RESEARCH ARTICLE

The effects of temperature extremes on survival in two semi-arid Australian bird communities over three decades, with predictions to 2104

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Abstract

Aim: Organisms in arid and semi-arid regions are frequently exposed to climatic extremes and accordingly among the most vulnerable to climate change. Studies of seasonal differences in vital rates, which mediate effects of climate on viability, are rare in arid species, limiting ability to project population trends. We quantified survival patterns for two bird communities as a function of exposure to temperature extremes in winter and summer, then projected survival patterns to 2104.

Global Ecology and Biogeography Location: Semi-arid eastern Australia.

Time period: 1986-2016; 1986-2104.

Major taxa studied: Birds.

Methods: Using mark-recapture time-dependent Cormack-Jolly-Seber models and data for 37 species from two >30-year ringing programmes, we tested for effects on 6-monthly survival of exposure to temperatures >38 and <0°C. We then predicted future survival for different emission scenarios, testing whether changes in survival associated with warming winters would be sufficient to offset the effects of rising summer temperatures.

Results: Survival probability declined strongly with increasing exposure to days >38°C and to a lesser extent to days <0°C, with temperature extremes explaining 43 and 13% of temporal variation in survival among years, respectively. Summer survival patterns were similar across avian guilds but only survival of nectarivores declined in winter. Our models predict that gains in winter survival will not offset reductions in summer survival. Annual survival is predicted to decline substantially by the end of the century: from .63 in 1986 to .43 in 2104 under an optimistic emission scenario and to .11 under a pessimistic scenario.

Main conclusions: We highlight the significance of temperature extremes for species' persistence in arid and semi-arid regions, comprising 70% of Australia's landmass, and 40% globally. Our demography-based results are consistent with physiological-based projections evaluating avian survival in arid and semi-arid regions globally and suggest rising summer temperatures pose a risk to population persistence in these regions.

KEYWORDS

arid zone, Australian birds, avian guilds, climate change, energy and water, population projections, species persistence, survival, temperature extremes, thermoregulation

1 | INTRODUCTION

A signature of contemporary climate change is the changing frequency, intensity and duration of extreme weather events (Stillman, 2019; Ummenhofer & Meehl, 2017). Birds in the arid and semi-arid regions of the world are particularly vulnerable to temperature extremes, in part, because their high body temperatures are close to the lethal limit for endotherms, and small changes in temperature can cause thermal stress at both the hot and cold ends of the temperature range. Exposure to weather extremes can disrupt energy and water budgets with consequences for fitness that affect both survival and reproduction (Boyles et al., 2011; Huey et al., 2012; Mitchell et al., 2018).

Mortality associated with exposure to summer extremes can be a direct result of succumbing to acute heat stress via hyperthermia or lethal dehydration, exemplified by mass die-offs of budgerigars *Melopsittacus undulatus*, zebra finches *Taeniopygia guttata* and Carnaby's cockatoos *Calyptorhynchus latirostris* during heatwave events in Australia (McKechnie et al., 2012; Saunders et al., 2011). In such cases, avian body temperature exceeding about 46°C is lethal (Boyles et al., 2011).

Fitness in terrestrial animals may also be affected by high temperatures well below those causing die-offs events. Growing evidence suggests that air temperatures in the mid to high 30s°C are harmful for endotherms (Cunningham et al., 2021). For example, prolonged exposure to temperatures >38°C has been shown to increase the cost of avian thermoregulation by increasing the need for evaporative cooling to maintain body temperatures below lethal limits (McKechnie et al., 2017). Increasing exposure to these sublethal conditions increases the risk of mortality, when exposure is prolonged over hours, days and weeks (Sharpe et al., 2019, 2021). Indeed, recent work on Australian desert birds in the laboratory showed that chronic heat stress can cause organ damage (e.g. liver or kidneys), which can contribute to avian mortality over time (Xie et al., 2020).

High temperatures are also associated with changes to foraging patterns and microhabitat use (Cooper et al., 2019; du Plessis et al., 2012; Edwards et al., 2015; Funghi et al., 2019; Sharpe et al., 2022), which can lead to a reduction in food intake and loss of body condition. Southern pied babblers, *Turdoides bicolor*, and southern yellow-billed hornbills *Tockus leucomelas*, for example, were unable to maintain body mass on days when temperatures exceeded thresholds in the mid 30s°C (du Plessis et al., 2012; van de Ven et al., 2019) and jacky winter, *Microeca fascinans*, lost 2% of their mass on days \geq 42°C (Sharpe et al., 2019). Given that body condition is closely linked to survival and reproductive success (Paniw et al., 2019), increasing exposure to high summer temperatures is likely to have major fitness consequences as the climate warms.

Exposure to cold extremes can also impose thermoregulatory and energetic challenges for endotherms, although we have much less understanding of how birds respond to reductions in cold extremes that are expected to be beneficial for fitness as the climate warms. Energetic constraints and cold stress can drive reductions in body condition and impose carry-over costs on subsequent survival and reproduction (Williams et al., 2014). In Australia, changes in survival were associated with temperature extremes for two coexisting bird species monitored over 37 years, red-winged fairywrens, Malurus elegans, and white-browed scrubwrens, Sericornis frontalis (Gardner et al., 2017). In white-browed scrubwrens, winter temperatures <5°C were associated with lower survival within the same season while in both species, survival was associated with body size, and there was evidence that size-dependent mortality was mediated by carry-over effects of climate in the previous season (Gardner et al., 2017). Moreover, energetic costs of thermoregulation in the cold during periods of low food availability can be greater than those in warmer conditions during the breeding season (Harrison et al., 2011; Williams et al., 2014). For example, energetic stress on cool days was greater than that associated with exposure to high temperatures between 40 and 45°C in an arid zone population of zebra finch (Cooper et al., 2019). Warming winters can, or are predicted to, reduce winter mortality and lead to improvement in body condition (Ozgul et al., 2010; Robinson et al., 2007). For example, warming winters led to longer growing seasons with concomitant improvement in the body condition of yellow-bellied marmots, Marmota flaviventris, and this was associated with changing patterns of survival and reproduction (Ozgul et al., 2010). Benefits of warming conditions in winter may therefore offset negative effects of warming summers on survival.

Studies of how changes in seasonal weather influence vital rates are rare in arid zone species, largely because of a paucity of long-term demographic data. This limits our ability to project population trends in coming decades. Here we investigate variation in survival associated with exposure to high summer and low winter temperatures for 37 avian species captured over a 30-year period (1986-2016) at two sites in a semi-arid landscape in western NSW, Australia. Using mark-recapture time-dependent Cormack-Jolly-Seber models we first test for the effects on 6-monthly survival of exposure to: (a) summer temperatures above 38°C, and (b) winter temperatures below 0°C. We classify these temperatures as extreme because chronic effects that reduce survival appear to begin at these thresholds in Australian bird species (Bailey et al., 2020; Gardner et al., 2016, 2017; McKechnie et al., 2017); obviously more extreme temperatures can have acute effects via immediate mortality. At our study sites these thresholds are currently reached on around 5% of days: cold extreme in winter 8% at Charcoal Tank Nature Reserve, 9% at Weddin Mt National Park; hot extreme

in summer 5% at Charcoal Tank, 3% at Weddin Mt. We then test whether the changes in 6-monthly survival associated with warming winters will be sufficient to offset the negative effects on survival of rising summer temperatures based on climate projections for the region to the year 2104. Current climate projections for Australia indicate more hot summer and fewer cold winter temperature extremes (BOM & CSIRO, 2020).

2 | METHODS AND MATERIALS

2.1 | Study sites and species

The study was carried out at two sites: The Charcoal Tank Nature Reserve (hereafter Charcoal: 33° 58' S, 147° 9' E, 147.1575° E) and Weddin Mountains National Park (hereafter Weddin: 33° 56' S, 147° 59' E, 147.9872° E) in western New South Wales in south-east Australia (Supporting Information Figure S1). Both sites have been the subject of long-term (>30 years) ringing programmes, with data collected in each year since 1986. The study sites are located 75 km apart within a fragmented agricultural landscape (see Supporting Information Appendix S1 for site description).

Birds were captured in mist nets and sampled 2–7 times annually (Gardner et al., 2016). At each capture, we recorded body mass using a Pesola balance (\pm 0.5 g). Wing length was measured as the length of the flattened wing chord from the carpal joint to the tip of the longest primary feather using a butt-ended ruler (\pm 1.0 mm), and primaries were scored for moult. Data collection was overseen by Mark Clayton (Charcoal) and Richard Allen (Weddin) ensuring consistency in methods over time and between sites.

We obtained weather data from the Australian Government Bureau of Meteorology, from the Grenfell (Manganese Rd) station for the Weddin site, and from the West Wyalong Airport station for the Charcoal site. We defined 6-month periods from 1 September to 29 February as "summer" or from 1 March to 31 August as "winter". For each 6-month period between 1970 to 2016 we extracted (a) mean daily extreme temperatures for each season (mean daily maximum in summer, mean daily minimum in winter); (b) the sum of precipitation for each 6-month period; (c) the number of days with temperatures beyond an extreme threshold for each season (days above 38°C in summer, days below 0°C in winter).

2.2 | Future climate predictions

To predict the number of temperature extremes until the end of the century under different scenarios of greenhouse gas concentration we chose the model CESM1-CAM5 (Community Earth System Model version 1 that includes the Community Atmospheric Model version 5, Neale et al., 2010). The model CESM1-CAM5 performs very well for short-term predictions of climate in Eastern and Southern Australia (Moise et al., 2015). We extracted daily predicted minimum and maximum temperatures for the years 2016 to 2104 from the West Wyalong Airport weather station, located 10.5 km from Charcoal, under three representative concentration pathway (RCP) scenarios: RCP 2.6 corresponding to a very stringent scenario of reductions in greenhouse gases emissions, RCP 4.5 an intermediate scenario and RCP 8.5 the worst-case climate change scenario (Meinshausen et al., 2011). We combined climate projections with observed data (1986 to 2015) and for each 6-month period calculated the number of days below 0°C in winter and above 38°C in summer. For both seasons and for each of the three RCP scenarios we fitted generalized additive models of the number of extreme temperature days as a function of year. Year was modelled as a thinplate regression spline (Wood, 2003). We used the predictions from each of these generalized additive models to project survival in the future.

2.3 | Mark-recapture data

The full data set contains captures for 39 species for which >100 captures were recorded between 1986 and 2016 (Supporting Information Table S1) with a total of 33,550 captures for 21,621 individuals. These data included only adults that were identified on the basis of plumage. We classified birds as belonging to one of four feeding guilds: nectarivore, insectivore, omnivore or granivore. Most individuals are captured only once, presumably due to movements of non-resident birds or post-fledging dispersal. Our study populations, typical for much of the Australian arid zone, contain both resident and migratory species, including partial migrants and local nomads, making it difficult to classify movement patterns for individual species (see Chan, 2001). This means that apparent local mortality represents a mixture of true mortality and permanent emigration. To reduce the influence of emigration we removed the first capture of each individual to focus our analysis on resident birds, increase the proportion of apparent survival (or mortality) related to local survival (or mortality) rather than emigration and decrease computation time. In two species, not a single individual was recaptured so we were left with only 37 species totalling 4,136 individuals. We present results derived from the full data set in Supporting Information Figure S8. We used capture data to calculate a temporal proxy of bird density within each guild (see Supporting Information Appendix S2).

To create regular time intervals corresponding to seasons and to decrease the number of variables in models we aggregated capture sessions by 6-month periods from 1 September to 29 February ("summer") or from 1 March to 31 August ("winter"). Thus, we obtained 62 virtual capture occasions instead of the initial 748. This procedure violates the assumption of mark-recapture models that survival intervals are long relative to the marking intervals but was essential to obtain a manageable number of capture occasions and reasonably high recapture probabilities. The noise introduced by this violation is expected to only blur the statistical signal and not bias it (see Supporting Information Appendix S3, Figure S2).

2.4 | Statistical analyses

2.4.1 | Mark-recapture model

We modelled apparent survival probability across species and time periods, as a function of summer and winter weather. We used timedependent Cormack–Jolly–Seber models, which describe capture histories as the product of a survival probability and a recapture probability. We modelled variation among species, among time periods and among locations for survival and recapture probabilities (see Supporting Information Appendix S4).

For the linear predictor corresponding to recapture probability, the fixed effects were a global intercept, the effect of site (Weddin versus Charcoal), the effect of season (the 6-month capture period being the non-reproductive or the reproductive season), and the effect of a bird being caught on a previous occasion to control for trap-dependence.

For the linear predictor corresponding to survival probability, the fixed effects were a global intercept for the effect of site (Weddin versus Charcoal), a linear effect of time (i.e. 6-month periods fitted as a continuous covariate) to de-trend the response and avoid over-estimating the effect of climate (Grobois et al., 2008), the effect of the 6-month survival period being in winter (as opposed to summer), a dummy variable indicating whether an individual was captured for the first time to account for transience effects, a proxy for within-guild-site bird density fitted as a continuous covariate (see Supporting Information Appendix S2, Figures S3 and S4), and the effect of weather variables, for which we tried different combinations involving our three weather variables, measured for each site and each 6-month period: (a) the number of days with temperature reaching a threshold (either above 38°C for summer survival periods or below 0°C for winter survival periods); (b) the sum of precipitation because extreme temperatures are correlated with the sum of precipitation, and precipitation is known to affect bird survival (Gardner et al., 2016; Kennedy, 1970; Robinson et al., 2007); (c) the average daily temperature (average winter minimum, average summer maximum). Weather variables were standardized to a mean of zero and a standard deviation of one.

In a first model (Model 1 hereafter), we fitted the linear effects of the number of days with temperatures beyond thresholds in each season as these were the main predictors of interest, and a linear effect of the sum of precipitation in each season. This model is at the centre of our work because it estimates the independent effect of extreme temperatures when accounting for the confounding effect of precipitation. For both seasons, separately, we calculated the proportion of temporal variance in mean survival among years explained by extreme temperatures (see Supporting Information Appendix S5 for details). To predict the net effect of changes in the balance of deleterious winter versus deleterious summer temperatures, we predicted seasonal-survival and year-survival based on Model 1 and on predictions of temperature extremes based on the CESM1-CAM5 model for the three RCP scenarios, from 1986 to 2104. Survival was predicted while integrating the random effects of year and species.

Beyond Model 1, we fitted four extra models to address secondary questions regarding the effect of weather on survival probability. In a second model (Model 2 hereafter) we added the interaction between sum of precipitation and the numbers of days >38 or <0°C in each season. In wetter summers the negative effect of extreme high temperatures may be reduced because water availability helps birds cope with heat, while in wetter winters the negative effect of extreme cold may be exacerbated because the insulating capacity of wet feathers is poor (Kennedy, 1970; Robinson et al., 2007). These expectations, however, assume that extreme temperatures co-occur with increased precipitation or water availability, within each time period, which may not be the case. Next we fitted Model 3, an extension of Model 2, in which we also included a linear effect of mean maximum or minimum daily temperature in each season. With the model we test whether it is possible to disentangle the effects of the number of days of extreme temperatures from the effect of the average season temperature.

We first fitted Models 1 to 3 for all species together. However, dietary guilds are expected to respond differently to weather conditions because food availability varies with temperature and rainfall, and because water content varies between diets, so we fitted Models 1 to 3 separately for each of the four guilds.

Model 4 included random slopes of species for the effects of the number of days of extreme temperatures to test for differences among species in their responses (see Supporting Information Appendix S4, results in main text). Model 5 included species average size and its interaction with the number of days of extreme temperatures (see Supporting Information Appendix S4, results Figure S7). With Model 6 we tested whether our results were robust to the exclusion of the first capture: Model 6 is identical to Model 1 but is fitted on the full data set, which includes all captures of all individuals, and includes a second transience fixed effect (see Supporting Information Appendix S4, results Figure S8).

We fitted all models in the Bayesian probabilistic programming language Stan (Carpenter et al., 2017), using No-U-Turn Hamiltonian Monte Carlo sampling with Rstan (Stan Development Team, 2020). For fixed effects we used normalizing Gaussian priors with a mean of 0 and a standard deviation of 3. For random effect standard deviations we used half-Cauchy priors of location 0 and scale 0.1. We used 4 chains each with 2,000 warm-up iterations and 2,000 samples. We assessed model convergence using visual diagnostics (trace plots, pairwise posterior plots), in particular using Bayesplot (Gabry et al., 2019) and checked that all R-hat values were below 1.05 and effective sample sizes were above 200. We report posterior means and 95% highest posterior density credible intervals. All derived parameters and model predictions were calculated by integrating over the full posterior distribution. The code to run all models is provided in Supporting Information Appendix S1.

3 | RESULTS

Unless mentioned otherwise, parameter estimates are from Model 1, fitted to all species together. Survival probability was slightly higher at Weddin compared to Charcoal ($\beta = 0.25, 95\%$

highest posterior density credible interval [0.02; 0.50]) and did not clearly differ between summer and winter ($\beta = -0.04$ [-0.68; 0.59]) (Supporting Information Table S2). The effect of transience was negative ($\beta = -0.78$ [-0.998; -0.55]), meaning that birds have a lower probability of apparent survival just after being captured for the first time. This effect may correspond to non-resident birds that permanently leave the study site after first capture. There was heterogeneity in survival probabilities both among occasions, even after accounting for weather variables (random standard deviation, $\sigma = 1.09$ [0.77; 1.54]) and among species ($\sigma = 0.28$ [0.14; 0.49], Figure 1). Species mean 6-month survival probabilities varied from .88 [.83; .92] in the white-throated treecreeper, to .76 [.67; .83] in the superb fairy-wren (Figure 1).

Recapture probability was consistently lower at Weddin compared with Charcoal and did not clearly differ between seasons (Supporting Information Table S2). Trap dependence was positive

White-throated treecreeper

Rufous whistler Brown treecreeper Inland thornbill Eastern yellow robin Brown-headed honeyeater

Speckled warbler White-browed babbler White-eared honeyeater Golden whistler Grey shrike-thrush White-plumed honeyeater

Yellow thornbill

Willie wagtail

Striated pardalote

Spiny-cheeked honeyeater Yellow-tufted honeyeater Dusky woodswallow

Yellow-faced honeyeater Buff-rumped thornbill 6-month apparent survival

 $(\beta = 0.33 [0.23; 0.43])$, meaning that a living bird is more likely to be recaptured just after having been captured. There was heterogeneity in recapture probabilities both among occasions ($\sigma = 0.55 [0.46; 0.66]$) and among species ($\sigma = 0.68 [0.44; 1.05]$). Species recapture probabilities varied from .34 [.27; .42] in the white-throated treecreeper, to .074 [.038; .12] in the spiny-cheeked honeyeater (Figure 1).

3.1 | Effects of number of days of extreme temperatures

Recapture

The effect of the number of extreme summer days was strongly negative ($\beta = -0.57$ [-1.01; -0.08]), corresponding to a decline in survival probability from .86 [.78; .95] when there are no days above 38°C to .59 [.45; .77] for 30 days above 38°C (Figure 2). The effect of the number of extreme winter days was marginally negative

Guild

Granivore

Insectivore

Nectarivore



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Number of days beyond extreme

FIGURE 2 Predicted probability of 6-monthly survival as a function of the number of days of extreme summer temperatures recording daily maxima >38°C and extreme winter temperatures recording minima <0°C. Average predictions, over all species, are shown in thick lines with shaded areas representing 95% credible intervals, and were derived from Model 1. Thin lines represent species-specific predictions derived from Model 4. Predictions were estimated for a median rainfall and population density, but integrated over temporal variation, and in the case of the average predictions, over species variation

($\beta = -0.39$ [-1.01; 0.04]), corresponding to a decline in survival probability from .84 [.76; .90] for 0 days below 0°C to .53 [.28; .78] for 44 days below 0°C (Figure 2; Supporting Information Table S2). The effect of extreme temperatures explained 43% [16%; 70%] of temporal variation in survival among years in summer and 13% [0%; 36%] in winter. The effects of the number of extreme summer and winter days were also apparent when including transients, in model 6 (summer $\beta = -0.33$ [-0.57; -0.10], winter $\beta = -0.37$ [-0.62; -0.15]), with the effect in summer being a bit weaker and the effect in winter being of similar strength but more precisely estimated (Supporting Information Figure S8).

Model 4 revealed that species differed significantly in their responses to extreme summer temperatures ($\sigma = 0.14$ [0.02; 0.32]) and to extreme winter temperatures ($\sigma = 0.12$ [0.02; 0.27]), but these differences were biologically small so that the pattern of survival was qualitatively consistent across species (Figure 2, Supporting Information Figure S5, Table S8). Moreover, as is often the case in mixed models (Houslay & Wilson, 2017), despite significant variance among species the uncertainty in species-specific slopes was large and so it is not possible to identify which species responded more or less strongly (Supporting Information Figure S5). In particular, the differences were not significantly explained by differences in the mean body size of species (model 5, Supporting Information Table S9).

Guild-specific analyses confirm the consistency of the responses among species. The negative effect of extreme temperatures in summer was independently found in insectivore, nectarivore and omnivore species (Supporting Information Table S3, Figure S6). On the other hand, the effect of extreme temperatures in winter was present only in nectarivore species, where it was significant and strong ($\beta = -0.66$ [-1.56; -0.43]), with a predicted decline in survival probability from .89 [.78; .97] with Odays below 0°C to .41 [.05; .81]

with 44 days below 0°C. For the granivore guild, a small sample size prevented a precise estimation of any parameter for weather effects. Winter precipitation had a negative effect on survival ($\beta = -0.52$ [-0.94; -0.17]). The effect was statistically supported in the nectarivore guild model ($\beta = -0.92$ [-1.56; -0.43]) but not found in other

rivore guild model ($\beta = -0.92$ [-1.56; -0.43]) but not found in other guilds (Supporting Information Table S3). Summer precipitation had no clear effect on survival across species ($\beta = -0.24$ [-0.57; -0.57]), or in any of the guilds (Supporting Information Table S3).

When fitting Model 2 to all species together (Supporting Information Table S4), there was no evidence of interactions between number of days beyond extreme temperatures and precipitation, in summer ($\beta = 0.04$ [-0.4; 0.52]) or in winter ($\beta = 0.13$ [-0.44; 0.13]). In guild models, there was support for an interaction only in omnivorous species, for summer, with increased survival to extreme temperatures at higher precipitation ($\beta = 0.67$ [0.03; 1.42]) (Supporting Information Table S5).

Fitting Model 3 to all species together allowed us to disentangle the effects of mean temperatures from the number of days with extreme temperatures. For summer, there was sufficient evidence that the number of days above 38°C had a negative effect on survival probability after accounting for effects of mean temperature ($\beta = -0.32$ [-0.55; -0.03]) (Supporting Information Table S6). In winter the trend for the effect of the number of days beyond 0°C was marginally negative but the uncertainty was large ($\beta = -0.28$ [-0.68; 0.04]).

In summary, winter extremes had a weak effect on 6-monthly survival, except in the case of nectarivores, which are predicted to have low survival (c. 41%) in the coldest winters with >40 days below freezing. In contrast, the negative effect of summer extremes was strong and consistent across species (Model 4), showing little variation among species (Supporting Information Figure S5) and all three guild-models showing similar trends (Supporting Information Figure S6). Our results are robust to the inclusion of the correlated effects of mean extreme temperatures (Model 3, Supporting Information Table S6), to the inclusion or exclusion of transient individuals (Model 6, Supporting Information Figure S8, Table S10), and in accounting for species (Model 4, Supporting Information Figure S5) and guild differences (Supporting Information Figure S6).

3.2 | Climate predictions

At Charcoal the number of winter days below 0°C is projected to decrease from 12.0 in the year 2016 to almost 0 in 2104 (2.4 RCP 2.6, 1.4 RCP 4.5, 0.17 RCP 8.5), while the number of summer days above 38°C is projected to increase from 13.8 in 2016 to 28.7 (RCP 2.6), 36.4 (RCP 4.5) and 67.4 (RCP 8.5) in 2104 (Figure 3). Based on these climate projections, model predictions for survival to 2104 showed broad-scale



FIGURE 3 Predictions of daily temperature extremes under three emission scenarios from the model CESM1-CAM5 (Community Earth System Model version 1 that includes the Community Atmospheric Model version 5). (a) Number of days on which temperatures are below 0°C in winter; (b) number of days on which temperatures are above 38°C in summer. Numbers are observed from 1986 to 2015 (black line) and simulated according to the model from 2016 to 2104. Smoothed lines and 95% confidence intervals are produced with negative-binomial generalized additive models using thin-plate smooths of year from 1986 to 2104. RCP = representative concentration pathway

declines in annual survival across species (Figure 4). Assuming median precipitation, in winter, 6-month survival is projected to increase slightly as winters warm, whereas summer survival and annual survival were predicted to decline substantially, with the severity of the decline depending on the RCP scenario (Figure 4).

4 | DISCUSSION

We quantified patterns of adult survival for two bird communities in semi-arid south-eastern Australia as a function of exposure to





FIGURE 4 Projected 6-monthly survival as a function of predicted change in the number of (a) winter and (b) summer days with temperature extremes >38 or <0°C, respectively; (c) annual survival to 2104 (averaged over all species, sites and time periods), for three scenarios of emissions and associated climate change. For winter the predictions from the three scenarios largely overlap. Dashed lines indicate the initial predicted survival probability to provide context for trends in predicted survival. Shaded areas represent 95% credible intervals

temperature extremes in winter and summer, using data from 37 species that have been the subject of continuous ringing programmes over >30 years. Survival probability did not differ between summer and winter, but survival declined at a higher rate with increasing exposure to summer days with thermal maxima >38°C, than with increasing exposure to winter days with minima <0°C. The effect of

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hot days in summer was consistent across species and guilds whereas the effect of cold days in winter was consistent across species but only statistically clear in nectarivores. Model projections to 2104 suggest that survival may be reduced by a third from current levels; the increase in survival associated with milder, warming winters will be insufficient to offset the negative effects on survival of more frequent extreme days above >38°C in summer.

4.1 | Survival

Our study does not elucidate the causes of temperature-related summer mortality or the specific timeframe over which such mortality occurs, but several mechanisms might be at play. Mortality might be a direct result of hyperthermia or lethal dehydration during heatwave events as previously reported in arid Australia (McKechnie et al., 2012; Saunders et al., 2011). However, increasing exposure to high temperatures >38°C is also likely to increase mortality over broader timeframes via increasing the need for evaporative cooling to maintain body temperatures below lethal limits or reducing food intake with consequences for water and energy budgets (Mitchell et al., 2018). Recent work by McKechnie et al. (2017) examined the evaporative cooling capacity and heat tolerance of five insectivorous and nectarivorous passerine species in Australia's arid zone, among them the spiny-cheeked honeyeater Acanthagenys rufogularis included in this study. They confirmed the reliance of these species on evaporative heat loss via panting at high air temperatures. When air temperatures exceeded 38°C, rates of evaporative water loss increased rapidly and linearly to at least sevenfold (670-860%) above basal rates under field laboratory conditions (McKechnie et al., 2017). Previous work at both Charcoal and Weddin showed that prolonged exposure to days with air temperature >38°C was associated with reductions in body condition of white-plumed honeyeaters Ptilotula penicillatus (Bailey et al., 2020), and at Charcoal, heat-exposed individuals in poor condition were less likely to be recaptured the following spring (Gardner et al., 2016). This apparent mortality may have been a result of thermoregulatory constraints but could also result from heat-related changes in foraging patterns and microhabitat use (du Plessis et al., 2012; Edwards et al., 2015; Funghi et al., 2019) that lead to a reduction in food intake and loss of body condition, although we have no direct evidence in our study species.

Diet is an important factor influencing the way birds respond to high temperatures (Albright et al., 2017; Smit et al., 2019). Diets vary in water content, potentially making some dietary guilds more vulnerable to rising temperatures than others. For example, the dry seeds eaten by granivores have the lowest water content of any food, leading to a high dependency on surface water (Fisher et al., 1972). Nectarivores are similarly dependent on surface water because they need water to process diets high in sugar (Fleming et al., 2008). Both groups drink more frequently as ambient temperature increases (Fisher et al., 1972). By contrast, omnivores and insectivores have animal-based diets or a combination of animal and plant-based (omnivores) diets, drink infrequently from freestanding water, and rely on water from their prey during the hottest, driest times of year (Smit et al., 2019). This has led to the suggestion that drinkers would be more vulnerable to mortality in hot conditions when surface water is unavailable (Smit et al., 2019).

Czenze et al. (2020) found that drinkers had greater heat tolerance than non-drinkers and could withstand air temperatures of \geq 52°C based on metabolic chamber measurements for wildcaught individuals of 12 passerine species in arid South Africa that had ad libitum access to water prior to testing. However, in the absence of surface water or during long periods of inactivity in hot conditions, they concluded that drinking species are likely to exceed their limits of dehydration tolerance at lower temperatures than non-drinkers, and thus may be more vulnerable to mortality in dry, hot conditions.

In an attempt to understand the causes of collapse of bird communities in the Mojave Desert, USA, over the last century (Iknayan & Beissinger, 2018), Riddell et al. (2019) modelled changing water requirements for thermoregulation using biophysical models and found that species declines were associated with increasing water requirements for body cooling in hot conditions. They found that birds inhabiting the hottest, driest sites without surface water had the lowest probability of persistence. Increasing water requirements were correlated with declines in insectivores and carnivores (nondrinkers with animal-based diets) but not herbivores and omnivores (drinkers with plant-based diets), in conditions where surface water was present.

In contrast to these studies, we found that dietary guilds displayed similar patterns of summer survival with increasing exposure to daily maxima >38°C. We found no evidence for an interaction between rainfall and increasing exposure to extremes >38°C across species, although the negative effect of summer extremes was reduced in higher rainfall conditions in the omnivorous guild. Despite this result, our study design is unlikely to detect the effects of rainfall-related water availability on summer survival because we calculated rainfall as the sum of rain for each 6-month period and so the values are not temporally related to the occurrence of extreme days >38°C. The structure of our analyses does not permit finerscale resolution of the co-occurrence of rainfall and temperature >38°C, which seems critical for understanding responses to heat. Indeed, previous study of mass loss in white-plumed honeyeaters at Charcoal found that apparent mortality was associated with high summer temperatures but only in low rainfall conditions, characterized as rainfall in the 4 weeks prior to capture (Gardner et al., 2016). This suggests that water availability in hot conditions may be critical for drinking species, but we have no comparable data for nondrinking species. Although these studies suggest that drinkers might fare worse in the absence of surface water in hot conditions, the broad-scale ecological significance of such findings are unclear. Behavioural field studies are needed to understand the trade-offs individuals make while foraging in the heat in conditions of varying water availability, and the influence dietary guild has on mortality risk, to complement lab-based studies of physiology.

4.2 | Climate projections and survival

Under all RCP scenarios the number of hot days >38°C is predicted to increase and the number of cold days <0°C is predicted to decrease until the end of the century. Given that increasing exposure to cold winter days is associated with decreased survival, warmer winters are projected to increase 6-monthly survival. Conversely, hot summer days are deleterious to survival and projected to become more common reducing 6-monthly survival by 2104. The increase in winter survival will be more than offset by decreasing survival in summer. Indeed, annual survival is projected to decrease from .631 to .430 at best, .11 at worst, by 2104. We note that these calculations come with assumptions and should not be taken as a prophecy. First, we predicted survival based only on the predicted changes in extreme temperatures, while ignoring other changes that may affect bird survival in the next 80 years. Second, in the case of hot days the calculation is based on an extrapolation since a summer with more than 25 days above 38°C has never been observed at our study sites, whereas climate models predict yearly averages of 30 to 70 days above 38°C. It is possible that the effect of days above 38°C is not consistent for the range of values observed at our study sites and for the larger values in the range predicted by climate models. Third, our calculations assume no significant adaptation of the bird populations to the changing climate (see below).

Nevertheless, the prediction of a substantial decrease in annual survival for the bird community currently present in our study sites is likely robust. Indeed, the deleterious effects of temperature extremes we identified statistically are consistent with physiological mechanisms (see next paragraph). Even if the shape of the relationship between survival and number of hot days is not accurately represented by our extrapolation (for instance, being optimistic there may be a plateau beyond which survival does not decline), we know of no plausible mechanism that would reverse the trend of decreasing survival across a broader range of hot days. Therefore, more hot days on average will certainly decrease mean survival compared to the current situation. In addition, cold days are already guite rare in our study sites and are predicted to almost disappear within a few decades under all RCP scenarios, whereas hot days will become more and more common until the end of the century (Figure 3). Trading very few cold days for a dozen or more hot days logically decreases overall survival.

Our results add to concerns about the persistence of avian populations in arid and semi-arid regions of Australia and on other continents. Modelling avian water requirements for temperatures predicted for the 2080s, McKechnie and Wolf (2010) concluded that desert birds in Australia will experience reduced survival times more frequently during summer due to large increases in thermoregulatory water requirements, regardless of water availability. Similarly, Conradie et al. (2020) modelled the risks of lethal hyperthermia and dehydration for 10 Australian arid zone bird species to 2104 based on thermal physiology data. They concluded that increased water demands for evaporative cooling will greatly increase mortality risk and several species will also be vulnerable to lethal hyperthermia, particularly smaller species. In combination, increasing temperatures and unpredictable water availability pose a significant risk to the avifauna of the Australian interior, particularly in the far western parts of the continent (Conradie et al., 2020). Our analyses, based on demographic data, suggest that climate change also poses a threat to birds in semi-arid regions of eastern Australia.

Elsewhere, Albright et al. (2017) modelled the consequences of 4°C warming to the year 2104 for desert passerines in the United States, and concluded warming would greatly increase the extent, frequency and intensity of dehydration risk over large parts of the south-western United States, affecting water balance, daily activity and geographic distribution of desert birds in these regions. Building on that work, simulation models of heat flux showed that observed declines over the last century in the Mojave Desert were positively associated with climate-driven increases in water requirements for evaporative cooling: predictions suggest an increase in water reguirements of 50 to 78% under future climate scenarios, all else held equal (Riddell et al., 2019). Finally, Conradie et al. (2019) synthesized physiological and behavioural data to evaluate the risks of lethal extreme heat events versus sublethal costs of chronic exposure to hot weather for birds in the Kalahari Desert. They concluded that the risk of acute heat exposure will remain relatively low to the end of the century compared with Australia and south-western USA due to lower rates of warming. By contrast, sublethal costs of chronic heat exposure are likely to drive large declines in avian diversity in the southern African arid zone by the end of the century.

These laboratory-based studies provide a physiological basis for climate-driven local extinctions that are likely to apply to the current study. Birds in our study will inevitably be exposed to greater risk of acute hyperthermia and dehydration as summers warm in these semi-arid environments. Model projections for the region indicate a 50% increase in the frequency of days with air temperatures >38°C, a temperature threshold known to affect white-plumed honeveaters at both sites (Bailey et al., 2020; Gardner et al., 2014, 2016). Moreover, recent heatwaves in semi-arid South Australia, provide some insights into the consequences of a 4°C rise for the survival of small passerines. In January 2019 the mean daily maximum temperature was 37.5°C, 4.2°C above average, identical to the temperature increase predicted for that region in 2090. Birds at the site were exposed to up to 10 hr per day of air temperatures above body temperature (40°C; Sharpe et al., 2019), the threshold at which evaporative cooling is required to maintain body temperatures below lethal limits (Albright et al., 2017; Boyles et al., 2011). Apparent mortality among the colour-ringed population of insectivorous jacky winter, Microeca fascinans, increased almost threefold during the 2-month heatwave period (20% of the population died) and all breeding attempts were abandoned. Birds were never observed to forage, provision nestlings or incubate at air temperatures >38°C (Sharpe et al., 2021). More recently, in December 2019, 29% of the ringed population disappeared, and presumably died, within 24hr of air temperatures reaching 49°C (Sharpe et al., 2022).

Body size will inevitably affect avian responses to high temperatures, with smaller birds at particular risk of mortality. Balancing WILEY-

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energy and water budgets against the risk of fatal hyperthermia is a challenge for smaller birds because they have smaller energy stores and body water pools but higher rates of heat gain and higher mass-specific rates of evaporative water and energy use (Albright et al., 2017; Smit et al., 2016). Consequently, smaller birds have shorter survival windows during extreme heat events than larger species. Albright et al. (2017) estimate that a 9.7-g lesser goldfinch Spinus psaltria will lose body mass at about twice the rate of a 71-g curve-billed thrasher Toxostoma curvirostre (3.4 vs. 1.8% body mass per hour). An increase in air temperature from 40 to 44°C will result in a 150% increase in rates of evaporative water loss, but time to death through dehydration differs greatly because of differences in mass-specific rates of evaporative water loss (Albright et al., 2017). However, we found no effect of body size on responses to temperature extremes, although the response to temperatures >38°C was consistent with poorer survival of smaller individuals. Our data may be too limited to detect strong effects, as we analysed only 37 species with a limited range of sizes (from 48 to 133 mm).

Our study looks at just one component of fitness: longitudinal adult survival. Clearly, estimates of reproduction are necessary to model population viability per se, but such data are not available for our study species. Nevertheless, our estimates of survival are likely to correlate with population decline, regardless of recruitment. Even if populations maintain recruitment at current levels by advancing the start of seasonal breeding as winters warm, increasing exposure to extreme heat represents a clear threat to survival, affecting all individuals, suggesting a downward trend in population size is likely. Assuming the decrease in annual survival of around 30% (RCP 2.6), recruitment would have to increase by c. 40% to offset the decline in survival [1/(1-0.3) = 1.43], which seems unrealistic. In general, adaptive microevolution may be substantial over a few generations (Bonnet et al., 2022), but current evidence suggests that adaptive responses are most likely insufficient to offset the current rate of climate change (Radchuk et al., 2019). Moreover, the potential for genetic adaptation to higher temperatures that could reduce mortality is unclear given the lack of evidence for such effects in birds (Chevin & Hoffmann, 2017; Giennap et al., 2008). In Australia, there is evidence for microevolution in genes that are associated with heatrelated desiccation in Drosophila melanogaster (Umina et al., 2005), but we are unaware of similar examples in birds. This reflects the rarity of examples of microevolution in response to climate change in general, and heat tolerance in particular (Chevin & Hoffmann, 2017; Giennap et al., 2008). In addition to microevolutionary changes in the mean response to extreme temperatures, a genetic response to natural selection may mitigate the negative impact of climate change on survival by reducing the temporal variation of vital rates, via demographic buffering (Hilde et al., 2020).

5 | CONCLUSIONS

Our study highlights the significance of temperature extremes for species' persistence in arid and semi-arid regions, comprising some

70% of the terrestrial landmass of Australia, and about 40% globally. Our results are likely to have broader implications, however, because the negative effects of heat extremes are not restricted to arid and semi-arid regions (see Cunningham et al., 2021; Jiguet et al., 2006). We used long-term ringing data and a mark-recapture framework to estimate survival as a function of temperature extremes, rather than make projections based on the physiological costs of heat exposure. Despite differences in methodology and approach, our conclusions are similar to physiological-based projections, and suggest that rising summer temperatures pose a risk to population persistence for birds in arid and semi-arid regions.

AUTHOR CONTRIBUTIONS

JLG conceived the study and with TB designed the analyses; MC, RA, JS collected the data; TB conducted the analysis; JLG and TB wrote the manuscript, and all authors contributed manuscript feedback.

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CONFLICTS OF INTEREST

We declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data openly available in a public repository that issues datasets with DOIs.

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BIOSKETCH

Our research focuses on understanding the impacts of climate change on the Australian avifauna. We seek to understand the effects of climate change on demography, breeding systems, and life history strategies, especially for arid and semi-arid zone species.

We integrate long-term bird banding data sets, extensive museum-based studies and targeted field-based research, working at a range of scales from local, within-population dynamics up to continental-wide comparisons of different species in different climatic regions and regimes.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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