

Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves

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Severe heat waves have occasionally led to catastrophic avian mortality in hot desert environments. Climate change models predict increases in the intensity, frequency and duration of heat waves. A model of avian evaporative water requirements and survival times during the hottest part of day reveals that the predicted increases in maximum air temperatures will result in large fractional increases in water requirements (in small birds, equivalent to 150–200 % of current values), which will severely reduce survival times during extremely hot weather. By the 2080s, desert birds will experience reduced survival times much more frequently during mid-summer, increasing the frequency of catastrophic mortality events.

Keywords: dehydration; desert; evaporative water loss; thermoregulation

1. INTRODUCTION

Desert environments are characterized by high environmental temperatures and scarce, unpredictable water resources, and birds inhabiting these ecosystems face a fundamental physiological conflict between evaporating water to maintain body temperature (T_b) below lethal limits, and the need to conserve water and avoid dehydration (Dawson 1954). During the last century, extremely hot weather events have occasionally led to catastrophic avian mortality (Finlayson 1932; Keast 1960; Miller 1963). Arguably, the most dramatic of these reports was Finlayson's (1932) account of tens of thousands of zebra finches, budgerigars and other small birds dead or dying at Rumbalara, central Australia, during January 1932. More recently, in January 2009, *PerthNow* (Towie 2009) reported the deaths of thousands of birds near Carnarvon in Western Australia during a severe heat wave (see the electronic supplementary material).

Large-scale avian die-offs, and heat-related mortality in other species (e.g. flying foxes, Welbergen *et al.* 2007), highlight the importance of considering

extreme weather events for predicting climate change impacts on animal populations. Most recent research has focused on climate envelope modelling that predicts range shifts (e.g. Erasmus *et al.* 2002; Peterson *et al.* 2002) and relatively few studies have examined the direct effects of extreme events (Parmesan *et al.* 2000; Welbergen *et al.* 2007), or developed physiological models directly linking predicted climates to survival and/or reproduction (Kearney & Porter 2009).

General circulation models predict increases in maximum temperatures and frequency, intensity and duration of heat waves (Meehl & Tebaldi 2004; IPCC 2007). Birds, because of their small body size, predominantly diurnal habits and limited use of thermally buffered microsites, are particularly vulnerable to extreme heat waves. Even when inactive in completely shaded microsites, small species can experience rates of evaporative water loss (EWL) exceeding 5 per cent of body mass per hour (Wolf & Walsberg 1996), conditions under which they rapidly reach their limits of dehydration tolerance.

In this study, we examine avian water requirements as a function of body size on extremely hot days, using current maximum air temperature data and values predicted for the 2080s. We model water requirements and survival times during the hottest time of the day, when EWL rates are high, but drinking and foraging behaviours are curtailed (Ricklefs & Hainsworth 1968; Smyth & Coulombe 1971; Fisher *et al.* 1972). We focus our model on two sites representative of many hot subtropical deserts in terms of current and predicted future air temperature maxima.

2. MATERIAL AND METHODS

(a) Evaporative water loss model

We used literature data for 27 bird species in which EWL was measured at air temperatures (T_a) > 41°C (mean active-phase T_b for resting birds (Prinzinger *et al.* 1991)) to construct a model predicting EWL rates from T_a and body mass (M_b) (see the electronic supplementary material). The model combined an equation for EWL in desert birds at $T_a = 25^\circ\text{C}$ (Williams 1996) with our equations for the inflection T_a above which EWL rapidly increases ($T_{\text{inflect}} = 40.38 - 2.29 \log M_b$, $r^2 = 0.487$, with T_{inflect} in degrees Celsius and M_b in grams) and the rate of EWL increase at high T_a ($\log b = 1.153 - 0.495 \log M_b$, $r^2 = 0.859$, where b is the slope ($\text{mg H}_2\text{O g}^{-1} \text{h}^{-1} \text{ }^\circ\text{C}^{-1}$) of a linear regression relating EWL to T_a).

(b) Current and future evaporative water requirements and survival times

To illustrate the effects of higher maximum T_a , we obtained current maxima and predicted increases for the 2080s for two locations that routinely experience $T_a >$ avian T_b : Yuma AZ, USA (32°42' N 114°37' W), and Birdsville, Queensland, Australia (25°54' S 139°21' E). We used the 95th percentiles of maximum T_a recorded during the 1990s as current maxima, and increases of 5.5°C for Yuma and 3.5°C for Birdsville for 2080s maxima (modal values from 18 general circulation models (IPCC 2007)). We modelled water requirements during the hottest part of the day, between 12.00 and 18.00, by predicting EWL over 15 min intervals to obtain estimates of cumulative EWL associated with current and future T_a maxima (see the electronic supplementary material). We estimated survival times as the time required for cumulative EWL to exceed dehydration tolerance. Because of the paucity of dehydration tolerance data for birds exposed to high T_a , we modelled survival times for water loss equivalent to 11 per cent (Wolf 2000) and 22 per cent of body mass (see the electronic supplementary material).

Predicting the frequency of die-offs is complicated by the lack of accurate quantitative data on the conditions under which these events occurred previously. To model current and future patterns of exposure to lethal conditions, we estimated survival times for birds at Yuma for daily T_a maxima recorded during the hottest month (July) during the 1990s, and the corresponding values predicted for the 2080s.

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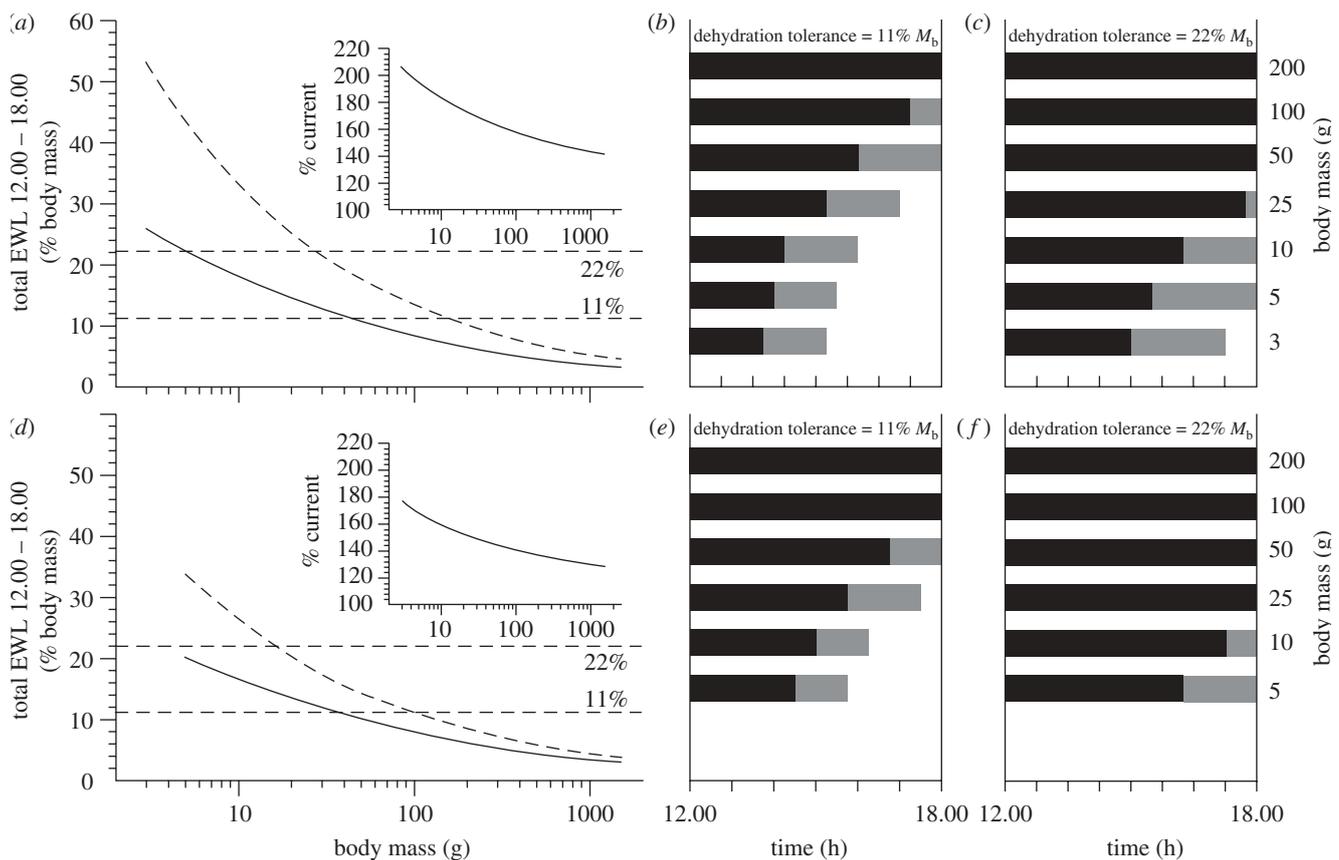


Figure 1. Predicted increases in air temperature (T_a) maxima for (a–c) Yuma AZ, USA, and (d–f) Birdsville, Australia, will cause large (a,d) increases in evaporative water requirements and (b,c,e,f) substantially decreased survival times. Evaporative water requirements and survival times are modelled for birds resting in the shade between 12.00 and 18.00. The inset graphs show water requirements predicted for the 2080s as percentages of current values. In (b,c,e,f), the x-axes correspond to the period 12.00–18.00, with the horizontal bars indicating the time (to the nearest 15 min) at which evaporative water losses exceed dehydration tolerance values ((b,e) 11% or (c,f) 22% of body mass (M_b), indicated by horizontal dashed lines in (a,d)). The M_b minima are 3 g for Yuma (corresponding to small hummingbirds, e.g. *Selasphorus* spp.) and 5 g for Birdsville (thornbills, *Acanthiza* spp.). (a,d) Solid line, 1990s; dashed line, 2080s. (b,c,e,f) Black shade, 2080s; grey shade, 1990s.

3. RESULTS

Avian water requirements are much higher at T_a maxima predicted for the 2080s compared with current values (figure 1). The strong M_b dependence of EWL means that fractional increases will be much larger in smaller species (figure 1). For example, a 5.5°C increase in T_a for Yuma (44.6°C to 50.1°C; current and future 95th percentiles, respectively) will result in water requirements between 12.00 and 18.00 increasing by 95 per cent in a 5 g bird, 64 per cent in a 50 g bird and 47 per cent in a 500 g bird (figure 1). The increases in water requirements on very hot days will cause significantly reduced survival times, most evident in smaller species (figure 1), and a greater frequency of these events (figure 2).

4. DISCUSSION

Increasing air temperatures will lead to large increases in avian thermoregulatory water requirements during extremely hot weather. Because mass-specific EWL rates increase with decreasing body mass, vulnerability to acute dehydration will be most pronounced in small birds. Our model applies to birds resting in complete shade in still air and provides a minimum estimate of increases in water requirements and decreases in

survival times, since solar radiation and forced convection can greatly increase heat gain (Wolf 2000). Increases of 3–5°C in summer T_a maxima are predicted for many deserts, including the Sahara, Arabian and Kalahari (IPCC 2007), and our predictions for Yuma and Birdsville are broadly applicable to many subtropical deserts.

Our model's most critical assumption, that water intake is negligible during the hottest part of the day, is supported by behavioural studies of desert birds (Ricklefs & Hainsworth 1968; Smyth & Coulombe 1971; Fisher *et al.* 1972). Although birds could conceivably adjust their behaviour patterns so as to drink and/or forage during the hottest part of the day, the heat gains associated with activity and/or exposure to intense solar radiation make it extremely unlikely that birds will be able to balance water supply and demand through behavioural adjustments.

A related determinant of avian survival during hot weather is hyperthermia, which can interact with dehydration in two ways. First, water demands can be reduced through sublethal, reversible increases in T_b (mean for 28 species = $43.5 \pm 1.2^\circ\text{C}$, Tieleman & Williams 1999). Many studies of avian EWL at high T_a involved birds that were slightly hyperthermic during measurements, but the non-steady state T_b of

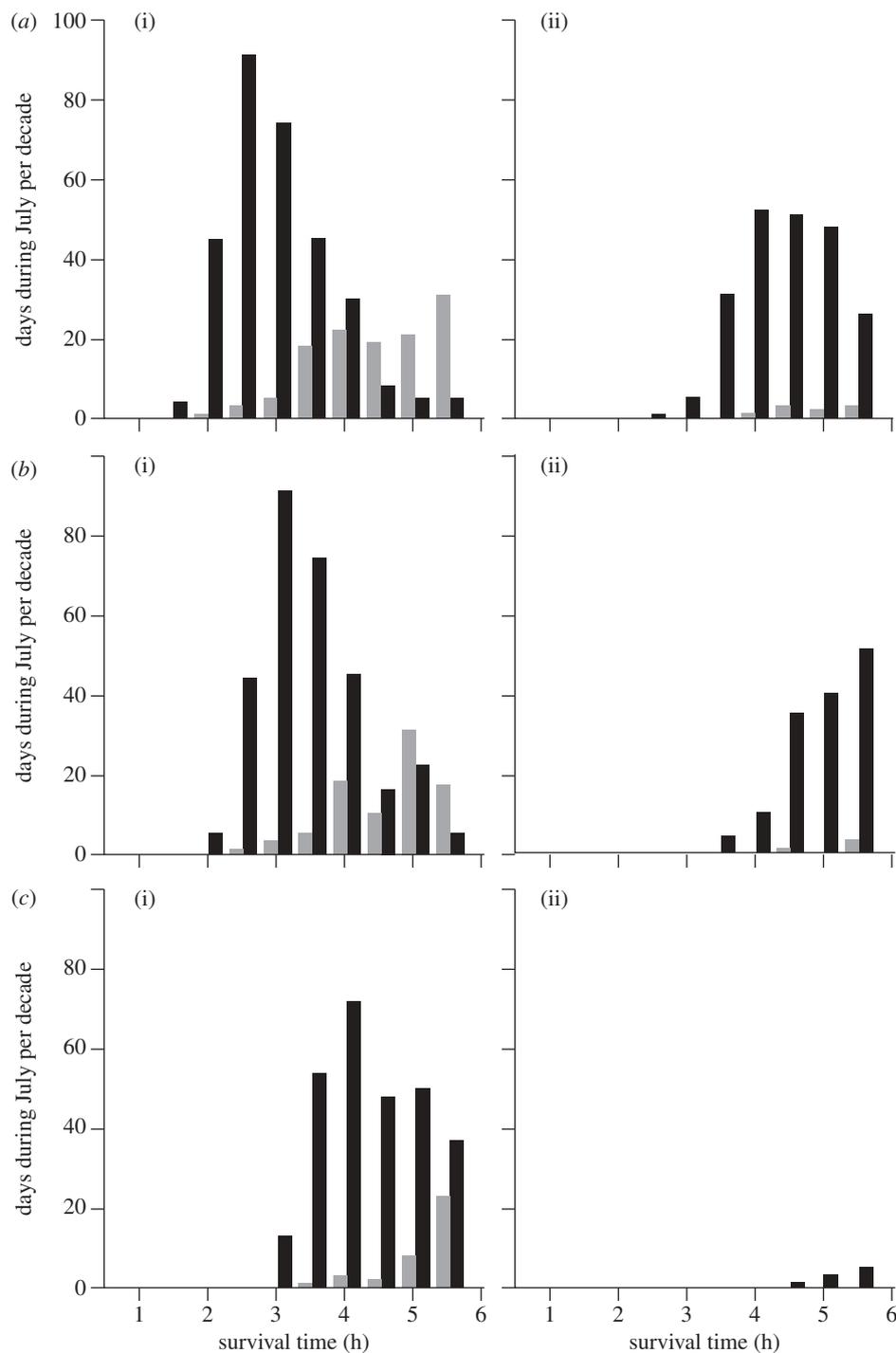


Figure 2. Small birds at Yuma AZ, USA, will be exposed to survival times less than 6 h much more frequently during mid-summer in the 2080s (black shade) compared with the 1990s (grey shade). Survival time distributions are shown for three body mass (M_b) values ((a) 5 g, (b) 25 g and (c) 50 g) and dehydration tolerances equivalent to (a(i), b(i) and c(i)) 11 per cent of M_b and (a(ii), b(ii) and c(ii)) 22 per cent of M_b . Survival time distributions were modelled using daily maximum air temperature (T_a) data for the hottest month (July) during the 1990s, and the predicted increase in maximum T_a for this location (IPCC 2007).

these individuals probably resulted in the water savings associated with hyperthermia being underestimated (Tieleman & Williams 1999). Second, an inability to evaporate water rapidly enough to balance heat gain can lead to T_b increasing to lethal levels. For instance, towhees (*Pipilo* spp.) exposed to $T_a > 40^\circ\text{C}$ rapidly became hyperthermic, lost coordinated movement at $T_b > 45^\circ\text{C}$ and died at $T_b \approx 47^\circ\text{C}$ (Dawson 1954). As T_a maxima increase from current (approx. 45°C) towards future values (approx. 50°C), we anticipate

that (i) water savings achievable through facultative hyperthermia will decrease, and (ii) many birds will die from hyperthermia, even if sufficient water is available, through simply being unable to dissipate heat rapidly enough.

Historical and contemporary reports of catastrophic avian die-offs, taken together with predicted increases in frequency, intensity and duration of heat waves, strongly suggest that future climates will cause more frequent mortality events. These die-offs will periodically

reduce populations, potentially by millions of individuals, over large areas (Keast 1960; Serventy 1971). Although birds are highly mobile, the short time scale over which dehydration occurs makes it unlikely that they will be able to escape such events, other than through longer term range shifts. In addition to increasing direct mortality of adult birds during heat waves, increased T_a maxima will have significant consequences for reproductive success. Avian embryos are highly vulnerable to hyperthermia (Webb 1987), and incubation in very hot environments requires continuous evaporative cooling of eggs (Grant 1982; Walsberg & Voss-Roberts 1983). Finally, several major migratory flyways cross hot subtropical deserts, and migrants crossing such areas during extremely hot weather may be susceptible to high mortality (Miller 1963). The predicted consequences of increasing air temperatures for avian survival in hot deserts reiterate the need for physiological modelling of direct impacts of climate change on birds and other animals.

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