Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration

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Extreme high environmental temperatures produce a variety of consequences for wildlife, including mass die-offs. Heat waves are increasing in frequency, intensity, and extent, and are projected to increase further under climate change. However, the spatial and temporal dynamics of die-off risk are poorly understood. Here, we examine the effects of heat waves on evaporative water loss (EWL) and survival in five desert passerine birds across the southwestern United States using a combination of physiological data, mechanistically informed models, and hourly geospatial temperature data. We ask how rates of EWL vary with temperature across species; how frequently, over what areas, and how rapidly lethal dehydration occurs; how EWL and die-off risk vary with body mass; and how die-off risk is affected by climate warming. We find that smaller-bodied passerines are subject to higher rates of mass-specific EWL than larger-bodied counterparts and thus encounter potentially lethal conditions much more frequently, over shorter daily intervals, and over larger geographic areas. Warming by 4 °C greatly expands the extent, frequency, and intensity of dehydration risk, and introduces new threats for larger passerine birds, particularly those with limited geographic ranges. Our models reveal that increasing air temperatures and heat wave occurrence will potentially have important impacts on the water balance, daily activity, and geographic distribution of arid-zone birds. Impacts may be exacerbated by chronic effects and interactions with other environmental changes. This work underscores the importance of acute risks of high temperatures, particularly for small-bodied species, and suggests conservation of thermal refugia and water sources.

avian ecology | physiological ecology | climate change | heat waves | water balance

Extreme weather events are increasingly seen as an important factor in ecology and conservation, with consequential effects on individuals, populations, communities, and ecosystems (1–3). Recent data indicate an increase in the incidence of heat waves and extreme high temperatures (4, 5). Despite difficulties in quantifying trends in mass mortality events, heat waves are known to have caused a number of large-scale die-offs among birds, pteropodid bats, and other taxa in recent years (6, 7). Moreover, current (8) and projected (9) increases in the frequency, duration, and severity of heat waves are likely to make these mortality events more common as the century progresses (10).

Birds may be particularly susceptible to heat waves given their typically diurnal activity periods, small size, and high mass-specific rates of metabolism and water loss. Small birds also have a very limited capacity to store vital resources such as water, and consequently must balance their water budgets over time scales of minutes to hours during hot weather (10). Constraints on water availability and heat stress are known to produce changes in behavior, reproductive success, occupancy, and mortality in birds (11). Heat-related mortality can arise from two categories of physiological constraints: (i) limits to the balancing of water budgets and maintenance of adequate hydration under conditions requiring evaporative cooling (dehydration), and (ii) limits to rates of heat dissipation and the maintenance of body temperature (T_b) below lethal limits (hyperthermia). When environmental temperatures exceed a bird's normothermic T_b, evaporative heat loss becomes the only avenue of heat dissipation available to offset increasing environmental and internal heat loads. Rates of evaporative water loss (EWL) increase markedly when environmental temperatures are above T_b and can exceed 5% of body mass (M_b) per hour, leading to rapid and acute losses of water (12); this creates a fundamental tradeoff between the dangers of dehydration and of hyperthermia. Given these challenges, birds typically curtail activity during the hottest periods of the day and seek relatively cool, shaded microsites to minimize heat loads and EWL (13).

Body mass is one of the most important factors affecting bird–environment interactions, with smaller species showing higher mass-specific rates of EWL and hence greater relative water demands. In a modeling study, McKechnie and Wolf (10) showed that warming temperatures in hot deserts could be expected to produce large fractional increases in EWL rates, and that future extreme heat events could result in very short survival times for smaller birds (<2 h for birds <10 g). However, this study was limited to physiological data obtained from the literature, and models were implemented for only two sites. Furthermore, the authors did not address the effects of geographic variation in
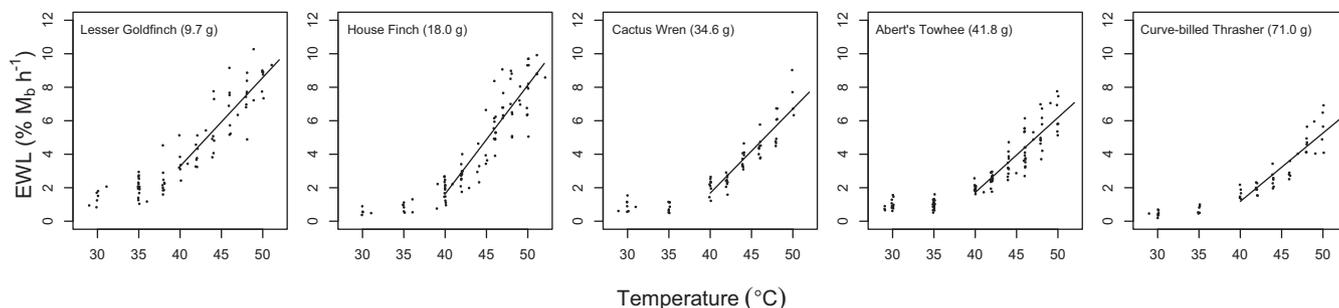
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Fig. 1. Evaporative water loss (EWL) as a percentage of body mass (M_b) for five passerine bird species across a range of elevated chamber T_{air}. Mean body masses (M_b) are indicated and a linear fit line ($P \ll 0.001$) has been added for T_{air} above T_{uc} of 40 °C. A small amount of jitter (10% minimum distance between adjacent unique values) has been added to minimize overplotting.

temperature across major portions of species' ranges, thus excluding a dimension critical for conservation planning.

Here, we examine the effects of heat waves on rates of EWL and survival in desert-dwelling birds in the United States using a combination of physiological data, mechanistically informed models, and hourly geospatial temperature data. We use measurements of EWL as a function of T_{air} above 40 °C (the approximate diurnal T_b of desert passerines) for five passerine birds common to the desert southwest. We model EWL and map the occurrence of current (1980–2013) conditions of lethal dehydration, which we define as cumulative EWL exceeding 15% of M_b. Given daily activity patterns and temperature profiles, we consider survival times of ≤5 h to pose an ecologically important (moderate) risk of lethal dehydration, and base most of our spatial modeling on this scenario. In addition, we characterize the occurrence of survival times ≤3 h (high risk). We then explore the implications of a 4 °C warming scenario, consistent with climate projections for this region in 2070–2100 (9, 14). Using

these five passerines, we ask (*i*) How do rates of EWL vary as a function of M_b across a range of T_{air}? (*ii*) How frequently, in what areas, and over what time scales do conditions associated with lethal dehydration currently occur? (*iii*) How will a warmer climate affect the frequency and spatial extent of conditions under which lethal dehydration occurs?

Results

Evaporative Water Loss Rates as a Function of Body Mass and T_{air}. At $T_{air} < 40$ °C, rates of EWL were universally well below 1 g·h⁻¹, with larger species having slightly higher rates than smaller species. However, at $T_{air} > 40$ °C, rates of total EWL increased markedly in a linear fashion. In the largest species, the Curve-billed Thrasher (71 g), EWL exceeded 4 g·h⁻¹ at 50 °C. However, small species evaporated water at proportionally higher rates than larger species (Fig. 1). For example, at 50 °C, Lesser Goldfinch (9.7 g) and House Finch (18.0 g) evaporated 8–9% of M_b·h⁻¹, whereas the larger Abert's Towhee (41.8 g)
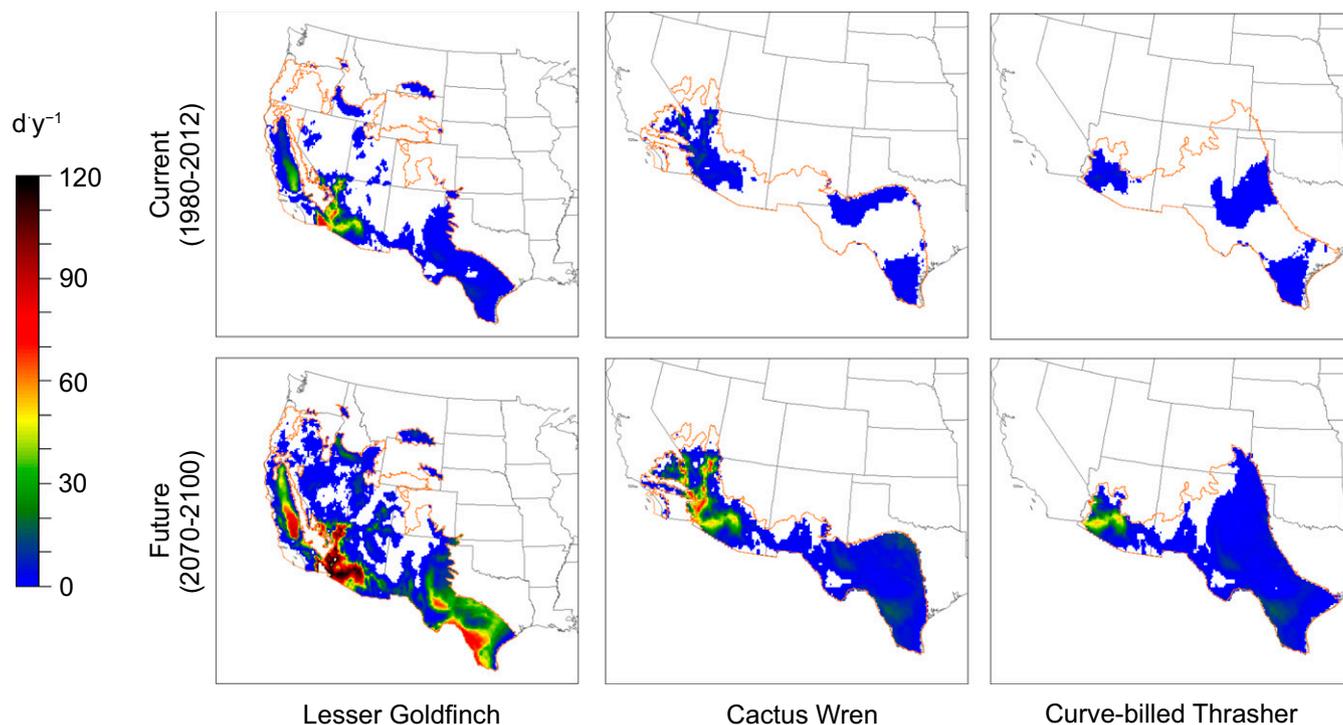

Fig. 2. Current (1980–2012) and future (2070–2100) number of days between April 1 and September 30 with survival time of ≤5 h across the range (orange lines) of three passerine species in the southwestern United States, arranged in order of increasing M_b. Maps of additional species and for ≤3-h dehydration risk are found in Fig. S1.
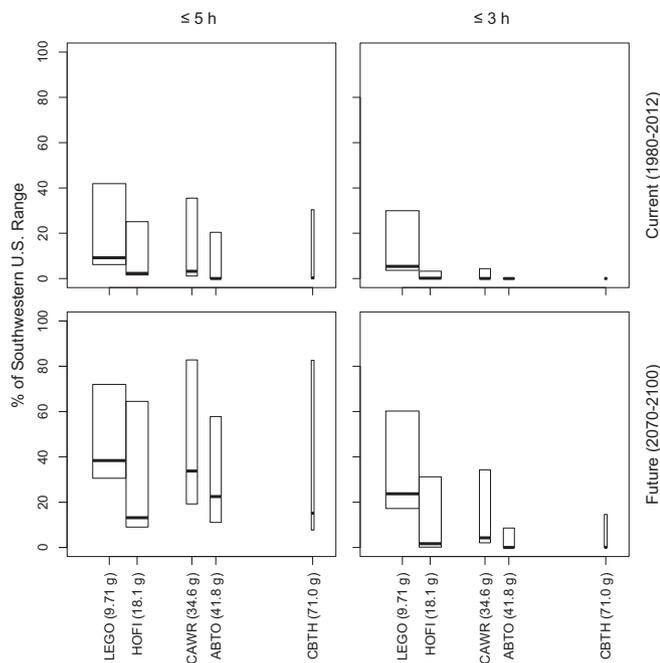
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Fig. 3. Percentage area of species ranges in the Southwest study region subject to conditions associated with lethal dehydration under current (*Upper*) and future 4 °C warmer (*Lower*) climates for moderate (survival time ≤5 h; *Left*) and high (survival time ≤3 h; *Right*) dehydration risk. LEGO, Lesser Goldfinch; HOFI, House Finch; CAWR, Cactus Wren; ABTO, Abert's Towhee; CBTH, Curve-billed Thrasher. The bottom of box, heavy central line, and top of box indicate areas experiencing ≥10 d·y^{-1}, ≥5 d·y^{-1}, and ≥1 d·y^{-1}, respectively. The width of each box is proportional to the range area of species within the conterminous United States, and abscissa position is determined by body mass.

and Curve-billed Thrasher evaporated ~7% and 5% of M_b·h^{-1}, respectively.

Spatiotemporal Dynamics of Lethal Dehydration: Current Conditions.
Maps of weather conditions associated with lethal dehydration reveal variable spatial patterns among our suite of passerine birds (Fig. 2 and Fig. S1). First, small passerines experienced lethal dehydration risk much more frequently than larger species, often with more than 50 d·y^{-1} over large portions of their range. For instance, at Yuma, AZ (32° 42′ N, 114° 37′ W), Lesser Goldfinch is modeled to experience an average 58 d·y^{-1} with survival time of ≤5 h, whereas the larger Curve-billed Thrasher only experiences 4 d·y^{-1} of comparable risk. Second, conditions associated with high dehydration risk (i.e., survival times ≤3 h) are presently limited to only the smallest species considered, with Lesser Goldfinch experiencing only a few days per year in limited low-elevation portions of their range (Fig. 1). Among our focal species, modeled survival times are currently never ≤3 h for Abert's Towhee or Curve-billed Thrasher.

Spatially, large portions of the US ranges of these species are subject to at least occasional risk of lethal dehydration (Fig. 2). Considering the normal conterminous US breeding ranges, the percentage of area experiencing an average of at least 1 d·y^{-1} of lethal dehydration risk ranged from 42% for Lesser Goldfinch to 20% for Abert's Towhee (Fig. 3). However, areas in which these species currently experience more than 10 d·y^{-1} of these conditions were much more restricted. The occurrence of high lethal dehydration risk (≤3 h) was similarly limited to parts of the Sonoran, Colorado, and Mojave deserts of western Arizona, southern Nevada, and southeastern California in smaller species, with these conditions not occurring at all in average years for larger species.

Climate Warming Effects on Spatiotemporal Dynamics of Lethal Dehydration. Warming of 4 °C greatly expands the extent, frequency, and intensity of dehydration risk for desert passerines in the United States. All species modeled will be subjected to increased risk of lethal dehydration over large parts of the southwestern United States (Fig. 2). Across the entire study region, there will be a large increase in the area of a species' range experiencing at least 1 d·y^{-1} with moderate (<5 h) dehydration risk; this is particularly true for the two larger-bodied, range-restricted birds, the Cactus Wren and Curve-billed Thrasher, with >80% of their ranges affected. Increases in the frequency of extreme dehydration risk are perhaps more dramatic, especially for the smaller species (Fig. 2). In the southwest desert ecoregion, the average number of days per year with lethal dehydration risk increases from 13 to 44 d for Lesser Goldfinch, from 2 to 9 d for Cactus Wren, and from <1 to 4 d for Curve-billed Thrasher (Fig. 4). Days with high lethal dehydration risk will remain rare for the largest species, but for smaller species, such days become far more frequent. For Lesser Goldfinches in the southwestern deserts, high risk of lethal dehydration increases from 7 to 25 d·y^{-1} (Fig. 4). In some portions of their range, particularly the Sonoran Desert of southwest Arizona and extreme southeastern California, the Lesser Goldfinch will experience survival times ≤3 h for virtually the entire summer and portions of spring and fall (Fig. S1).

Discussion

Our models reveal that increasing T_{air} and the concomitant increase in the frequency and severity of heat waves will have potentially important impacts on the water balance, daily activity, and geographic distribution of birds in deserts of the southwestern United States. Even modest increases in maximum T_{air} during heat waves result in greatly increased demands for evaporative cooling. Increases in rates of EWL are strongly dependent on M_b, with smaller species showing higher mass-specific rates. Consequently, smaller species will be subject to much greater dehydration risk than larger species. Because activity is reduced at high T_{air}, the impact of higher EWL rates will be exacerbated by reduced foraging and hence water intake. Thus, the selection of relatively cool microhabitats may be expected to become increasingly important. Finally, diet will also play an important role in determining future avian distributions, with granivorous birds challenged by their relatively dry diet and need for scarce, unpredictable free water resources. In the following paragraphs, we discuss each of these topics and how their integrative effects under conditions of rapid warming may affect the future distributions of arid-zone passerines.
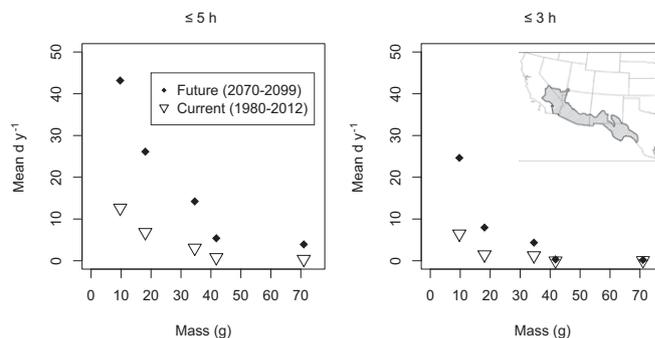

Fig. 4. Average days per year with 5-h (*Left*) and 3-h (*Right*) lethal dehydration intensities in current and future climates. Averages are calculated over each species' range within the US hot desert ecoregion, comprising the Mojave, Sonoran, and Chihuahuan deserts (ecoregion data from ref. 39).

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Scaling of Rates of Evaporation and Time to Lethal Dehydration. The effects of M_b on resting rates of EWL at moderate T_{air} are well described in birds (15, 16). Less well understood is how EWL and upper limits to evaporative cooling capacity vary with T_{air} above normothermic T_b (10, 17). As expected, our data confirm that smaller species lose water at higher mass-specific EWL than larger species. At $T_a = 40$ °C, for example, the Lesser Goldfinch (9.7 g) loses 3.4% $M_b \cdot h^{-1}$, a rate approximately twice that of the approximately sevenfold-larger Curve-billed Thrasher (71 g; 1.8% $M_b \cdot h^{-1}$). At $T_a \sim 10$ °C above normothermic T_b, rates of EWL in goldfinches can exceed 8% $M_b \cdot h^{-1}$, and may approach 5% $M_b \cdot h^{-1}$ in thrashers. During extreme heat events, goldfinches may reach their limits of dehydration tolerance ($\sim$15% M_b) in less than 2 h, and even thrashers approach these same limits in as little as 3 h (Fig. 3).

In both the Lesser Goldfinch and Curve-billed Thrasher, an increase in T_a from 40 to 44 °C results in a $\sim$150% increase in rates of EWL. However, time to death through dehydration differs greatly between these two species because of differences in mass-specific rates of EWL (5.4% $M_b \cdot h^{-1}$ vs. 2.7% $M_b \cdot h^{-1}$; Fig. 1). These values are similar to the fractional increases in EWL required for evaporative cooling predicted by the model presented by McKechnie and Wolf (10) for 27 avian species, and provide the basis for mapping EWL with daily changes in T_a across each species' range.

Dehydration Risk Under Current and Future Climates. Maps of dehydration risk (Fig. 2) provide the basis for quantifying the proportion of species' ranges where lethal dehydration ($\leq$5 h) is likely to occur, and the frequency of occurrence ($d \cdot y^{-1}$). Interactions among body mass, geographic range, and dehydration risk reveal that, under certain scenarios, the smallest, most heat-sensitive species are the least affected from a distribution and abundance standpoint. House Finches and Lesser Goldfinches provide excellent examples, both having widespread distributions that span the latitude range of the study region. Under current climate conditions, both species exceed their 5-h dehydration limits on 1–10 $d \cdot y^{-1}$ over large areas ($\sim$1,500,000 km² and $\sim$960,000 km², respectively; Fig. 2 and Fig. S1). Even though these areas of risk include 25% and 42% of the total ranges for House Finches and Lesser Goldfinches, respectively, the very large ranges ($\sim$6 million and 2.3 million km², respectively) indicate that the majority of populations are at low risk of mortality from acute heat stress under current conditions. Under future climates, however, these large ranges may not provide adequate population buffers, given likely additional stressors. Under the +4 °C scenario, House Finches will experience at least 1 $d \cdot y^{-1}$ of lethal dehydration risk over $\sim$65% of the species' total range, and Lesser Goldfinches will encounter potentially lethal events over $\sim$72% of the total range.

A different scenario applies to Abert's Towhee, Cactus Wren, and Curve-billed Thrasher, all of which are arid-zone specialists with relatively small distributional ranges ($\sim$200,000–900,000 km²; Fig. 2 and Fig. S1). Under current conditions, the risk of lethal dehydration for these larger passerines is reduced by their modest mass-specific rates of EWL. Thus, despite being restricted to hot deserts, the fractions of their ranges (Cactus Wren 36%; Abert's Towhee 20%; Curve-billed Thrasher 31%) over which there is a risk of lethal dehydration are comparable to those of the smaller, but more widely distributed Lesser Goldfinches and House Finches; however, because their total ranges are small and mainly confined to hot deserts, a 4 °C warming scenario produces very different consequences. Temperatures under projected warming exceed the threshold for lethal dehydration on at least a handful of days each year over the majority of each species' range (Fig. 3; Cactus Wren 83%; Abert's Towhee 58%; and the Curve-billed Thrasher 83%). Possibly of even greater concern, however, is the observation that 4 °C warming in an already hot desert will yield long periods when chronic effects of heat and water limitation may pose problems, as discussed below.

Expanding Risks Under Climate Change. Our model reveals that the portion of species' ranges with risk of lethal dehydration during heat waves will dramatically expand under future climate scenarios (Fig. 3), as will the average frequency at which such conditions are encountered (Fig. 4), and this is most apparent for the Lesser Goldfinch. By 2100, this species will be exposed to 60–120 $d \cdot y^{-1}$ of potentially lethal conditions over a large region that includes the entire lower Colorado River basin, southern Arizona, the lower central valley of California and southern Texas (Fig. 2). A similar pattern emerges for House Finches, where in the central valley of California and the entire lower Colorado River basin there is a sustained risk of lethal dehydration much of the year. Under the current climate, exposure of these two species to such extreme conditions is mostly limited to the lower Colorado River basin and constrained to 20–40 $d \cdot y^{-1}$. As granivores, these two species may be at particular risk because of their reliance on free water sources, an ecological trait that may well exclude them from large parts of their current range by the end of this century. For the larger three species, Cactus Wren, Abert's Towhee, and Curve-billed Thrasher, prolonged periods of acute stress may be limited to the Sonoran Desert portion of their range. Among these three, the wren and thrasher are insectivores and so have constant access to preformed water in their diet, whereas the granivorous Abert's Towhee may have very limited access to water resources.

Other Factors Affecting Species Distributions in Hot Deserts. Avoidance of environmental extremes is a common strategy used by animals to balance their water and energy budgets under physiologically challenging conditions, and the availability of thermally buffered microsites is potentially important in modeling the consequences of hotter future climates. During the hottest part of the day, small birds completely cease all foraging activities (18, 19) and seek relatively cool, shaded thermal refugia to reduce exposure to extreme heat (20, 21). Our model focuses on meteorological T_{air}, which for birds in hot desert environments, is typically a minimum index of thermal stress in the absence of radiative and convective heat fluxes, and approximates the thermal conditions in a completely shaded and ventilated meteorological thermoscreen. There is also evidence that North American Land Data Assimilation System (NLDAS) and other gridded climate products often underestimate maximum temperatures by 1 °C or more (22), underscoring the conservative nature of our analysis. Nevertheless, it may be possible for individuals to use cooler microsites (e.g., burrows and sites in dense vegetation) (23). The role of microsites is emphasized by the observation that, in hot areas like the Sonoran Desert, many species already experience periods of significant dehydration risk on a small number of days per year (Fig. 2). However, the availability of microsites, given habitat conditions and competition, may not be guaranteed, presently or under future environmental changes.

The increased mortality risk associated with acute heat stress under climate change that we have modeled here will be superimposed on a range of fitness impacts of chronic, but sublethal on a daily scale, heat exposure that we are only just beginning to understand; these include reductions in body condition driven by tradeoffs between foraging efficiency and heat dissipation behaviors (24), and temperature effects on offspring provisioning rates with consequences for chick development and survival (25). Evidence from arid and semiarid ecosystems indicates that shifts in avian abundance associated with heat waves and drought are already occurring (1, 26, 27).

In this study, we have focused on arid environments and modeled EWL under conditions near the ceiling of avian physiological capacity. However, the increases in the frequency dehydration risk for Lesser Goldfinch in the humid eastern half of the United States (Fig. S1) raises the question of how humidity will modify the impacts of higher air temperatures. By reducing the efficiency of evaporative cooling during extremely hot conditions (28), elevated humidity will increase the likelihood that birds cannot dissipate heat rapidly

Table 1. Sampled passerine species and measured body masses

Name	Mass (g; X ± SD)	N	Notes (https://www.allaboutbirds.org)
Lesser Goldfinch (*Spinus psaltria*)	9.7 ± 0.5	33	Open habitat dweller, granivore, tree-nester, foliage gleaner
House Finch (*Haemorhous mexicanus*)	18.0 ± 1.3	75	Human/wild habitat dweller, granivore, tree-nesting, ground forager
Cactus Wren (*Campylorhynchus brunneicapillus*)	34.6 ± 2.7	22	Desert dweller, insectivore, shrub-nesting, ground forager
Abert's Towhee (*Melozone aberti*)	41.8 ± 1.3	28	Desert riparian habitat dweller, granivore, tree-nester, ground forager
Curve-billed Thrasher (*Toxostoma curvirostre*)	71.0 ± 8	18	Scrub habitat dweller, insectivore, shrub-nester, ground forager

enough to avoid lethal hyperthermia. Extremely hot, humid weather will create conditions in which avian mortality events analogous to those that have affected pteropodid bats along the east coast of Australia (29) may be expected to become more frequent.

Future Changes in Avian Distributions and Community Structure. The 4 °C warmer climate scenario produced dramatic increases in the frequency, intensity, and extent of lethal dehydration conditions. These conditions may overwhelm population-level (e.g., density dependence and metapopulation dynamics) and individual-level (behavior and movement) coping mechanisms. The spatial expansion of lethal dehydration may be of greatest concern for conservation of desert avifaunas. At an individual level, birds may be able to cope with extreme heat events near the lower end of the severity range we have modeled here. At a population/species level, birds may be able to cope with more severe scenarios (e.g., ≤3-h survival times), because such extreme events are unlikely to affect entire ranges simultaneously. However, when such intense events begin to occur on a regular and sustained basis, as will be the case for Lesser Goldfinch and other small passerines later in this century, one must question the ability of birds smaller than 10–20 g to avoid extirpation in some portions of their US Southwest range. The relationship between body size and dehydration risk may ultimately drive shifts in community structure in hot regions, as smaller birds experience more rapid declines in survival and productivity compared with larger species.

Conservation Implications. These findings suggest several key conservation and management implications for avifaunas of the desert Southwest and other hot desert regions of the world. The US Southwest enjoys a relatively high avian diversity, distinctive avian assemblages, and a number of threatened birds that may be vulnerable to extreme heat waves (30). The present model was limited to the US portion of the range of our focal species. However, we expect that the more southern Mexican portions of Sonoran and Chihuahuan species' ranges may experience similar current and future regimes of high temperature extremes. In general, because passerine birds rely on the metabolically costly process of panting to evaporate water and lack more efficient evaporative mechanisms (e.g., gular flutter and cutaneous evaporation) (12, 31), small species may experience a new level of threat from hot extremes in this region.

This study provides further motivation for limiting the magnitude of climate warming, because there is already evidence the majority of high temperature extremes are attributable to anthropogenic warming (32). Our study also identifies an urgent need for conservation professionals to consider the effects of hot extremes on desert fauna and promote adaptive measures. For example, efforts to conserve vegetation providing thermal refugia and the maintenance of sources of open water may be important. Similarly, we emphasize that conservation planning should consider the implications of high temperature extremes and climate change by ensuring the availability and conservation of more thermally moderate habitats.

Materials and Methods

Evaporative Water Loss Measurements. We conducted evaporative water loss experiments on 193 individuals of five passerine bird species during June and July of 2012 and 2013 in an area just north of Tucson, AZ (Table 1; ~32° 30′ N,

110° 55′ W). These regionally common species range from 9.7 to 71.0 g and include insectivore and granivore species. During the sampling period at the Tucson, AZ, MET weather station, daily maximum T_{air} ranged from 31 to 42 °C, and the dew point ranged from −15 to 23 °C.

Experiments were conducted with the approval of University of New Mexico Institutional Animal Care and Use Committee (protocol no. 12-100537-MCC) and under permits issued by the US Fish and Wildlife Service and the Arizona Game and Fish Department. The birds were captured using standard walk-in traps baited with seed; upon capture, the birds were held outdoors in shaded, darkened screen cages. All birds were subjected to thermoregulatory trials and released on the same day of capture.

Before each experimental run, a temperature-sensitive passive integrated transponder (PIT) tag (model TX1411BBT; Biomark) was injected into each bird's abdominal cavity and used to monitor T_b during trials (33). Measurements of resting metabolic rate and EWL were made using a flow-through respirometry system (33). The respirometry chamber consisted of a transparent plastic container (5 L) sealed by an opaque lid and modified by addition of inlet and outlet ports; it contained a stainless steel hardware cloth floor above a 2-cm layer of medium-weight mineral oil to trap excreta. The respirometry chamber was placed inside a modified ice chest where a microprocessor-controlled Peltier device regulated T_{air} to ±0.5 °C. Dry air provided by a compressor and pushed through a membrane air dryer was supplied to a mass flow controller that regulated airflow to the respirometry chamber at a rate that ranged from 5 to 40 standard liters per minute. Chamber excurrent chamber air was sampled at 250 mL·min⁻¹ and directed to a CO_2/H_2O gas analyzer (model LI-840A; LICOR) with an accuracy of ±1 ppm for CO_2 and 1% of the reading for H_2O. Rates of whole-animal EWL (grams of water per hour) were calculated from the H_2O ppt readings (less baseline values) for the same data points using equation 10.9 in Lighton (34).

Following PIT tag insertion, each bird was weighed (±0.01 g) and placed in the respirometry chamber. The chamber was darkened during runs and an infrared light and video camera enabled continuous viewing of the animal in the chamber on a computer monitor. The bird was exposed to one or more thermoneutral temperatures (30 °C or 35 °C) and one or more higher temperatures (40–54 °C in 2 °C increments) in a continuously stepped pattern of temperature trials over the span of 1–3 h. To maintain H_2O content of the respirometry chamber at values that would not impede evaporation (dew point <5 °C), flow rates were maintained between 5 and 40 L·min⁻¹, depending on the chamber temperature and the bird's evaporative rate. The initial thermoneutral trial temperature allowed a bird to calm from handling; H_2O and CO_2 production were monitored and observed to drop to resting levels (typically 30–45 min). Temperatures were then increased and birds were allowed to adjust to each for 10–20 min and stabilize before moving to the next temperature. Most birds had few problems coping with T_{air} below 46 °C, but at higher temperatures, birds sometimes showed intermittent activity such as flapping escape attempts; these periods were not included in the analysis. Because airflow rates through the chamber ranged from 5 to 40 L·min⁻¹, chamber equilibrium times ranged from ~30 s to 4.5 min (35), which allowed for accurate observations of both activity metabolism and resting metabolism. As chamber T_{air} were increased above thermoneutrality, T_b and activity were monitored closely to prevent mortality. Experimental runs were also timed to end before total losses, including fecal, were less than 10% of M_b to minimize the effects of hypohydration on thermoregulatory performance.

Geospatial Temperature Time Series. To characterize 1979–2012 T_{air} across the conterminous US study region, we used the multiinstitution NLDAS-2 (36). In this dataset, the temperature forcing fields are spatially interpolated from 32-km resolution to a 1/8° grid (~14 km) and temporally disaggregated from 3-h to hourly frequency. This combination of spatial and temporal resolution makes NLDAS-2 well suited for simulation of many ecologically relevant land surface processes over large geographic areas. The data are available from 1979 onward on the NASA Goddard Earth Science Data and Information Services Center website (https://disc.sci.gsfc.nasa.gov/).

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Water Balance Model. At T_{air} below normothermic T_b, EWL rates are typically modest and determined by the obligatory losses associated with gas exchange at respiratory surfaces and minimum evaporative losses across the skin. Most heat loss is passive via conduction, convection, and radiation, and determined by the thermal gradient between the animal and its environment. As environmental temperatures exceed T_b, rates of EWL increase rapidly because both metabolic and environmental heat loads must be dissipated solely thorough evaporative processes. In passerines, this active heat dissipation is characterized by panting, which increases both EWL and metabolic rate. As T_{air} exceeds T_b, birds retreat to shaded microsites and often remain inactive during the heat of the day; this minimizes EWL, but water intake from foraging is also curtailed. In this model, we assume that birds remain in shaded areas during the hottest periods of the day and forgo foraging. For simplicity, we use T_{air} to define the thermal stress on the animal and its rate of evaporative water loss (12, 37), while recognizing that complex thermal and radiative environments outside of still-shaded microsites may produce additional thermal stress.

For each species, a linear regression model was fitted to EWL rate against chamber $T_{air} > {\sim}40\,°C$ where active evaporative heat dissipation is occurring. The resulting linear model for each species was used to estimate hourly EWL rates and water balance at T_{air} above upper critical temperature (T_{uc}). In this analysis, we estimate the total evaporative water loss by the animal between 10 AM and 6 PM (8 h) local time, a period when continued foraging would likely produce a net water deficit because of increased heat loads during high-temperature events. We view this estimate as conservative because T_{air} in this region may exceed 40 °C for 10 or more hours each day during a heat wave.

Survival Time Modeling. We use the concept of survival time as an indicator of the intensity of a high-temperature event and the probability of death. Survival time was estimated as the number of hours during which cumulative water loss via evaporation was equivalent to <15% M_b for each passerine species. Given daily activity patterns and temperature profiles, we focus on two ecologically important survival times: ≤5 h (moderate risk of lethal dehydration) and ≤3 h (high risk). Although data for birds are sparse, we selected the loss of 15% of M_b as a conservative estimate of dehydration tolerance (21, 38), and assume that mortality occurs when this threshold is exceeded. For each species, survival times during warm season (April to September) were calculated daily at each NLDAS-2 grid cell location. Our measurements of EWL subsume the effects of hyperthermia, but we do not assess the chronic effects heat on potential mortality. Interactive Data Language code is available in Dataset S1.

Regional and Climate-Change Analyses. With the goal of identifying relevant areas prone to lethal dehydration, we obtained bird ranges from US Geological Survey National Gap Analysis Program portal (https://gapanalysis.usgs.gov/species/data/download/) and overlaid these with the NLDAS-2 grid. We calculated and mapped regional summaries (dehydration climatologies) across species' US ranges as well as within the more-restricted southwest desert ecoregion comprising the Mojave, Colorado, Sonoran, and Chihuahuan deserts (39) to minimize the influence of variations in range size across our suite of species. We then repeated dehydration and mapping analyses using a warming scenario, wherein all NLDAS-2 temperatures during our 1979–2012 dataset were increased by 4 °C, in line with current regional projections for summer warming by 2070–2099 under Special Report on Emissions Scenarios A2 (14) and with mean global surface temperature increases under Representative Concentration Pathway 8.5 (9).

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