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CLIMATE CHANGE

Exposure to climate change drives stability or collapse of desert mammal and bird communities

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High exposure to warming from climate change is expected to threaten biodiversity by pushing many species toward extinction. Such exposure is often assessed for all taxa at a location from climate projections, yet species have diverse strategies for buffering against temperature extremes. We compared changes in species occupancy and site-level richness of small mammal and bird communities in protected areas of the Mojave Desert using surveys spanning a century. Small mammal communities remained remarkably stable, whereas birds declined markedly in response to warming and drying. Simulations of heat flux identified different exposure to warming for birds and mammals, which we attribute to microhabitat use. Estimates from climate projections are unlikely to accurately reflect species' exposure without accounting for the effects of microhabitat buffering on heat flux.

With one of six species threatened by future warming (*1*), conserving biodiversity depends on identifying the factors that make a species vulnerable to climate change. Exposure, sensitivity, and adaptive capacity are fundamental components of climate vulnerability (*2*), but it is the magnitude of exposure—determined by the degree of change at a given site and by behavioral buffering from microhabitat use—that establishes whether organisms experience the direct effects of climate change (*3*). Despite diverse strategies used by animals to reduce exposure to lethal temperatures and desiccation (*4*, *5*), species inhabiting a site are typically assumed to experience similar magnitudes and rates of exposure (*6*–*9*). However, comparisons of exposure among taxa at the same sites—especially where climate change has pushed organisms toward their physiological limits—are lacking and are rarely connected to long-term community responses.

To assess the impact of exposure on communities, we compared the responses of small mammals and birds of the Mojave Desert to warming and drying by resurveying sites originally visited by Joseph Grinnell and colleagues in the early 20th century (*10*). Our comparison leveraged the recently documented collapse of the Mojave bird community (*11*, *12*) to evaluate how exposure affects vulnerability across taxa. Multiday surveys were conducted for 34 small mammal species at 90 sites and 135 bird species at 61 sites located primarily on protected lands (Fig. 1A) (see supplementary materials). We used a dynamic multispecies occupancy model to estimate occupancy probabilities for species in each era, accounting for differences in detection between time periods. The model also evaluated the influence of climate change as well as other causes of turnover, such as habitat change from fire and grazing (*11*). We then estimated the degree of exposure for birds and mammals using a heat flux model that simulates thermoregulatory costs on the basis of behavioral strategies, morphology, thermal properties, and microhabitat conditions (see supplementary materials). We expected that small mammals would mirror the collapse of the Mojave bird community (*11*) because they are endotherms, occupy similar trophic levels (*13*), have comparable life history traits and ecological strategies (*13*), and have exhibited similar sensitivities to warming, including elevational and latitudinal range shifts (*14*–*17*). Alternatively, small mammals may buffer their exposure to climate change by accessing cool fossorial microhabitats. In that case, biotic interactions, such as competition, should influence changes in community assembly of desert mammals (*18*, *19*).

Over the past century, occupancy of small mammals remained stable while birds severely declined (Fig. 1B and fig. S1). The mean occupancy probability of small mammals during the historical time period [μ = 0.26; 95% credible interval (CRI), 0.24 to 0.29] was indistinguishable from the value derived from modern surveys (μ = 0.26; 95% CRI, 0.24 to 0.29). Occupancy of 3 (9%) mammal species decreased, 27 (79%) did not change, and 4 (12%) increased (Fig. 1B and table S1). In contrast, bird community occupancy declined over the past century from 0.24 (95% CRI, 0.17 to 0.32) to 0.11 (95% CRI, 0.07 to 0.15). Of 135 bird species, occupancy of 39 (29%) decreased, 95 (70%) did not change, and 1 (<1%) increased (*11*).

Species richness was characterized by stability over the past century for the small mammal community but collapse for the bird community. Richness declined significantly at 55 of 61 sites for birds (90.1%) versus only 3 of 90 sites for mammals (3.3%) (Fig. 1C). Sites supported an average of 8.79 mammal species (95% CRI, 8.18 to 9.72) in historical surveys compared to 8.92 species (95% CRI, 8.47 to 9.73) in modern surveys. However, the stability of mammal species richness conceals moderate species turnover at survey sites (Fig. 1D). There was an average gain of 2.02 mammal species (95% CRI, 1.50 to 2.60) colonizing per site and an average loss of 1.89 species (95% CRI, 1.58 to 2.30) extirpated per site. Thus, a 23% gain in species per site was offset by a 22% loss relative to historical species richness. In contrast, site-level richness for birds collapsed by 42% (–17.9 species per site; 95% CRI, –15.5 to –20.5; Fig. 1C). For birds, colonization rarely occurred, resulting in species loss without replacement at surveyed sites (Fig. 1D). Moreover, the mean probability of persistence was much lower for birds (μ = 0.43; 95% CRI 0.31 to 0.55) than for mammals (Fig. 1E; μ = 0.79; 95% CRI, 0.70 to 0.86).

Warming and drying over the past century was not associated with persistence or colonization in small mammals, but drove bird turnover. Only 1 of 34 mammal species (3%) responded to precipitation change and none to temperature change (table S2). Likewise, habitat degradation from fire and grazing was not associated with persistence and colonization in small mammals (table S3). Instead, long-term turnover in the composition of the small mammal community reflected a combination of putative interspecific interactions, habitat requirements, and stochastic processes (fig. S3). For desert birds, however, a reduction in precipitation drove the community collapse over the past century, as persistence was positively associated with precipitation for 35 (26%) of 135 bird species (*11*). The effect was compelling at sites that both warmed and dried (*12*), which suggests that desert birds are particularly vulnerable to increased water requirements for evaporative cooling.

Exposure to climate change differed markedly between bird and small mammal communities, despite widespread warming (Fig. 2A). However, differences were apparent only upon simulating exposure with downscaled microhabitat conditions, which we accomplished using high-resolution climate models incorporating behavioral buffering. Differences were especially evident in the amount of water required for evaporative cooling to maintain homeothermy ("cooling costs"), a critical aspect of survival for desert birds and mammals (*20*–*22*). Cooling costs were higher in birds than in mammals by a factor of 3.3 across a representative landscape, and climate change

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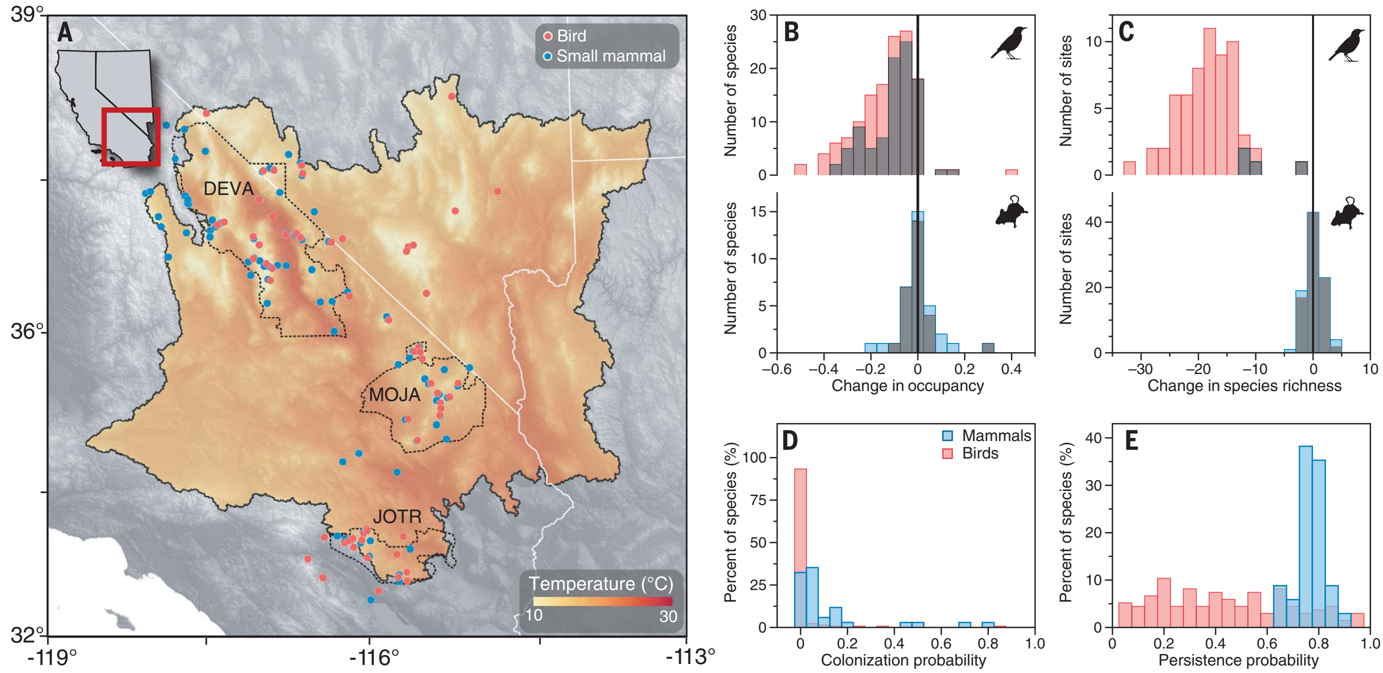

Fig. 1. The simultaneous collapse of bird communities and stability of small mammal communities over the past century in the Mojave Desert. (**A**) Survey sites for birds (red) and small mammals (blue) within the Mojave Desert, with average annual temperature from 1970 to 2000 (Worldclim v.2.1) and park boundaries for Death Valley National Park (DEVA), Mojave National Preserve (MOJA), and Joshua Tree National Park (JOTR). (**B** and **C**) Change (modern – historical) in occupancy and species richness at survey sites. Species and sites in gray did not change over the past century, whereas birds (red) and mammals (blue) changed significantly. (**D** and **E**) Colonization and persistence probabilities.

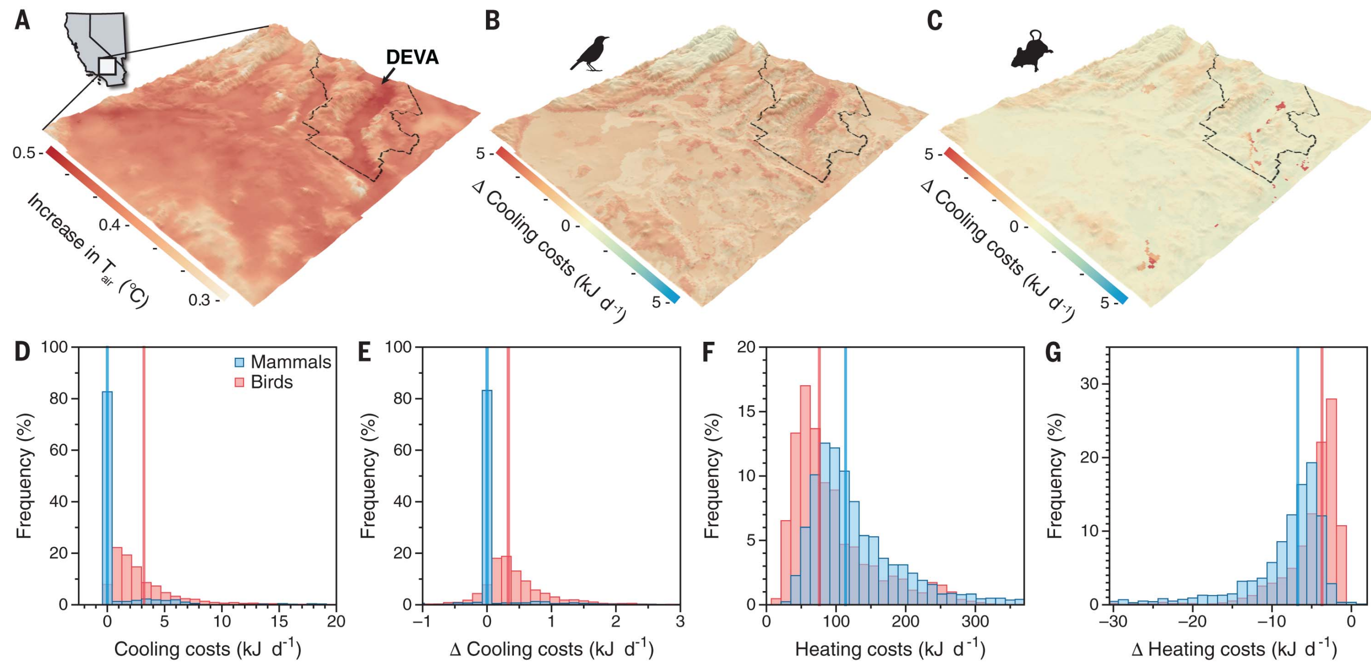

Fig. 2. Small mammals and birds differ in exposure over the past century. (**A**) Increase in average spring air temperature (see supplementary materials) for a landscape representative of climatic extremes. Dotted black line shows DEVA boundary; arrow points to Death Valley. (**B** and **C**) Average daily change in evaporative cooling required for homeothermy ("cooling costs") for birds (B) and mammals (C) assuming 50% cover in locations with vegetation. (**D**) Birds exhibited higher cooling costs than mammals at survey sites (Mann-Whitney U test; $W = 1018$, $P < 0.001$). (**E**) Changes in cooling costs at survey sites were higher for birds than for mammals ($W = 1076$, $P < 0.001$). (**F** and **G**) Relative to birds, mammals experienced higher heating costs ($W = 309$, $P < 0.001$) (F) and a greater reduction in heating costs due to climate change ($W = 936$, $P < 0.001$) (G) at survey sites. Vertical lines indicate medians for birds (red) and mammals (blue).

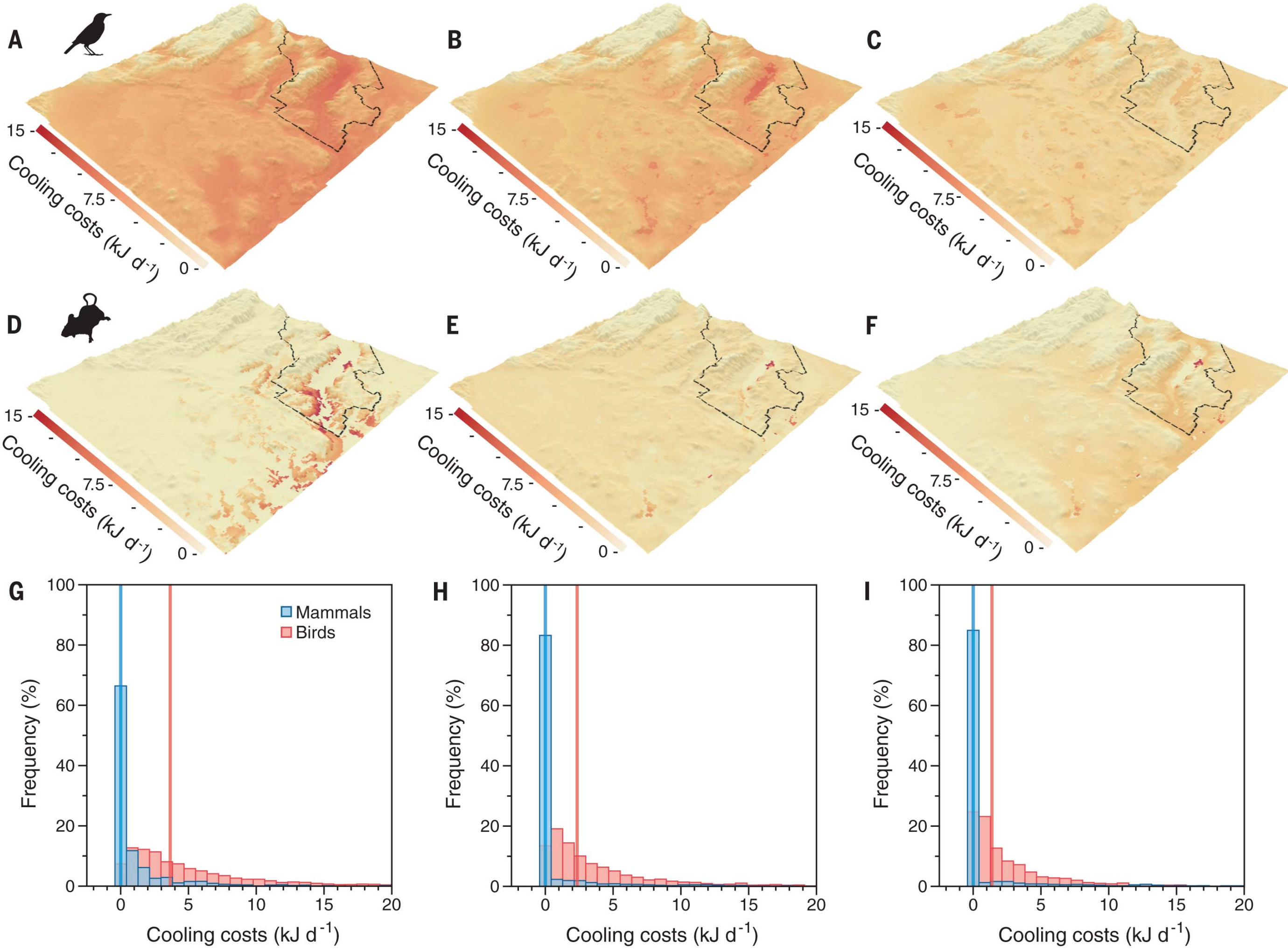

Fig. 3. Small mammals are more buffered from future climate change than birds. (**A** to **F**) Water requirements for evaporative cooling costs in a Mojave Desert landscape representative of climatic extremes for birds [(A) to (C)] and mammals [(D) to (F)] under a moderate warming scenario (RCP 6.0) and shaded 0% [(A) and (D)], 50% [(B) and (E)], and 100% [(C) and (F)] by vegetation. Dashed black line is DEVA boundary. (**G** to **I**) Cooling costs at survey sites were always higher for birds than for small mammals under warming scenario RCP 6.0 and shaded 0% (Mann-Whitney U test; $W = 1084$, $P < 0.001$) (G), 50% ($W = 1018$, $P < 0.001$) (H), and 100% ($W = 996$, $P < 0.001$) (I) by vegetation. Vertical lines indicate medians for birds (red) and mammals (blue).

increased these costs by 58.5% for birds but only 17.4% for mammals (Fig. 2, B and C). Similarly, relative to mammals, birds experienced higher cooling costs and increases in cooling costs at survey sites (Fig. 2, D and E). In fact, more than 80% of small mammals experienced low to no change in cooling costs (Fig. 2E). Metabolic heat production was similarly reduced for birds and mammals over the past century (Fig. 2, F and G). Restrictions on activity from hot temperatures were also similar for birds and mammals (fig. S4) and do not explain the contrasting community dynamics, unlike the proposed mechanism underlying population declines in some ectotherms (*23*). Despite small geographic differences between bird and mammal survey sites (Fig. 1A), climatic conditions were nearly identical between the two sets over the past century (fig. S5 and table S4).

Projections of exposure to future climate change indicate that birds will experience higher thermoregulatory costs than small mammals. Cooling costs are projected to be greater for birds than for mammals by a factor of 3.8 across a representative Mojave landscape by 2080 (Fig. 3). In general, microhabitat use produces lower physiological exposure for small mammals (Fig. 3, A to F), except for isolated locations where shallow soil depths constrain burrowing. At survey sites, birds are projected to experience greater cooling costs than small mammals, and both nocturnal and diurnal small mammals can avoid thermoregulatory cooling costs in underground burrows, even without vegetation cover (Fig. 3, G to I, and fig. S6).

Adaptations to desert life may contribute to divergent responses of birds and small mammals over the past century, but microhabitat buffering likely played a more influential role. Desert rodents are well known for dietary, physiological, and behavioral adaptations that reduce reliance on free water from their environment (*24*). However, not all rodents are well adapted to desert life. *Neotoma lepida* requires preformed water from vegetation and lacks a well-developed ability to concentrate urine (*25*). Yet this species exhibited high persistence and colonization probabilities (figs. S1 and S2), which suggests that microhabitat use offsets physiological sensitivity to warming by reducing exposure. Mammal species exhibited stable occupancy regardless of specialization to desert habitats (fig. S7) and changes were not concentrated in any family (table S1). Diurnal mammals, which have immediate, unrestricted access to cool microhabitats below ground, experienced similar, although more variable, exposure to warming than their nocturnal counterparts (fig. S6). Among birds, desert specialists and habitat generalists declined similarly (*11*), which suggests that desert adaptation was not a buffer from climate change.

The impending threat of climate change to global biodiversity underscores the need to rapidly evaluate climate vulnerability (*2*), which is often done by assuming that changes in conditions estimated from climate projections reflect exposure for all taxa at a site (*6–9*). In contrast, we have demonstrated that sympatric mammals and birds with comparable physiological and ecological requirements experienced fundamentally different exposures to warming due to microhabitat buffering, which enabled stability or drove collapse of their respective communities. Moreover, among Mojave birds, species-specific exposure was strongly related to species declines (*12*). Thus, each species likely experiences different magnitudes of exposure that may affect population persistence through physiological requirements. Modeling approaches that combine physiology and behavior are needed to predict how exposure differences affect species' persistence in the face of a rapidly changing climate.

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SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/371/6529/633/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S15
Tables S1 to S7
References (*27–89*)

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Microhabitat matters
Understanding how our warming climate affects vulnerable species is of paramount importance. However, predicting responses is complicated because species are complex and may adapt or respond in distinct ways. Riddell *et al.* compared a century-old dataset on species richness in the Mojave against modern surveys to measure climate-related changes in bird and small mammal communities. They found little change in mammal richness or occupancy but large declines across birds. They attribute these differences to differences in microclimate opportunities: Specifically, mammals can mitigate temperature impacts through burrowing, whereas birds are generally more exposed.

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