2, which is the estimated occupied penguin habitat (65). We adjusted the breeding pair density estimates prior to 2016 using a ratio of 1.36, because earlier penguin surveys counted unpaired males potentially as part of a breeding pair (17, 65).

To measure body size and inheritance, we measured the lengths of the bill, flipper, and foot, and the depth of the bill in adult penguins and fledged juveniles from 1983 to 2019. In sum, we collected 1,920 parent–offspring pairs, where we measured the juvenile trait measurements of the offspring and its parent when they were juveniles. We focused on juvenile rather than adult measurements, as these were found to have a significant impact on recruitment to the colony, and later, survival as fledglings age to become prebreeding and breeding adults (Fig. 2*A*) (20). In cases where we had measurements for both parents, we averaged their measurements. Extrapair copulations are rare, and although mate switching can occur, we checked eggs well after mate switching happens, ensuring that we were confident in parentage (21). Due to strong positive correlations between the 4 morphological traits, we calculated a synoptic body size measurement using principal components analysis (21). The first and second principal components represented 66.4% and 13.9% of the variation in these morphological traits, respectively. Following Koehn *et al.* (21), we used the first principal component as a body size measurement as it represented an increase in all morphological characteristics in these penguins. We note here that body size in Magellanic penguins at Punta Tombo is significantly heritable as estimated by animal models and parent–offspring regressions (h^2 = 0.123 to 0.526) (21), similar to our estimates found here (mean biometric heritability = 0.16, 95% CI = 0.08 to 0.24). Although maternal and/or environmental effects could lead

to biases in heritability estimates, both experiments and quantitative estimates suggest these effects have little to no effect on heritability estimates in similar long-lived vertebrates (21, 41).

Climate Variables. Warm, unproductive oceans in the colony's foraging area drive penguins to search further out from the colony to find food, leading to reduced reproductive success and survival under increasingly warmer ocean conditions (30, 31). We extracted sea surface temperature anomalies (SSTA) during breeding season using the Coral Reef Temperature Anomaly Database (69), which has global ~4 km resolution data on a weekly time scale. We extracted these data in a rectangle bounded from 65.6 to 61°W and 45 to 40°S, which is >95% of the maximum foraging distance of breeding penguins at Punta Tombo (30, 31). We calculated the SSTA covariate by spatially and temporally averaging the data from October to February to align with the breeding season.

Dynamics of the Rio de la Plata plume are captured by an index that integrates spatial patterns in sea surface temperatures (32), and has been experiencing a long-term increase (indicating a decrease in the plume strength). The plume provides important spawning and nursing habitat for key prey species of Magellanic penguins (e.g., Argentine anchovy (*E. anchoita*), Argentine hake (*Merluccius hubbsi*), Brazilian sardine (*Sardinella brasiliensis*)) (32). Higher plume index values have been shown to increase body condition, fledging success, and survival, as prey are expected to be concentrated in pockets of oceanographic productivity and thereby easier for penguins to encounter (17, 20, 32). To calculate the plume index, we extracted SSTAs during migration for an area from 40 to 23°S and from the coast to the 1,000 m isobath. We excluded data further out than 1,000 m because Magellanic penguins commonly migrate over the continental shelf (32, 63). We conducted a principal components analysis of the SSTA data to quantify the spatial and temporal patterns following Rebstock et al. (32). The first three principal components represented 30.4, 14.0, and 6.3% of the variance in the SSTAs. Following Rebstock et al. (32), we used the first principal component and temporally averaged the monthly plume index from May to August to align with the migratory period for our colony.

IPM². To understand eco-evolutionary processes in this population, we built an IPM², which is a combination of an integrated population model (29) and an integral projection model (28), following Plard et al. (27). The integrated population model links survival and reproduction to population datasets, whereas the integral projection model links body size and inheritance datasets to survival. We did not model the effect of body size on reproduction (but still estimate annual fecundity), as preliminary analyses indicated that this effect was minimal, and previous analyses showed that reproduction was not a significant driver of population dynamics or fitness (17, 21).

The population model is a prebreeding, six-stage, female-only state-space model with immigration. Males were excluded from this model as males are not limiting factors for reproduction or population growth in this colony (70). Magellanic penguins do not breed until age 4+ and sometimes skip breeding due to poor body condition, so we assumed a relatively simple stage structure (17, 67). Population stages (a) included juveniles (n_{juv}), second years (n_2), third years (n_3), prebreeders (n_P), breeders (n_B), and nonbreeders (n_N). The population projection over years is given by

$$n_{juv,t+1} = I(0.5f_t S_{J,t} n_{B,t})',$$

$$n_{2,t+1} = S_{P,t} n_{juv,t},$$

$$n_{3,t+1} = S_{P,t} n_{2,t},$$

$$n_{P,t+1} = (S_{P,t} n_{3,t}) + (1+\gamma)(S_{P,t} n_{P,t}),$$

$$n_{B,t+1} = \gamma(S_{P,t} n_{P,t}) + \delta(S_{A,t} n_{B,t}) + (1-\varepsilon)(S_{A,t} n_{N,t}) + \omega_t(S_{A,t} n_{B,t}),$$

$$n_{N,t+1} = (1-\delta)(S_{A,t} n_{B,t}) + \varepsilon(S_{A,t} n_{N,t}),$$

where *I* is the inheritance matrix (see paragraph below). F_t is the fecundity (number of fledged chicks per nest with eggs), which we multiply by 0.5 to reflect an even sex ratio at hatching (64). S_J, S_P, and S_A represent the survival vector over size of the apparent juvenile (from fledging to first year), apparent prebreeder (2–4), and apparent adult (4+) survival probability, respectively, of individuals. We assumed 3 age classes for survival due to evidence that survival among adults is similar, regardless of breeding state (67). γ is the probability of transitioning from a prebreeder to a

breeder, δ is the probability for a breeder to remain a breeder, and ε is the probability for a nonbreeder to remain a nonbreeder. ω_t is the immigration rate, which is a latent variable expressed as a per capita rate relative to the population size the year before. We assumed immigration due to evidence of metapopulation dynamics among Magellanic penguin colonies (53, 71); however, evidence of emigration out of our colony is known to be very small (17).

The population size column vectors, n_a, describe the population size for each population stage (a = juveniles, second-years, third-years, prebreeders, breeders, and nonbreeders) as a frequency distribution over the body size trait, z, similar to traditional integral projection models (27). The body size trait is fixed and does not change with age, as penguin body size stabilizes early on in development (33). The body size trait z is divided into 50 bins from standardized PCA values of −5 to 5, where the bin-value midpoints $z = [Z_1, Z_2 … Z_M]$ are the medians of these body size trait classes. We found that the number of bins/midpoints did not affect our results from varying them from 25 to 100 (72). To better visualize the effect of these body size trait classes, we divided up the values into "small", "medium", and "large" categories, representing values from −5 to −1.667, −1.667 to 1.667, and 1.667 to 5, respectively. The survival matrix S_c are diagonal matrices describing the survival of each survival age class (c) according to the individual trait z. The inheritance matrix, *I*, describes the probability for the juvenile of a parent with juvenile body size trait z inheriting the body size trait z′. The change in the distribution of all individuals in the vector n is calculated based on S and I, influenced by body size and environmental variables, as described in the section "Assessing the effect of climate variables and individual traits".

The likelihood of the observed number of adult breeding penguins in each year (Y_t) is a truncated normal distribution with mean equal to the sum of the breeding population vector over size:

$$Y_t \sim Truncated\ Normal\left(\sum_z n_{B,z,t}, \tau_Y\right),$$

where τ_Y is the observation error for the population counts. The normal distribution is truncated to prevent population values falling below zero.

To estimate annual survival per age class, $S_c(z)$, and recapture probabilities, p, we used the individual histories of capture-recapture, Φ, and a Cormack–Jolly–Seber model with a multinomial likelihood. See ref. 27 for more information on the model likelihood.

The observed body size trait Z′ of fledgling *I* whose parent had the body size trait Z is given by

$$Z'_i \sim N(\mu_I(Z_i), \sigma_I),$$

where μ_I and σ_I are the mean and variance of the inheritance function.

The observed number of fledglings J_t in a given year t was used to estimate annual fecundity, f_t:

$$J_t \sim Pois(f_t R_t),$$

where R_t is the total number of surveyed nests per year.

The likelihood of the four datasets (population size, survival, reproduction, and inheritance) are multiplied to form a joint likelihood for the IPM², made up of state-space, multinomial, Poisson, and normal distribution models, respectively:

$$L_{IPM^2} = L_{Ob}(Y|n,\tau) * L_{Pr}(n|S, f, \gamma, \delta, \varepsilon, \omega, \mu_I, \sigma_I) * L_{Bi}(\Phi|S, p)$$
$$* L_{Po}(J, R|f) * L_{No}(Z'|\mu_I, \sigma_I).$$

Assessing the Effect of Climate Variables and Individual Traits. We fitted the relationships of our IPM² using logit-linear and normal regressions to estimate the effect of climate variables (SSTA and plume) and body size on survival and inheritance, respectively. We modeled inheritance as a function of climate variables and body size with an identity link:

$$\mu_I(z) = i_I + \alpha_1 * z + \alpha_2 * SSTA + \alpha_3 * Plume + \alpha_4 * z$$
$$* SSTA + \alpha_5 * z * Plume,$$

where i_I is the intercept of the inheritance function, and α are the slopes for the body size and climate covariates.

We modeled juvenile, prebreeder, and breeding adult survival using the same function of climate variables and body size with a logit-link:

$$logit\left(S_c(z)\right) = i_{S,c} + \beta_{1,c} * z + \beta_{2,c} * SSTA + \beta_{3,c} * Plume + \beta_{4,c}$$
$$* z * SSTA + \beta_{5,c} * z * Plume,$$

where $i_{S,c}$ is the intercept of the survival function of survival age class c, and β are the slopes for the body size and climate covariates. Each covariate was standardized to have zero mean and unit variance to compare the effect sizes of α and β to each other. We computed the mean and 95% CRI for the regression coefficients. During preliminary analyses, some of the model coefficients had 95% CRIs that overlapped zero. In subsequent analyses, we removed them from the model using a stepwise model selection process. *SI Appendix*, Table S1. In addition, we also considered the importance of density dependence in the survival function and found that these regression coefficients overlapped zero, so we removed this variable from the model. These relationships are shown in Figs. 2*A* and 3, and *SI Appendix*, Fig. S1.

To independently quantify the form and strength of selection on penguin body size, we used regression-based methods to calculate selection gradients (73, 74). We estimated directional and quadratic selection gradients for adult and juvenile survival as a function of body size by calculating the first-order and second-order derivatives of the model describing the relationship between survival, climate variables, and body size following (74). Directional selection gradients are shown in *SI Appendix*, Fig. S2, indicating varying selection over time in accordance with fluctuating climate. Quadratic selection gradients were found to be very small and overlapped with zero. This is consistent with past research finding fluctuating selection where fitness was measured by reproductive success (21). We also calculated lifetime directional selection (75) across juvenile and adult survival, estimating it to be 0.966, or 0.0261 per year, which confirms the evidence for the weak directional change in body size we found (Fig. 2*B*). There is likely a much stronger effect of fluctuating selection where fitness is measured by adult survival than juvenile survival, as adult survival has a much stronger effect on penguin fitness and population dynamics than juvenile survival (17, 21).

Model Implementation and Selection. We used a Bayesian framework using Nimble (76, 77) run from program R to fit the IPM[2]. As prior distributions, we modeled the intercepts of the demographic/inheritance parameters (e.g., i_S, i_I) and slopes of covariates (α, β) using vaguely informative prior distributions of N(0, 0.34). Transition parameters ($\gamma, \delta, \varepsilon$) were given a uniform distribution over the interval [0,1]. Observation error (τ_y) was given a vague prior of U(0, $4*10^{-10}$). Variance of the inheritance function was given a vague uniform distribution over the interval [0,100] (78). Three independent MCMC chains of 10,000 iterations were used with a burn-in period of 5,000. Final inferences were derived from a sample of 3*5,000 iterations that resulted from merging the chains. Convergence of chains was assessed using the Gelman–Rubin convergence diagnostic (R < 1.5) (79) and chains were well mixed.

Eco-Evolutionary Projection Scenarios. To determine the effects of interannual environmental variability, as measured by the interannual SD in SSTA and the plume index, we ran 1,000 simulations projected forward 100 years using our IPM[2] in Nimble and the parameter values we estimated previously. In these simulations, we generated oceanographic data for SSTA and the plume index by drawing 100 random values from normal distributions that were fit to the prior observed climate data, varying the SD of the normal distribution from 0 to 2. We measured changes in the penguin population size using geometric mean lambda, which is the product of annual population growth rates over 100 years and more useful for characterizing fluctuating populations. We measured changes in penguin body size by calculating the difference between the mean body size at the beginning and end of the sensitivity analysis.

To estimate the likelihood of evolutionary rescue under different scenarios, we projected 100 simulations of the population forward 100 years using our IPM[2]. Scenario 1 (climate based on current rate of change) was run using generated oceanographic data from normal distributions based on the prior observed climate data. Scenario 2 (increasing plume variability) was run by doubling the rate of plume index interannual variability. Scenario 3 (decreasing age at first breeding) was run by altering breeding parameters and removing the n_1, n_2, and n_P population stages in the model, thereby allowing individuals to breed after their first year. We note here that age at first breeding may evolve, but we have no evidence in this population that this trait is changing (64, 67). We also compared 1-, 2, and 3-year age at first breeding scenarios (*SI Appendix*, Fig. S3). Scenario 4 (increasing heritability) was run by setting the slope of the inheritance function (α_1) to 0.8 based on levels of high heritability in Darwin's finches (23). For all scenarios, we calculated the mean and 95% CIs across the 100 simulations and calculated population and body size change using methods discussed previously.

Data, Materials, and Software Availability. The code and data needed to reproduce this analysis can be found on Github and is archived on Zenodo (80).

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