Cooling requirements fueled the collapse of a desert bird community from climate change

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Climate change threatens global biodiversity by increasing extinction risk, yet few studies have uncovered a physiological basis of climate-driven species declines. Maintaining a stable body temperature is a fundamental requirement for homeothermic animals, and water is a vital resource that facilitates thermoregulation through evaporative cooling, especially in hot environments. Here, we explore the potential for thermoregulatory costs to underlie the community collapse of birds in the Mojave Desert over the past century in response to climate change. The probability of persistence was lowest for species occupying the warmest and driest sites, which imposed the greatest cooling costs. We developed a general model of heat flux to evaluate whether water requirements for evaporative cooling contributed to species' declines by simulating thermoregulatory costs in the Mojave Desert for 50 bird species representing the range of observed declines. Bird species' declines were positively associated with climate-driven increases in water requirements for evaporative cooling and exacerbated by large body size, especially for species with animal-based diets. Species exhibiting reductions in body size across their range saved up to 14% in cooling costs and experienced less decline than species without size reductions, suggesting total cooling costs as a mechanism underlying Bergmann's rule. Reductions in body size, however, are unlikely to offset the 50 to 78% increase in cooling costs threatening desert birds from future climate change. As climate change spreads warm, dry conditions across the planet, water requirements are increasingly likely to drive population declines, providing a physiological basis for climate-driven extinctions.

thermoregulation | climate change | desert birds | evaporative cooling | Bergmann's rule

Climate change threatens to accelerate the ongoing, rapid loss of biodiversity (1, 2), prompting an urgent need to identify the mechanisms that make species vulnerable (3). Vulnerability to climate change increases when environmental conditions challenge an organism's capacity to balance heat and water budgets (4), suggesting physiological mechanisms will underlie some population declines (5). However, the physiological bases of climate vulnerability are often inferred indirectly from population declines (6), and empirical evidence supports the uncoupling of species interactions as the most common cause of climate-driven extinctions (7). A major impediment to detecting the physiological bases of climate vulnerability is the complex nature of the organism–climate interaction, especially for endotherms. Heat transfer through avian plumage and mammal pelage complicates our understanding of the homeothermic requirements of endotherms (8, 9). Establishing meaningful links between physiology and long-term population responses to climate change would represent a major advance for predicting endotherm climate vulnerability.

At a fundamental level, energy imbalance between an organism and its environment—manifested as changes in mass, water, and heat—drives climate vulnerability (4). The primary determinants of energy exchange are environmental temperature and body size (10). Body size determines an organism's total energetic

requirements, whereas temperature modulates this relationship (11). Warming temperatures can influence the spatial and temporal patterns in body size by causing local energetic imbalances (12). Large-bodied endotherms, for instance, simultaneously experienced rapid extinction (13) and reductions in body size during Pleistocene warming (14), with analogous patterns occurring in response to human-caused climate change (15). Similar negative associations between body size and average annual temperature have also been reported across species' geographic ranges in a pattern generally referred to as Bergmann's rule (16). However, models of heat flux have not supported a mechanistic explanation of Bergmann's rule (17), possibly due to their focus on the benefits of greater heat retention in large-bodied endotherms inhabiting cool climates. Given that geographic variation in body mass is more strongly associated with maximum than minimum temperatures (18), shifting perspectives to evaluate size-dependent cooling costs in hot environments might produce different insights.

We developed simulation models of heat flux to evaluate whether water requirements for evaporative cooling contributed to the collapse of the Mojave Desert bird community over the last century that has been explicitly linked to climate change (19). Since the original surveys by Joseph Grinnell and others in the early 20th century, Mojave sites, situated mostly within national parks and reserves with minimal land use change, have lost on average 43% of their bird species. Occupancy probability

Significance

Climate change—especially accelerated warming and drying—threatens to increase extinction risk, yet there is little evidence that physiological limitations have contributed to species declines. This study links species-specific water requirements for cooling body temperature to the collapse of a Mojave Desert bird community over the past century from climate change. Species occupying the hottest, driest sites were less likely to persist. Birds with the greatest water requirements for cooling their body temperature experienced the largest declines. Large-bodied carnivores and insectivores were especially vulnerable to cooling costs because they obtain water primarily from their food. Climate warming increases the evaporative cooling demand for birds, which will affect geographic patterns in body size and future extinction risk.

ECOLOGY

significantly declined for 39 of 135 (29%) breeding birds, while only one species significantly increased. Climate change, particularly a long-term decline in precipitation, was the most important driver of site-level persistence of species (19). Drying conditions should impose the greatest pressure on homeothermy in warming environments by increasing water requirements for cooling, while simultaneously limiting the availability of water. Here, we evaluated the prediction that persistence of bird species over the past century should be lowest at hot, dry sites due to greater water requirements for cooling. We then estimated species-specific cooling requirements in 50 species using a simulation-based approach that linked climate warming to biophysical traits, such as body size, shape, and plumage properties. We focused on cooling costs because water requirements for homeothermy in birds increase exponentially under warm conditions, leading to potentially lethal dehydration under climate change (20). We used our simulations to 1) test whether increases in cooling requirements over the past century were associated with occupancy declines species experienced in the Mojave, and 2) explore cooling requirements as a mechanism underlying Bergmann's rule.

Results

Persistence of Desert Birds and Climate. Community-level occupancy analyses revealed the probability of persistence at a site over the last century was lowest for birds in hot, dry environments (Fig. 1 and *SI Appendix*, Table S1). Moreover, the presence of standing water increased persistence probabilities across all climatic conditions (Fig. 1 and *SI Appendix*, Table S1). Low persistence probabilities at the hottest, driest sites with the greatest water requirements for cooling and limited access to water suggests an underlying mechanism of species declines related to cooling costs. Moderately lower persistence also occurred in the coolest, wettest sites located in the high elevation sites when surface water was absent (Fig. 1).

A General Model of Cooling Costs for Birds. We developed estimates of cooling requirements using an energy balance equation:

$$Q = M - E - C\frac{dT_b}{dt} = K_e(T_b - T_e),$$ [1]

where Q is the net sensible heat flux, M is the heat generated through metabolic processes, E is the heat lost via evaporative processes, C is the heat capacitance of the isothermal core, T_b is body temperature, K_e is the effective conductance, and T_e is the operative temperature (*SI Appendix, Heat flux simulation*). To generate estimates of chronic heat stress, we estimated daily water requirements for evaporative heat loss ($Q < 0$ in red; Fig. 2 *B*, *E*, and *H*), using physical calculations that incorporated variation in 10 thermally relevant, avian traits that affect heat flux from measurements of museum specimens (Fig. 2 *A*, *D*, and

G) for 50 species (*SI Appendix*, Table S2). Our approach uses first principles to simulate the combined influence of air temperature, radiation, and solar exposure on the amount of cooling required to maintain a stable body temperature. Our model is similar to endothermic simulations of heat flux (9), except we focus on the increase in thermoregulatory costs over the last century to isolate the impact of climate change.

Our general model of endotherm thermoregulation accurately simulated avian evaporative water loss (Fig. 2). Simulations revealed that water requirements for evaporative cooling are greatest 2 h after midday, reduced by seeking shade, and greater in large-bodied species (Fig. 2 *B*, *E*, and *H*). Model estimates of water requirements were strongly correlated to Q measured from controlled laboratory studies of birds (Fig. 2 *C*, *F*, and *I*), validating that our model accurately predicted intraspecific and interspecific homeothermic requirements. Model outputs of T_e also closely matched empirical measurements from field studies in complex thermal environments (*SI Appendix*, Fig. S1).

Declines in Avian Occupancy, Cooling Costs, and Behavioral Traits. Our simulations indicated that the increase in cooling costs over the past century was a likely mechanism underlying avian declines from climate change. On average, cooling costs increased by 18.8% (±5.0%) relative to historic climates (*SI Appendix*, Fig. S2E). The increase in cooling costs was positively correlated with body mass (Fig. 3A), with the largest species experiencing a 42-fold increase in cooling costs relative to the smallest species for the same degree of warming. Both mass and cooling costs were positively associated with the degree of species decline (Fig. 3 *A* and *B*), but AICc (Akaike information criterion corrected for small sample size) weights indicated the evidence in favor of cooling costs was 4.5 times greater than body mass (*SI Appendix*, Table S3). Phylogenetic analyses indicated that these relationships were unassociated with relatedness (*SI Appendix*, Fig. S4; median value of $P = 0.127$; see also ref. 19). The relationship between cooling costs and occupancy decline was robust upon incorporating hyperthermia and shade-seeking behavior (*SI Appendix*, Table S4), suggesting that physiological and behavioral strategies for seeking cooler microhabitats were unable to compensate for the increase in cooling costs.

Increased cooling costs may disproportionately affect species with certain behavioral traits. Diet is especially likely to affect cooling costs by determining the primary source of water intake. Compared to plant-eating species, birds with animal-based diets infrequently drink from freestanding water (21), rely on preformed water from their prey during the hottest, driest times of year (22, 23), and tend to have higher resting water loss rates (24). For birds with more plant-based diets, meeting their requirements for water intake depends on the distance to surface water (21, 25). We found that cooling costs explained nearly half of the variation in decline for insectivores and carnivores
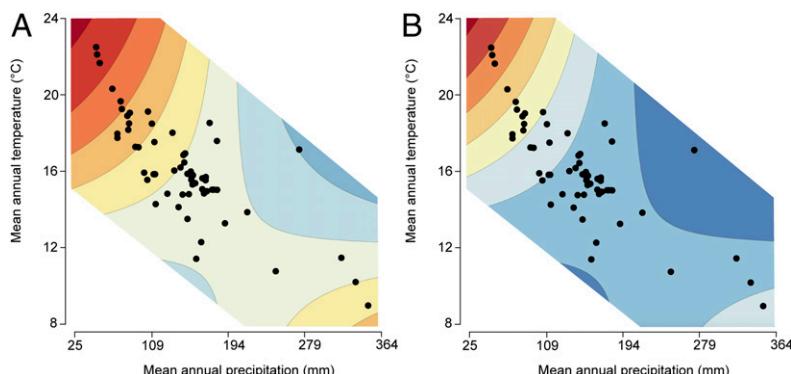
Fig. 1. Low persistence at hot, dry sites suggests water requirements underlie avian community collapse. (*A*) Avian persistence over the last century was lowest in the hottest, driest sites in the absence of surface water. Persistence was moderate in less hot and dry sites, and declined slightly in cool, wet sites likely due to factors not related to cooling costs. (*B*) Predictions for persistence in the presence of surface water indicate that persistence was much higher in areas except for hot, dry sites.

Riddell et al.
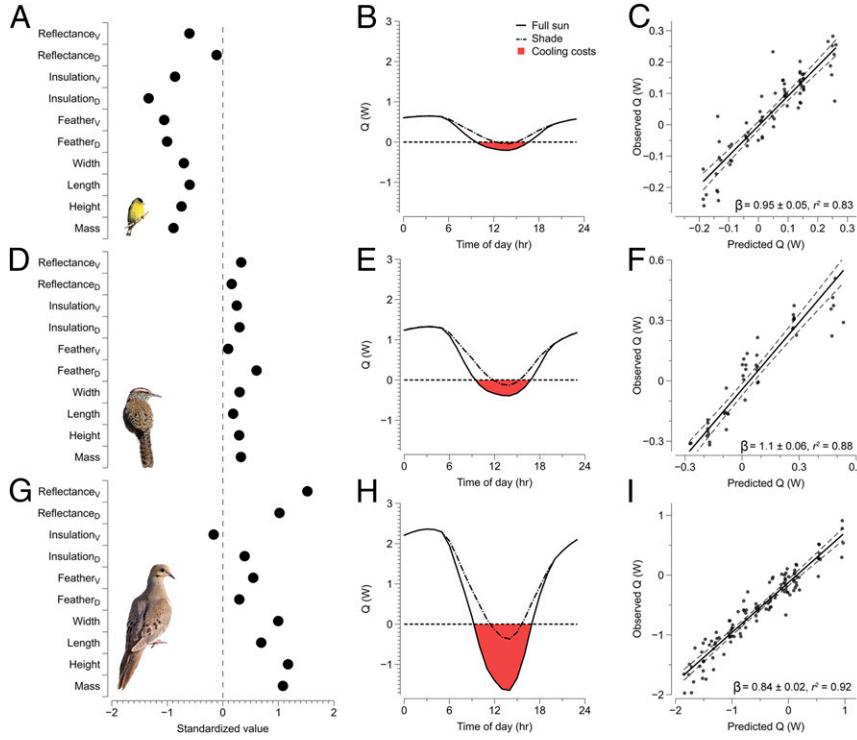
Fig. 2. Simulation-based model predicts intraspecific and interspecific variation in cooling costs. (*A*, *D*, and *G*) Standardized values of biophysical traits (defined in *SI Appendix*, Table S10) used to estimate thermoregulatory costs of the (*A*) lesser goldfinch (*Spinus psaltria*), (*D*) cactus wren (*Camplyohynchus brunneicapillus*), and (*G*) mourning dove (*Zenaida macroura*). Biophysical traits were standardized relative to all 50 study species. (*B*, *E*, and *H*) Net sensible heat flux (*Q*) during the hottest day of the year in the Mojave Desert while sitting in full sun (solid line) and 50% shade (dashed line). Cooling costs, or the amount of water required for evaporative cooling in watts (W), are displayed in red and do not incorporate thermoregulatory mechanisms (e.g., panting, gular flutter, or cutaneous water loss) that a particular species might use to thermoregulate. (*C*, *F*, and *I*) Performance of simulation in predicting *Q* from the integrated value of metabolic rate, evaporative heat loss, and changes in body temperature from physiological studies of the 3 species. Images for the species were downloaded from Google image search engine with the usage rights to use and share and modified in Adobe Photoshop.

(Fig. 3*B*), consistent with our expectations. Decline in birds with plant-based diets was unrelated to the variation in cooling costs (Fig. 3*B*). By converting cooling costs to insect requirements, we demonstrated that body size magnifies food demands for hydration, as larger species require approximately 7 times more prey biomass per day than smaller birds to offset increased cooling costs, regardless of prey size (Fig. 3*C*). Elevational preference, habitat preference, migratory mode, clutch size, and sexual dimorphism were not associated with occupancy decline after accounting for cooling costs (*SI Appendix*, Tables S5–S9). Long-term changes in wind speed and food availability were also unlikely factors underlying species declines (*SI Appendix*, *Supplementary Text*).

Body Size, Cooling Costs, and Bergmann's Rule. We examined the relationship between body mass and average annual temperature using 28,367 records from western North America (*SI Appendix*, *Analysis of geographic variation in avian body mass*). Most bird species tended to follow Bergmann's rule, as reflected by smaller masses in warmer climates (negative slopes for 80%, 40 out of 50 species, of which 22 were significant), while 20% tended to exhibit larger masses, counter to Bergmann's rule (positive slopes for 10 species, of which 2 were significant) (Fig. 4*A* and *SI Appendix*, Fig. S6). Positive relationships reflect the diverse mechanisms underlying geographic variation in body size (26). Nevertheless, the magnitude of variation, either supporting or countering Bergmann's rule, may have consequences for species in hot environments that can be explicitly evaluated using thermoregulatory simulations (27).

We estimated the consequences of body size variation by comparing cooling costs from simulations that used the observed geographic variation in body size to those that held body size constant. The analysis determined whether the increase or reduction in body mass with respect to latitude was related to the collapse of desert birds. Occupancy decline over the last century was unrelated to the reduction in cooling requirements for species that followed Bergmann's rule (Fig. 4*B*), suggesting that

reductions in body size alleviated some of the water requirements for Mojave birds. For species with a pattern counter to Bergmann's rule, however, occupancy declines were positively related to cooling costs resulting from increased body size in the Mojave (Fig. 4*C*). The benefits and costs of geographic variation in body size were localized to the hottest regions of the California desert (Fig. 4 *D* and *E*), possibly contributing to the limited support for Bergmann's rule at continental scales (26).

Impact of Future Climate Change on Cooling Costs. Our simulations provide a heuristic understanding for reductions in body size and activity to decrease cooling requirements under future climate change (Fig. 5). We estimated that Mojave birds will experience an increase in water requirements of 50 to 78% under future climate scenarios, all else held equal (Fig. 5*A*). To avoid this cost, birds would need to reduce body mass by 36 to 52% on average, depending upon the warming scenario and species (Fig. 5*B*). In extreme cases, body mass in birds has declined by as much as 27.2% over 49 y (28), but such reductions are rare and seem unlikely. Alternatively, birds might lessen vulnerability by reducing activity by 18 to 36% (Fig. 5*C*), but reductions in activity would likely reduce survival or reproductive success (29).

Reductions in basal water loss, excretory water loss, or feather absorptance are unlikely to offset cooling costs because thermoregulatory costs are commonly an order of magnitude higher than basal water loss rates (30–32), excretory water loss typically represents a small fraction of the total water budget (33), and climate warming requires unrealistic reductions in feather absorptance (*SI Appendix*, *Reductions in activity and body mass under climate change*).

Discussion

Cooling Costs as a Driver of the Desert Bird Community Collapse. Over the past century, the Mojave Desert bird community collapsed in association with a long-term reduction in precipitation from climate change (19). Despite being located primarily on protected lands, sites lost on average 43% of their breeding bird
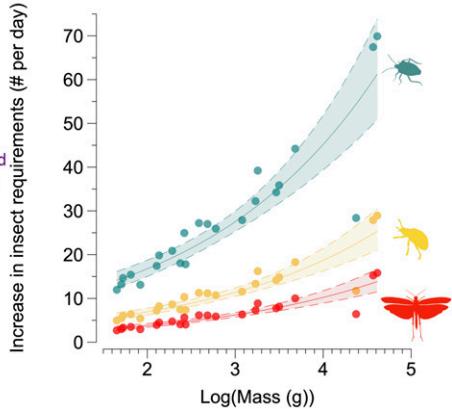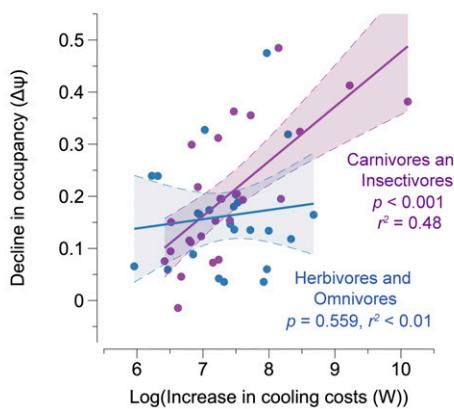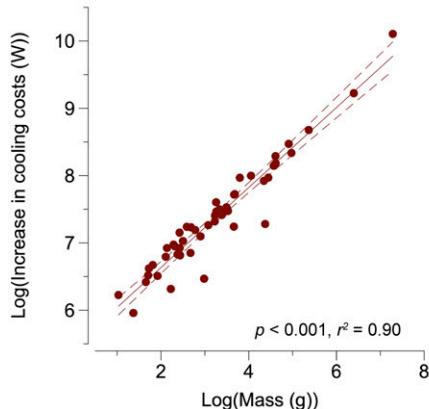
Fig. 3. Water requirements for evaporative cooling contributed to occupancy decline in desert birds. (*A*) The increase in cooling costs over the past century of warming (~1.5 °C) was positively related to avian body mass. (*B*) An interaction between diet and cooling costs revealed that occupancy decline in carnivores and insectivores (purple) was highly associated with water requirements but less so in herbivores and omnivores (blue). (*C*) The number of additional insects per day required to offset the increase in cooling costs assuming a diet of herbivorous stink bugs (*Dendrocoris contaminates* in green), beetles (*Edrotes ventricosus* in yellow), and grasshoppers (*Bootettix argentatus* in red). Larger birds need to find more prey than smaller birds, but they can reduce the number of prey needed by finding larger, yet more dispersed prey. Silhouettes were downloaded from www.phylopic.org and edited in Adobe Photoshop.

species and occupancy probability declined significantly for 29% of the 135 species. Our simulations revealed a potential physiological basis underlying the community collapse by linking climate with the fundamental need to thermoregulate. The probability of a species persisting was lowest at the hottest, driest sites and at sites without surface water (Fig. 1). Together, these conditions challenge the capacity of endotherms to offload excess heat via evaporative cooling. Persistence of species was also moderately lower at cooler, wetter sites at high elevations (Fig. 1*A*), suggestive of multiple underlying mechanisms. These high elevation sites were the wettest sites but also experienced the greatest increase in average temperature and a recent destructive fire (19). Although other factors may have contributed to the collapse, multiple lines of evidence indicate cooling costs as an important underlying mechanism.

We developed a heat flux model for birds that used similar equations derived from the same general theory as previous approaches (9, 34, 35), with 2 exceptions. We focused on the change in cooling costs without incorporating basal water requirements, and we modeled heat flux on the dorsal and ventral sides separately, as opposed to averaging across the whole organism. Quantifying the change in cooling costs isolated the impact of climate change on water requirements independent of the costs imposed by obligatory water loss to offset metabolic heat production (i.e., basal water requirements). Incorporating basal water requirements would not affect our interpretations, because basal cooling costs scale positively with body size (36). Thus, incorporating these rates would further exacerbate the size-mediated impact of climate change on cooling costs. We also modeled heat flux by considering morphological differences across the dorsal and ventral sides of birds (37). Simulating heat flux in this way offers an opportunity to incorporate the physiological role of morphological variation, such as differences in feather absorptance between the dorsum and ventrum (*SI Appendix*, Table S2).

We demonstrated that avian declines were strongly correlated with the increase in water requirements for homeothermy (Fig. 3). The increase in cooling costs potentially explains the greater declines in larger-bodied species (Fig. 3 and *SI Appendix*, Table S3) and appears robust to behavioral modifications such as seeking shade under vegetation (*SI Appendix*, Table S4). The increase in cooling costs also disproportionately affected species based upon their dietary preferences. Dietary preferences

influence the source of preformed water, a factor not considered in recent studies of water-related stress from climate change in birds (20, 38). Desert birds with animal-based diets infrequently drink surface water, instead relying predominantly on their prey for water (22, 23). Increased cooling costs translate into higher foraging rates, exacerbating water loss through increased activity (39) and solar exposure (40). Because birds with plant-based diets drink from free surface water, balancing water budgets appears less likely to be related to thermoregulatory costs and more likely to be affected by the distance from surface water (19, 41). Thus, the physiological basis of climate change in desert birds may act through its effects on the magnitude of cooling costs for insectivores and carnivores, whereas its relevance for herbivores and omnivores may be determined by the distance to surface water.

A bird's sensitivity to cooling costs may also depend on its behavioral repertoire and the availability of cooler microhabitats. During the hottest periods of the day, desert birds restrict foraging to shaded microhabitats or cease foraging entirely (23, 42). The ability of small insectivores, like the Verdin, to forage in the shade reduces heat gain from the environment while maintaining energy and water intake (42), possibly contributing to the higher persistence of smaller birds over the last century. Larger birds, however, likely struggle to access cooler conditions due to the small dimensions of commonly available microhabitats (43). Moreover, large carnivorous birds in the Mojave Desert are most often observed perching in direct sunlight (44), which increases water requirements for evaporative cooling from solar exposure. Desert birds can dramatically lower cooling costs by ceasing activity, finding cool microhabitats, or soaring to higher altitudes, but such behaviors involve spending less time foraging, defending territories, and finding mates (45)—all important components of fitness (46). Having less time for fitness-related activities might also have a disproportionate impact on larger bodied birds.

The observed declines in larger birds conflicts with recent predictions that smaller birds are more vulnerable to water-related challenges than larger birds due to high surface area-to-volume ratios (20). A higher ratio results in smaller birds more rapidly reaching critical dehydration tolerances, all else equal. However, this perspective does not capture the need for greater absolute water intake requirements of larger-bodied species. These opposing perspectives reflect the long-standing debate on whether higher mass-specific fluxes of water or heat, as opposed

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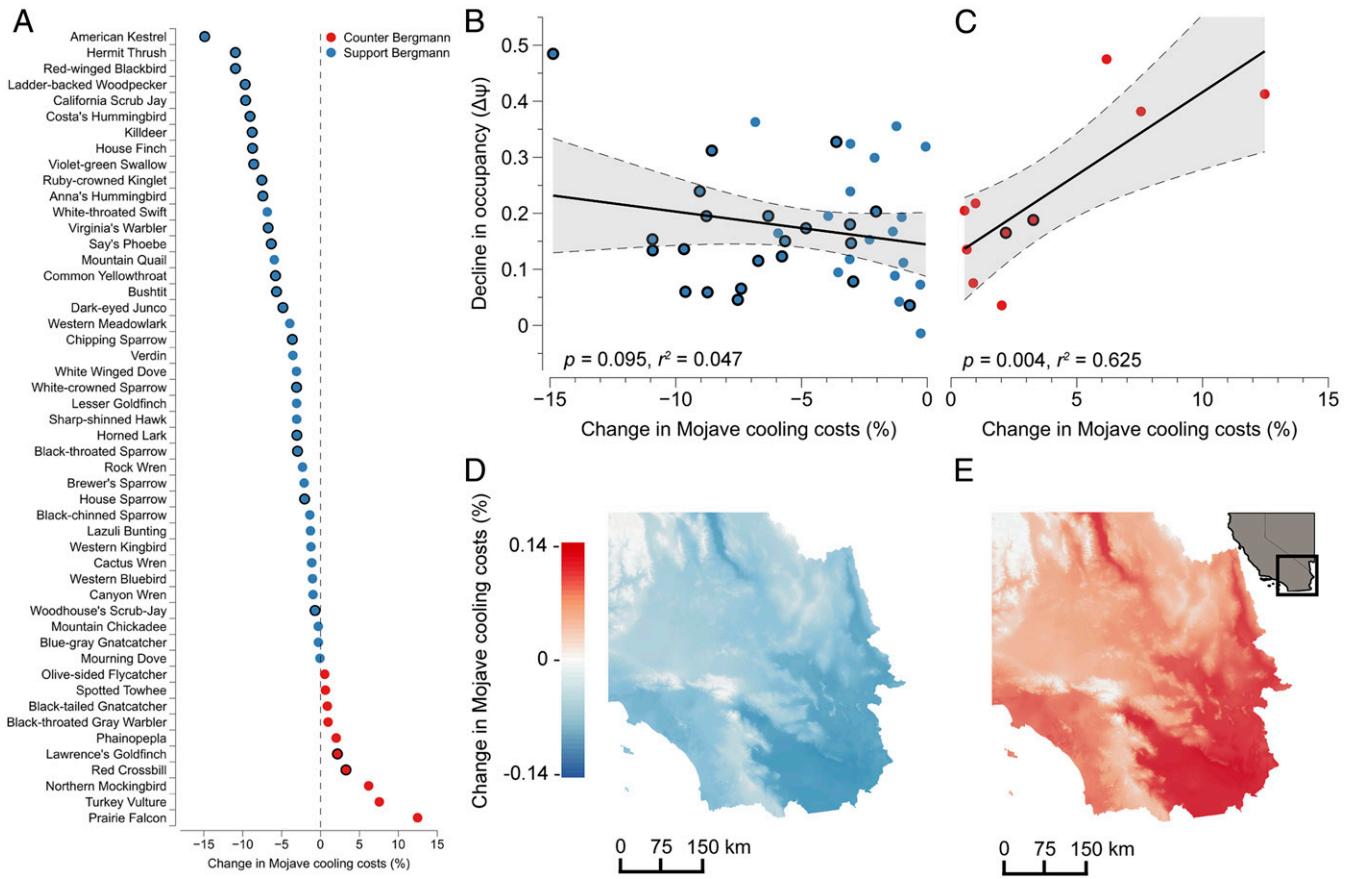
Fig. 4. The change in cooling costs due to geographic variation in body size and their relationship to decline in the Mojave. (*A*) The percent change in cooling costs between simulations with and without geographic variation in body size; colors indicate species with slopes that support Bergmann's rule (blue) and countered Bergmann's rule (red). Points with black outline indicate species that significantly supported or countered Bergmann's rule. (*B* and *C*) Percent change in Mojave cooling costs, weighted by uncertainty of body mass regressed against average annual temperature, was unrelated to occupancy decline for species that followed Bergmann's rule but positively associated with decline for species that violated Bergmann's rule; colors are as in *A*. (*D* and *E*) Spatial variation in size-related cooling costs for the American kestrel (*Falco sparverius*) and the prairie falcon (*Falco mexicanus*) illustrate the impact of body size variation is localized to the desert. These 2 species exhibited the greatest reduction and increase in mass in the Mojave Desert, respectively.

to the total flux, are more ecologically relevant (47). In our study, we found no support for mass- or surface area-specific rates explaining declines (*SI Appendix*, Fig. S2). Rather, large desert birds require nearly 7 times more prey than small-bodied birds to offset their cooling costs from a ~1 °C increase in mean air temperature, despite losing water at a proportionally lower rate (Fig. 3*C*). Models that explicitly incorporate water intake also indicate that small-bodied birds balance water budgets more easily (48). Birds might switch to larger, more hydrating prey (Fig. 3*C*, orange and red) to reduce the total number of insects required for hydration. However, densities are much lower for large insects in the Mojave (*SI Appendix*, Fig. S3) and are lowest during the hottest months of the year (*SI Appendix*, Fig. S4).

Cooling Costs and Bergmann's Rule: Cause or Consequence? The influence of body size pervades the biological hierarchy of life—from driving physiological rates at the cellular level to affecting the function of ecological networks (49). This wide array of interactions implies variation in body size can be driven by many mechanisms, including heat dissipation, resource availability, and dispersal limitations (16).

Our analysis suggests that cooling costs can be both a cause and a consequence of geographic variation in body size. Reductions in body size in hot environments was associated with sustained occupancy over the past century (Fig. 4), indicating total cooling costs as a mechanism underlying Bergmann's rule.

Species exhibiting a pattern counter to Bergmann's rule comprised 20% of our sample, implying mechanisms unrelated to thermoregulation to underlie geographic variation in body size (47). Nevertheless, increased body size in warm climates translated into negative consequences for species persistence.

Many bird species did not exhibit significant variation in body size with climate, consistent with other analyses (26). Our analysis indicates that the physiological mechanism underlying body size clines may be related to total cooling costs, rather than mass-specific heating and cooling as others have proposed (47). Geographic variation in body size likely depends upon the impact of behavior, physiology, and morphology on the magnitude of total cooling costs, as well as the extent to which species experience extreme environmental conditions across their geographic range. Exploring these interactions will reveal the multiple processes driving the high degree of interspecific variation in the support for Bergmann's rule (26).

Conclusions

Species interactions are thought to cause most climate-driven extinctions to date (7), partly because the physiological bases of climate vulnerability are complicated by thermodynamic relationships with the environment. By directly modeling the water requirements of desert birds, our study illustrates the importance of an intrinsic, physiological basis of avian decline that is associated with climate change (19). We uncovered greater climate
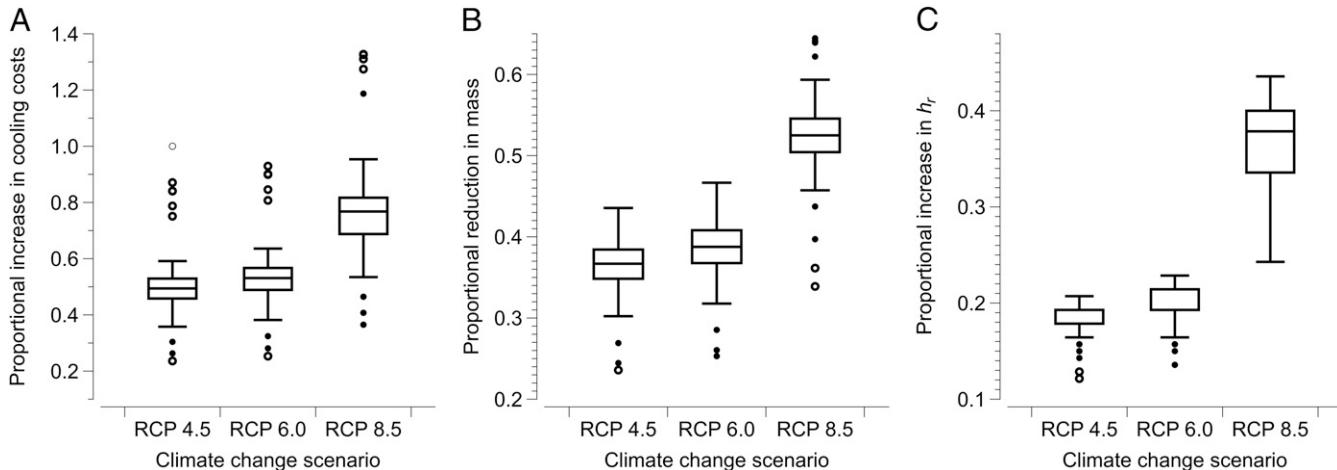
Fig. 5. The potential for reductions in body size or activity to alleviate cooling costs under climate change. (*A*) The increase in cooling costs for 3 climate change scenarios, Representative Concentration Pathway (RCP) 4.5, 6.0, and 8.5, assuming organisms maintain the same levels of activity as under contemporary climates. Global air temperatures are predicted to rise 1.8 °C, 2.2 °C, and 3.7 °C under these RCP scenarios, respectively. (*B*) Reductions in mass required to maintain contemporary levels of cooling costs. (*C*) Increase in hours of activity restriction (h_r) required to maintain contemporary levels of cooling costs. We expressed values relative to contemporary mass, cooling costs, or h_r. Box plots illustrate median values with interquartile ranges.

vulnerability in larger species from accelerated water requirements, which was especially relevant for birds with animal-based diets and at sites without surface water.

Water requirements are increasingly likely to drive population declines as climate change spreads warm and dry conditions across the planet over the next century (50). Thus, species with large body size, with animal-based diets, and that violate Bergmann's rule may become more vulnerable globally. Although our study focused on a physiologically challenging desert environment, ecologists can leverage climate–organism interactions to identify the relevance of other intrinsic, physiological factors. In tropical environments, for instance, rising temperatures may predispose ectotherms with high thermal sensitivities to greater climate vulnerability (51). Thus, linking physiology to relevant ecological traits may become a powerful approach to identifying biodiversity vulnerable to climate change.

Methods

Avian Occupancy and Persistence. Resurveys evaluated the response of desert birds to climate and environmental change at 61 sites throughout the Mojave Desert that were originally surveyed for avian diversity during the early 20th century by Joseph Grinnell and colleagues (19). Iknayan and Beissinger (19) used a dynamic, multispecies occupancy model (MSOM) that incorporated imperfect detection to yield species-specific estimates of occupancy probability (the proportion of sites occupied during historical and modern surveys) for 135 bird species. Values from their dataset S1 were used to calculate the difference between historic and modern occupancy ($\Delta\Psi$) for each species. Here, we modified their MSOM to test whether species occupying hot, dry sites, where the demand for evaporative water for cooling is greatest, were less likely to persist over the past century. Detection covariates included era to account for differences between the time periods, and Julian day and its quadratic term to allow detection to vary during the breeding season. Initial occupancy covariates included historic climate averages (annual precipitation, mean annual temperature) during the initial survey period (1906 to 1965) derived from the basin characterization model (BCM) (52), using a 5-km window to capture local variability. We included the same climate covariates measured from 1986 to 2015 for persistence. Colonization was modeled without covariates because it rarely occurred ($\gamma = 0.003$; 95% credible interval, <0.001 to 0.009). See ref. 19 for more model details and code.

Heat Flux Simulation. We developed an index of chronic water requirements for evaporative cooling using species-specific traits from Mojave birds. We focused on 50 species for this analysis, 39 species that significantly declined in occupancy and 11 species without significant change, which encompassed the range of occupancy decline over the last century. Our index of water requirements captures the interspecific differences in thermal conditions that species experience due to their unique body size, shape, and feather properties in the same environment. Although species may have behavioral and physiological strategies for coping with thermal stress, our approach generates a conservative and standardized estimate of thermal stress while also exploring the sensitivity of physiological and behavioral strategies for reducing heat loads (*SI Appendix, Heat flux simulation*).

Cooling costs were based upon the conditions a bird experiences in the Mojave Desert National Preserve (35°00′39″ N, −115°28′24″ W) during July, the average hottest month of the year (52). This site reflected the average altitude, and thus climatic conditions, of resurvey sites (simulation site, 1,285 m; average resurvey site, 1,250 m). We calculated water required for evaporative cooling for an average daily temperature cycle in July based on average air temperatures between 1900 to 1930 (when most historic surveys were conducted) and 1985 to 2015 (the period preceding our resurveys) from the BCM (52). We calculated the difference in cooling costs between historic and modern climates for each species and used these water requirements for cooling as a covariate in statistical analyses. We converted the daily increase in cooling costs into the number of insects needed to offset the increase in water requirements for insectivorous birds (*SI Appendix, Ecological relevance of cooling costs*). By using average climatic conditions, the index captures the increase in daily water requirements that a bird might experience over several weeks or months in the Mojave. We validated our simulations using published data on thermoregulatory profiles of desert birds (30) and operative temperatures from taxidermic mounts in nature (43) (*SI Appendix, Validation of the heat flux model*).

Model Parameterization from Museum Measurements. We parameterized our model by measuring biophysical characteristics of bird specimens in the Museum of Vertebrate Zoology at the University of California, Berkeley. We quantified the 1) shape of each species, 2) average feather length across the dorsum and ventrum, 3) plumage depth across the dorsum and ventrum, and 4) feather absorptance. We obtained the mean body mass of each species from the VertNet database (http://www.vertnet.org/) based upon collection points in western North America. (*SI Appendix, Museum measurements for parameterization of the heat flux model*).

Body Mass and Bergmann's Rule Analyses. We examined the consequences for 50 species of Mojave birds of geographic variation in body mass on water requirements for evaporative cooling. We evaluated the association between body mass and air temperature for each species (*SI Appendix, Analysis of geographic variation in avian body mass*). We grouped species based upon the sign of their slope to categorize species and determine whether the magnitude of body size variation (either supporting or countering Bergmann's rule) was associated with occupancy decline. We then used our simulation to determine whether geographic variation in body mass had consequences for cooling costs in the Mojave Desert. For each species, we calculated the cooling costs from simulations that used the body mass 1) associated with the Mojave Desert and 2) from the highest latitude from western North America for that species. The analysis was designed to estimate the relative

costs or benefits of body size difference in the Mojave Desert. We calculated the change in cooling costs (in watts) between each location and expressed the difference relative to the average mass in the Mojave. We then examined associations between these values and the change in occupancy.

Statistical Analyses. Statistical analyses were conducted in R (version 3.4) and Python (version 3.5) using linear regression and type II analysis of covariance (Figs. 2–4). We used the natural logarithm of mass and cooling costs to meet the assumptions of linear regressions. We used AICc to evaluate the effect of cooling costs and the interaction with life history traits (*SI Appendix*, Table S7). In a post hoc analysis, we analyzed the relationship between occupancy decline and cooling costs by grouping species that primarily eat animals (carnivores [$n = 4$] and insectivores [$n = 22$]) to compare with those primarily consuming plants (herbivores [$n = 7$] and omnivores [$n = 17$]), and used AICc to compare models (*SI Appendix*, Table S7). For the analysis of the decline in occupancy versus percent change in Mojave cooling costs (Fig. 4 *B* and *C*), we weighted each estimate by the inverse the SE of the regression between body mass and annual temperature to incorporate uncertainty (19). We also evaluated the potential for relatedness to underlie the observed species declines (*SI Appendix, Statistical Analyses*).

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