Re-evaluating model assumptions suggests that Australian birds are more tolerant of heat and aridity than predicted: a response to Conradie et al. (2020)

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Lay Summary
Conradie et al. (2020) recently modelled the vulnerability of Australian arid birds to a changing climate. While the approach used by Conradie et al. (2020) is valuable, we argue that key assumptions in their study are poorly supported and the risks of a changing climate to arid zone avifauna are consequently overstated.

Editor: Steven Cooke
Received 19 August 2021; Revised 5 November 2021; Editorial Decision 2 February 2022; Accepted 6 February 2022
Cite as: Pacheco-Fuentes H, Cooper CE, Withers PC, Griffith SC (2022) Re-evaluating model assumptions suggests that Australian birds are more tolerant of heat and aridity than predicted: a response to Conradie et al. (2020). Conserv Physiol 10(1): coac010; doi:10.1093/conphys/coac010.

Conradie et al. (2020) recently evaluated the risk of hyperthermia and dehydration for 10 species of Australian desert bird to projected climates, concluding that small species like the zebra finch (Taeniopygia guttata) were likely to decline throughout their range as a consequence of escalating lethal dehydration risk and hyperthermia. Their modelling was based on birds’ physiological response to air temperature (Tₐ) under experimental conditions in a laboratory relative to existing and projected climate throughout the Australian arid zone (Conradie et al., 2020). They predicted that smaller (10–42 g) bird species, particularly those with a westerly distribution, would be severely impacted by the end of the century, with the zebra finch identified as a species especially at risk, in the north-west of its range. While we agree that it is important to model the likely effects of climate change on the persistence of birds, and that a more extreme climate will likely impact on their abundance and distribution, we believe that the predicted outcomes underestimate the capacity of birds to withstand heat and aridity and consequently may overestimate the likely physiological effects of environmental change. Indeed, we have observed several species, including the zebra finch, withstanding predicted lethal limits in the field (e.g. zebra finches persisting when Tₐ > 46°C and with a maximum air temperature of 47.5°C; at Fowlers Gap, New South Wales, on the following dates: 16, 17 and 24 and 25 January 2019 and 29 November 2020; data from the Bureau of Meteorology Automated Weather Station #46128), despite the predicted dehydration and thermal limits of 41.5
and 46°C, respectively, (Conradie et al., 2020). Consequently, we will address the assumptions of Conradie et al. (2020) that most likely contribute to this discrepancy. We hope that the perspective we provide concerning the assumptions of predictive models improves the accuracy of future models and encourages a more comprehensive integration of laboratory and field observations of physiology and behaviour. This, combined with steps to ground-truth predictive models, will contribute to a better understanding of ecological physiology and its application to conservation and management in the face of climate change.

Assumption: water is unavailable to birds throughout much of Australia’s arid zone

The Australian arid zone is largely defined by low rainfall (Morton et al., 2011), along with high rates of evaporation and high variability of rainfall and $T_a$ (Bradshaw, 1986). Conradie et al. (2020) suggested that unavailability of water limits drinking for birds during hot periods and declining rainfall would further reduce access to drinking water under future climate scenarios. However, standing water is abundant throughout much of Australia’s arid zone, with the presence of natural water points currently reflecting their past distribution (Bird et al., 2016). Even if these water sources become more saline during dry periods, desert birds still drink (Skadhage and Bradshaw, 1974). Rainfall is predicted to decline in some parts of Australia as a consequence of human-mediated climate change, as recognized by Conradie et al. (2020), but the study they cited (Delworth and Zeng, 2014) predicts increasing rainfall in the north and north-west of the continent and the IPCC (2018) predicts only minor (0–5%) changes to mean rainfall for this region, but with increased variability. Therefore, there is unlikely to be less natural water available to birds in general in the region that Conradie et al. (2020) predict zebra finches to be most at risk from climate change. Indeed, higher rainfall has been observed in that region since 1981 (Davies et al., 2010; Delworth and Zeng, 2014) with a shift to increased summer rain (Hughes, 2003), which means water is more likely available when birds’ thermoregulatory demand for water is highest.

While the availability of naturally occurring water is largely driven by climatic variation, the Australian arid zone has been enriched with a high density of groundwater-fed artificial water points to support livestock (Fensham and Fairfax, 2008; James et al., 1999). Rangeland pastoralism is the predominant land use over 70% of Australia’s arid zone (James et al., 1999; Pickup, 1998) and in these areas there are few locations more than 5–7 km from water (Davies, 1972; Davies et al., 2010; Fensham and Fairfax, 2008; James et al., 1999; Pickup, 1998); water-dependant birds typically remain within 12 km of a water source but can travel up to 20 km to water (Harrington, 2002). These artificial water points are consequently a reliable water supply for fauna (Florance et al., 2011; Letnic et al., 2015; Letnic et al., 2014) and water is widely available ad libitum to most mobile animals throughout at least 70% of the arid zone (James et al., 1999).

Assumption: birds do not drink to replace water lost during periods of extreme heat

It is a common fallacy that high rates of evaporative water loss are unsustainable. If evaporated water is replaced by drinking, then evaporative heat loss can be sustained, although it is more challenging for small species (Mitchell et al., 2018). Conradie et al.’s (2020) calculations of dehydration tolerance assumed that birds do not replace water lost at high $T_a$. Even their most conservative model, which assumed that the birds started with a crop full of water, did not allow for birds drinking throughout the day, due to the assumption that birds do not have access to water if they do, they avoid activity and exposure to solar radiation at high $T_a$. However, water-dependant Australian species such as many granivores (including the zebra finch) and nectarivores are typically nomadic and only persist in close proximity to water (Davies, 1984; Harrington, 2002; Burbidge and Fuller, 2007; Jordan et al., 2017). Indeed, water-dependant birds such as the zebra finch are reliable indicators of proximity to water in Australia’s arid regions (Bayly, 1999). We established that birds inhabiting the majority of Australia’s arid zone have ready access to drinking water. We now demonstrate that they use this water throughout the day.

It has long been appreciated that many of quintessential Australian desert birds, including the iconic budgerigar (Melopsittacus undulatus) and zebra finch, are water dependant on days when $T_a \geq 25°C$ (Fisher et al., 1972). Zebra finches, along with other arid-habitat birds including painted finches (Emblema pictum), diamond doves (Geopelia cuneata) and spinifex pigeons (Geophaps plumifera) drink throughout the day on hot days (Davies, 1982). Cooper et al. (2019) established that zebra finches visit water to
Figure 1: Frequency of visits to water troughs at 30-min intervals throughout the day by a population of approximately 350 zebra finches (Taeniopygia guttata) for 17 days of maximum air temperature of >40°C between 1 December and 17 February 2018, together with mean hourly air temperature (black line) from Australian Bureau of Meteorology for Fowlers Gap (station number 046128). Grey panels indicate the period from sunset to sunrise; solar radiation increases from sunrise to peak at approximately midday, declining to 0 at sunset (Kondragunta et al., 1993). Figure re-drawn from the data of Cooper et al. (2019).

drink throughout the day during heatwaves on days with a maximum $T_a$ of up to at least 44.5°C, and found no evidence of zebra finches having to withstand any considerable time without access to water (Fig. 1). Solar radiation in arid environments increases in intensity throughout the day, peaking around midday and then declining to 0 at sunset (and there is a lag in the diel $T_a$ cycle compared to the radiation cycle due to thermal inertia and radiative cooling; Kondragunta et al., 1993). For a population of approximately 350 zebra finches of which a proportion were implanted with an identification Passive Integrated Transponder (PIT tag), there was a high frequency of visits to water between sunrise and sunset, with especially high drinking rates prior to 15:00 (Cooper et al., 2019; Fig. 1), during the period when solar radiation is most intense. Indeed, finches visited water more frequently during the middle of the day on hot days than they did on cooler days, to sustain the higher water intake required to counteract a lower metabolic water production during hot conditions (Cooper et al., 2019). Regular access to drinking water allows birds to maintain sufficient evaporative heat loss to defend a lower body temperature at high $T_a$ compared to dehydrated birds (e.g. Arad et al., 1987; Crawford Jr and Schmidt-Nielsen, 1967; Itsaki-Glucklich and Arad, 1992), reducing the likelihood of fatal hyperthermia.

Assumption: operative temperature experienced by a bird is equivalent to air temperature

Many authors (e.g. Gerson et al., 2014; Hetem et al., 2016; Williams and Tieleman, 2005; Withers et al., 2016; Wolf and Walsberg, 1996) state that evaporation is the only avenue of heat loss for animals when $T_a > T_b$. They assume that $T_a$ is equivalent to operative temperature (or more correctly environmental temperature; $T_e$), as do Conradie et al. (2020)—‘the operative temperature experienced by the bird is equivalent to air temperature’. However, $T_e$ incorporates evaporative, radiative, conductive and convective avenues of heat exchange (Bakken, 1976; Bakken et al., 1985) and, consequently, $T_e$ not $T_a$ determines heat exchange (Mitchell et al., 2018; Wolf, 2000). For an animal in a temperature-controlled cabinet or room, the assumption that $T_a$ approximates $T_e$ is reasonable; the thermal limits that Conradie et al. (2020) identified are realistic for birds under these laboratory conditions, as there is no object in the animal’s environment with a temperature less than $T_a$. The problem arises when extrapolating laboratory findings to wild, free-living individuals where the assumption that $T_a = T_e$ is unrealistic (Maloney and Dawson, 1994) due to the complexity of the animal’s thermal environment. This can substantially distort heat tolerance calculations (Mitchell et al., 2018).

Heat loss via radiation to objects cooler than $T_a$ and selection of cool microclimates where $T_e < T_a$ are two examples of how an animal may potentially lose, not gain, heat when $T_a > T_b$ without augmenting their own evaporative heat loss. The significance of radiative heat loss to the night sky, which is considerably lower than $T_a$ and often approaches the mean troposphere temperature of −23°C (Sun et al., 2017), has long been appreciated, e.g. Schmidt-Nielsen’s camels (Schmidt-Nielsen et al., 1956). However, not so widely appreciated by biologists is that daytime sky temperatures can also be considerably lower than $T_a$. Clear,
dry desert day-time skies are typically >20°C lower than $T_a$ and can be a significant heat sink (Adelard et al., 1998; Evangelisti et al., 2019). Thus, net radiative heat exchange with the daytime sky can be a potential source of heat loss for animals in their natural environment even when $T_a > T_b$.

We can use a simple heat balance model for zebra finches (Porter and Gates, 1969) to estimate the cooling effect of daytime sky temperatures (Fig. 2). If net radiative exchange is constant, then a bird in a metabolic chamber (surrounded by a black bulb = $T_a$) is effectively at a higher $T_a$ than the bird in its natural environment sheltered from solar radiation but experiencing heat loss to the sky (surrounded by a combination of ground black bulb = $T_a$ and daytime sky grey bulb at $<T_a$). At $T_a = 41.5°C$ (calculated dehydrational maximum for a zebra finch; Conradie et al., 2020), the heat loss of a bird in natural shade facilitated by radiation to the daytime sky, is equivalent to $T_a$ of $\sim$30°C for a bird in a metabolic chamber. At the calculated lethal heat $T_a$ of 46°C, the equivalent natural $T_a$ is only $\sim$33°C.

Birds can also exploit other aspects of their environment to achieve heat loss without augmenting their own evaporative heat loss at $T_a > T_b$. Conductive loss is possible if the animal can contact a surface cooler than $T_b$, and radiative loss will occur to objects with a surface temperature $< T_b$. Briscoe et al. (2014) suggested that cool trees can be a heat sink for many animals including birds, and Wolf et al. (1996) calculated that small desert birds reduced evaporative water loss by 50–66% by sheltering in hollows or against the trunks of trees that were $\sim$3°C $< T_a$. Evaporative cooling by the finches was likely lower due to evaporative cooling of their immediate environment (Griffith, pers. obs.). Sheltering in these favourable microclimates presumably imposes costs associated with foraging, reproduction and predation, but an observation of birds persisting during periods of extreme $T_a$ is evidence they can balance these costs. Our data for body mass and blood parameters of wild, free-living zebra finches indicates that withstanding $T_a$ of up to 45.2°C does not impose a significant physiological cost (Cooper et al., 2019, 2020b).

**Assumption: physiological traits that determine thermal tolerance are fixed**

Physiological change is an important but often overlooked component of animals’ response to environmental change (Mitchell et al., 2018; Wojciechowski et al., 2021). Animals can respond to changing environmental conditions by microevolution and by developmental or acclimatory plasticity. Failing to consider these responses in mechanistic climatic models produces inaccurate predictions (Clusella-Trullas et al., 2021; Fuller et al., 2010). There are a plethora of studies demonstrating adaptive and plastic physiological change by birds in response to environmental change, including zebra finches. In addition to an array of genetic, reproductive, morphological and behavioural effects of captivity (e.g. Forstmeier et al., 2007; Gilby et al., 2013; Mainwaring et al., 2010; Tschirren et al., 2009). Skadhauge and Bradshaw (1974) and Cooper et al. (2020a) reported that captive conditions impact on the metabolic and hygic physiology of zebra finches, demonstrating physiological consequences of differing environmental conditions. Developmental plasticity in response to exposure to, or signals of, high $T_a$ impacts body mass and growth (Andrew et al., 2017) of zebra finches. There is also considerable evidence of phenotypic plasticity; zebra finches respond to chronic and acute acclimation and acclimatization to varied $T_a$ and water availability by adjusting reproductive, cellular and thermal physiology, including metabolic...
heat production, evaporative heat loss and/or T\(_b\) (e.g. Salvante et al., 2007; Niedojadlo et al., 2018; Cooper et al., 2019, 2020a, 2020b; Szafrańska et al., 2020; Wojciechowski et al., 2021).

Cooper et al. (2019) demonstrated that the ability of zebra finches to predict periods of extreme T\(_b\) assisted them to withstand these conditions by implementing appropriate behavioural and physiological responses. As climate change realizes projected future T\(_b\) increases, the likelihood that birds will have already experienced extreme conditions will be greater, improving resilience of zebra finches and facilitating favourable plastic responses (Cooper et al., 2020a). An inability to predict and respond favourably to unexpected extreme events is one factor hypothesized to contribute to heat-induced avian mass mortality (Cooper et al., 2019). Attempts to model future responses of birds, including small passerines such as the zebra finch, to changing environmental conditions must consider their demonstrated capacity for micro-evolutionary or plastic adaption. In summary, we feel that the overall conclusions of Conradie et al. (2020) are overstated and that the degree to which Australia’s arid zone birds are vulnerable to the changing climate is currently unclear. Predicting the vulnerability of species to climate change is difficult, but a worthy objective and can be improved through a comprehensive consideration of physiological, ecological and evolutionary processes (Clusella-Trullas et al., 2021).

**Funding**

This work was supported by the National Agency for Research and Development of the Republic of Chile—International Macquarie Research Excellence Scholarship (BECAS Chile/International Doctorate Scholarships 2019-72200260 to H.P.-F.) and the Australian Research Council’s Discovery Project funding (DP170103619 to S.C.G. and C.E.C.).

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