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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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1 **The effects of temperature extremes on survival in two semi-arid Australian bird com-**
2 **munities over three decades, with predictions to 2104.**

3

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6

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9

10 **Running Title:** Temperature extremes and avian survival

11 **Abstract**

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

18

19 **Location:** semi-arid eastern Australia

20

21 **Time period:** 1986-2016; 1986-2104

22

23 **Major taxa studied:** Birds

24

25 **Methods:** Using mark recapture time-dependent Cormack-Jolly-Seber models and data for 37
26 species from two 30-year ringing programs, we tested for effects on 6-monthly survival of expo-
27 sure to temperatures $>38^{\circ}\text{C}$ and $<0^{\circ}\text{C}$. We then predicted future survival for different emission
28 scenarios, testing whether changes in survival associated with warming winters would be suffi-
29 cient to offset the effects of rising summer temperatures.

30

31 **Results:** Survival probability declined strongly with increasing exposure to days $>38^{\circ}\text{C}$ and to a
32 lesser extent to days $<0^{\circ}\text{C}$, with temperature extremes explaining 43% and 13% of temporal
33 variation in survival among years, respectively. Summer survival patterns were similar across

34 avian guilds but only survival of nectarivores declined in winter. Our models predict that gains
35 in winter survival will not offset reductions in summer survival. Annual survival is predicted to
36 decline substantially by the end of the century: from 0.63 in 1986 to 0.43 in 2104 under an opti-
37 mistic emission scenario and to 0.11 under a pessimistic scenario.

38
39 **Main conclusions:** We highlight the significance of temperature extremes for species' persis-
40 tence in arid and semi-arid regions, comprising 70% of Australia's land mass, and 40% globally.
41 Our [demography-based](#) results are consistent with physiological-based projections evaluating
42 avian survival in arid and semi-arid regions globally and suggest rising summer temperatures
43 pose a risk to population persistence in these regions.

44 **KEYWORDS:** arid zone, Australian birds, avian guilds, climate change, energy and water bud-
45 gets, population projections, species persistence, survival, temperature extremes, thermoregula-
46 tion.

47 INTRODUCTION

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

56
57 Mortality associated with exposure to summer extremes can be a direct result of succumbing to
58 acute heat stress via hyperthermia or lethal dehydration, exemplified by mass die-offs of
59 budgerigars (*Melopsittacus undulatus*), zebra finches (*Taeniopygia guttata*) and Carnaby's
60 cockatoos (*Calyptorhynchus latirostris*) during heatwave events in Australia (McKechnie et al.,
61 2012, Saunders et al., 2011). In such cases, avian body temperature exceeding about 46°C is
62 lethal (Boyles et al., 2011).

63
64 Fitness in terrestrial animals may also be affected by high temperatures well below those caus-
65 ing die-offs events. Growing evidence suggests that air temperatures in the mid to high 30°Cs
66 are harmful for endotherms (Cunningham et al., 2021). For example, prolonged exposure to
67 temperatures >38°C has been shown to increase the cost of avian thermoregulation by increasing
68 the need for evaporative cooling to maintain body temperatures below lethal limits (McKechnie
69 et al., 2017). Increasing exposure to these sub-lethal conditions increases the risk of mortality,
70 when exposure is prolonged over hours, days and weeks (Sharpe et al., 2019, 2021). Indeed, re-
71 cent work on Australian desert birds in the laboratory showed that chronic heat stress can cause
72 organ damage (e.g. liver or kidneys) which can contribute to avian mortality over time (Xie et
73 al., 2020).

74
75 High temperatures are also associated with changes to foraging patterns and microhabitat use
76 (du Plessis et al., 2012; Edwards et al., 2015; Cooper et al., 2019; Fungi et al., 2019) which can
77 lead to a reduction in food intake and loss of body condition. Southern pied babblers, *Turdoides*
78 *bicolor* and southern yellow-billed hornbills (*Tockus leucomelas*), for example, were unable to
79 maintain body mass on days when temperatures exceeded thresholds in the mid 30s°C (van de

80 Ven et al., 2019; du Plessis et al., 2012) and Jacky Winters *Microeca fascinans* lost 2% of their
81 mass on days $\geq 42^{\circ}\text{C}$ (Sharpe et al., 2019). Given that body condition is closely linked to sur-
82 vival and reproductive success (Paniw et al., 2019), increasing exposure to high summer temper-
83 atures is likely to have major fitness consequences as the climate warms.

84 Exposure to cold extremes can also impose thermoregulatory and energetic challenges for en-
85 dotherms, although we have much less understanding of how birds respond to reductions in cold
86 extremes that are expected to be beneficial for fitness as the climate warms. Energetic con-
87 straints and cold stress can drive reductions in body condition and impose carry-over costs on
88 subsequent survival and reproduction (Williams et al., 2014). In Australia, changes in survival
89 were associated with temperature extremes for two coexisting bird species monitored over 37
90 years, red-winged fairy-wrens *Malurus elegans* and white-browed scrubwrens *Sericornis*
91 *frontalis* (Gardner et al., 2017). In scrubwrens, winter temperatures $<5^{\circ}\text{C}$ were associated with
92 lower survival within the same season while in both species, survival was associated with body
93 size, and there was evidence that size-dependent mortality was mediated by carry-over effects of
94 climate in the previous season (Gardner et al., 2017). Moreover, energetic costs of thermoregu-
95 lation in the cold during periods of low food availability can be greater than those in warmer
96 conditions during the breeding season (Harrison et al., 2011; Williams et al., 2014). For exam-
97 ple, energetic stress on cool days was greater than that associated with exposure to high temper-
98 atures between 40 and 45 $^{\circ}\text{C}$ in an arid zone population of zebra finch (Cooper et al., 2019).
99 Warming winters can, or are predicted to, reduce winter mortality and lead to improvement in
100 body condition (Robinson et al., 2007; Ozgul et al., 2010). For example, warming winters led to
101 longer growing seasons with concomitant improvement in the body condition of yellow-bellied
102 marmots, *Marmota flaviventris* and this was associated with changing patterns of survival and
103 reproduction (Ozgul et al., 2010). Benefits of warming conditions in winter may therefore offset
104 negative effects of warming summers on survival.

105 Studies of how changes in seasonal weather influence vital rates are rare in arid zone species,
106 largely because of a paucity of long-term demographic data. This limits our ability to project
107 population trends in coming decades. Here we investigate variation in survival associated with
108 exposure to high summer and low winter temperatures for 37 avian species captured over a 30-
109 year period (1986-2016) at two sites in a semi-arid landscape in western NSW, Australia. Using
110 mark recapture time-dependent Cormack-Jolly-Seber models we first test for the effects on 6
111 monthly survival of exposure to: (1) summer temperatures above 38°C , and (2) winter tempera-
112 tures below 0°C . We classify these temperatures as extreme because chronic effects which re-

113 duce survival appear to begin at these thresholds in Australian bird species (Bailey et al., 2020;
114 Gardner et al., 2016; 2017; McKechnie et al., 2017); obviously more extreme temperatures can
115 have acute effects via immediate mortality. At our study sites these thresholds are currently
116 reached on around 5% of days: cold extreme in winter 8% at Charcoal Tank Nature Reserve, 9%
117 at Weddin Mt National Park; hot extreme in summer 5% at Charcoal Tank, 3% at Weddin Mt.
118 We then test whether the changes in 6 monthly survival associated with warming winters will be
119 sufficient to offset the negative effects on survival of rising summer temperatures based on cli-
120 mate projections for the region to the year 2104. Current climate projections for Australia indi-
121 cate more hot summer and fewer cold winter temperature extremes (BOM & CSIRO, 2020).

122 **METHODS AND MATERIALS**

123 **Study sites and species**

124 The study was carried out at two sites: The Charcoal Tank Nature Reserve (hereafter Charcoal; -
125 33.9831°S, 147.1575°E) and Weddin Mountains National Park (hereafter Weddin; -33.9386°S,
126 147.9872°E) in western New South Wales in south-east Australia (Fig. S1). Both sites have been
127 the subject of long-term (>30 years) ringing programs, with data collected in each year since
128 1986. The study sites are located 75 km apart within a fragmented agricultural landscape (see
129 Appendix S1 in Supporting Information for site description).

130

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

137

138 We obtained weather data from the Australian Government Bureau of Meteorology, from the
139 Grenfell (Manganese Rd) station for the Weddin site, and from the West Wyalong Airport sta-
140 tion for the Charcoal site. We defined 6-month periods from 1st September to 29th February as
141 “Summer” or from 1st March to 31st August as “Winter”. For each 6-month period between 1970
142 to 2016 we extracted (1) mean daily extreme temperatures for each season (mean daily maxi-
143 mum in summer, mean daily minimum in winter), (2) the sum of precipitation for each 6-month
144 period, (3) the number of days with temperatures beyond an extreme threshold for each season
145 (days above 38°C in summer, days below 0°C in winter).

147 **Future climate predictions**

148 To predict the number of temperature extremes until the end of the century under difference sce-
149 narios of greenhouse gas concentration we chose the model CESM1-CAM5 (Community Earth
150 System Model version 1 that includes the Community Atmospheric Model version 5, Neale et
151 al. 2010). The model CESM1-CAM5 performs very well for short-term predictions of climate in
152 Eastern and Southern Australia (Moise et al., 2015). We extracted daily predicted minimum and
153 maximum temperatures for the years 2016 to 2104 from the West Wyalong Airport weather sta-
154 tion, located 10.5km from Charcoal, under three Representative Concentration Pathway (RCP)
155 scenarios: RCP 2.6 corresponding to a very stringent scenario of reductions in greenhouse gases
156 emissions, RCP 4.5 an intermediate scenario and RCP 8.5 the worst-case climate change sce-
157 nario (Meinshausen et al, 2011). We combined climate projections to observed data (1986 to
158 2015) and for each 6-month period calculated the number of days below 0°C in winter and
159 above 38°C in summer. For both seasons and for each of the three RCP scenarios we fitted gen-
160 eralised additive models of the number of extreme temperature days as a function of year. Year
161 was modeled as a thin-plate regression spline (Wood, 2003). We used the predictions from each
162 of these generalised additive models to project survival in the future.

163

164 **Mark-recapture data**

165 The full data set contains captures for 39 species for which > 100 captures were recorded
166 between 1986 and 2016 (Table S1) with a total of 33550 captures for 21621 individuals. Those
167 data included only adults which were identified on the basis of plumage. We classified birds as
168 belonging to one of four feeding guilds: nectarivore, insectivore, omnivore or granivore. Most
169 individuals are captured only once, presumably due to movements of non-resident birds or post-
170 fledging dispersal. Our study populations, typical for much of the Australian arid zone, contain
171 both resident and migratory species, including partial migrants and local nomads, making it dif-
172 ficult to classify movement patterns for individual species (see Chan, 2001). This means that ap-
173 parent local mortality represents a mixture of true mortality and permanent emigration. To re-
174 duce the influence of emigration we removed the first capture of each individual to focus our
175 analysis on resident birds, increase the proportion of apparent survival (or mortality) related to
176 local survival (or mortality) rather than emigration and decrease computation time. In two spe-
177 cies, not a single individual was recaptured so we were left with only 37 species totalling 4136
178 individuals. We present results derived from the full data set in Fig. S8. We used capture data to
179 calculate a temporal proxy of bird density within each guild (see Appendix S2).

180
181 To create regular time intervals corresponding to seasons and to decrease the number of vari-
182 ables in models we aggregated capture sessions by 6-month periods from 1st September to 29th
183 February (“Summer”) or from 1st March to 31st August (“Winter”). Thus, we obtained 62 virtual
184 capture occasions instead of the initial 748. This procedure violates the assumption of mark-re-
185 capture models that survival intervals are long relative to the marking intervals but was essential
186 to obtain a manageable number of capture occasions and reasonably high recapture probabilities.
187 The noise introduced by this violation is expected to only blur the statistical signal and not bias
188 it (see Appendix S3, Fig. S2).

189

190 **Statistical analyses**

191 **Mark-recapture model**

192 We modelled apparent survival probability across species and time periods, as a function of
193 summer and winter weather. We used time-dependent Cormack-Jolly-Seber models which de-
194 scribe capture histories as the product of a survival probability and a recapture probability. We
195 modeled variation among species, among time periods and among locations for survival and re-
196 capture probabilities (see Appendix S4).

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

201 For the linear predictor corresponding to survival probability, the fixed effects were a global in-
202 tercept for the effect of site (Weddin vs. Charcoal), a linear effect of time (i.e. 6-months periods
203 fitted as a continuous covariate) to de-trend the response and avoid over-estimating the effect of
204 climate (Grobis et al., 2008), the effect of the 6-month survival period being in winter (as op-
205 posed to summer), a dummy variable indicating whether an individual was captured for the first
206 time to account for transience effects, a proxy for within-guild-site bird density fitted as a con-
207 tinuous covariate (see Appendix S2, Fig. S3, S4), and the effect of weather variables, for which
208 we tried different combinations involving our three weather variables, measured for each site
209 and each 6-month period: (1) the number of days with temperature reaching a threshold (either
210 above 38°C for summer survival periods or below 0°C for winter survival periods); (2) the sum
211 of precipitation because extreme temperatures are correlated with the sum of precipitation, and
212 precipitation is known to affect bird survival (Kennedy, 1970; Robinson et al., 2007; Gardner et

213 al., 2016); (3) the average daily temperature (average winter minimum, average summer maxi-
214 mum). Weather variables were standardized to a mean of zero and a standard deviation of one.

215 In a first model (model 1 hereafter), we fitted the linear effects of the number of days with tem-
216 peratures beyond thresholds in each season as these were the main predictors of interest, and a
217 linear effect of the sum of precipitation in each season. That model is at the center of our work
218 because it estimates the independent effect of extreme temperatures when accounting for the
219 confounding effect of precipitation. For both seasons, separately, we calculated the proportion of
220 temporal variance in mean survival among years explained by extreme temperatures (see Ap-
221 pendix S5 for details). To predict the net effect of changes in the balance of deleterious winter
222 versus deleterious summer temperatures, we predicted seasonal-survival and year-survival based
223 on model 1 and on predictions of temperature extremes based on the CESM1-CAM5 model for
224 the three RCP scenarios, from 1986 to 2104. Survival was predicted while integrating the ran-
225 dom effects of year and species.

226 Beyond model 1, we fitted four extra models to address secondary questions regarding the effect
227 of weather on survival probability. In a second model (model 2 hereafter) we added the interac-
228 tion between sum of precipitation and the numbers of days $>38^{\circ}\text{C}$ or $<0^{\circ}\text{C}$ in each season. In
229 wetter summers the negative effect of extreme high temperatures may be reduced because water
230 availability helps birds cope with heat, while in wetter winters the negative effect of extreme
231 cold may be exacerbated because the insulating capacity of wet feathers is poor (Kennedy, 1970;
232 Robinson et al., 2007). These expectations, however, assume that extreme temperatures co-oc-
233 cur with increased precipitation or water availability, within each time period, which may not be
234 the case. Next we fitted model 3, an extension of model 2, in which we also included a linear ef-
235 fect of mean maximum or minimum daily temperature in each season. With the model we test
236 whether it is possible to disentangle the effects of the number of days of extreme temperatures
237 from the effect of the average season temperature.

238 We first fitted models 1 to 3 for all species together. However, dietary guilds are expected to re-
239 spond differently to weather conditions because food availability varies with temperature and
240 rainfall, and because water content varies between diets, so we fitted models 1 to 3 separately
241 for each of the 4 guilds.

242 Model 4 included random slopes of species for the effects of the number of days of extreme
243 temperatures to test for differences among species in their responses (see Appendix S4, results
244 in main text). [Model 5 included species average size and its interaction with the number of days
245 of extreme temperatures \(see Appendix S4, results Fig. S7\).](#) With model 6 we tested whether our

246 results were robust to the exclusion of the first capture: model 6 is identical to model 1 but is fit-
247 ted on the full data set, which includes all captures of all individuals, and includes a second tran-
248 sience fixed effect (see Appendix S4, results Fig. S8).

249
250 We fitted all models in the Bayesian probabilistic programming language Stan (Carpenter,
251 2017), using No-U-Turn Hamiltonian Monte Carlo sampling with Rstan (Stan Development
252 Team, 2020). For fixed effects we used normalising Gaussian priors with a mean of 0 and a
253 standard deviation of 3. For random effect standard deviations we used half-Cauchy priors of lo-
254 cation 0 and scale 0.1. We used 4 chains each with 2000 warm-up iterations and 2000 samples.
255 We assessed model convergence using visual diagnostics (trace plots, pairwise posterior plots),
256 in particular using Bayesplot (Gabry et al., 2019) and checked that all R-hat values were below
257 1.05 and effective sample sizes were above 200. We report posterior means and 95% highest
258 posterior density credible intervals. All derived parameters and model predictions were calcu-
259 lated by integrating over the full posterior distribution. The code to run all models is provided
260 (see Appendix Code S1).

261

262 **RESULTS**

263 Unless mentioned otherwise, parameter estimates are from model 1, fitted to all species to-
264 gether. Survival probability was slightly higher at Weddin compared to Charcoal ($\beta=0.25$, 95%
265 highest posterior density credible interval [0.02; 0.50]) and did not clearly differ between sum-
266 mer and winter ($\beta=-0.04$ [-0.68; 0.59]) (Table S2). The effect of transience was negative ($\beta=-$
267 0.78 [-0.998;-0.55]), meaning that birds have a lower probability of apparent survival just after
268 being captured for the first time. This effect may correspond to non-resident birds that perman-
269 ently leave the study site after first capture. There was heterogeneity in survival probabilities
270 both among occasions, even after accounting for weather variables (random standard deviation,
271 $\sigma= 1.09$ [0.77;1.54]) and among species ($\sigma= 0.28$ [0.14; 0.49], Fig. 1). Species mean 6-month
272 survival probabilities varied from 0.88 [0.83; 0.92] in the white-throated treecreeper, to 0.76
273 [0.67; 0.83] in the superb fairy-wren (Fig. 1).

274

275 Recapture probability was consistently lower at Weddin compared with Charcoal and did not
276 clearly differ between seasons (Table S2). Trap dependence was positive ($\beta=0.33$ [0.23;0.43]),
277 meaning that a living bird is more likely to be recaptured just after having been captured. There
278 was heterogeneity in recapture probabilities both among occasions ($\sigma= 0.55$ [0.46;0.66]) and
279 among species ($\sigma= 0.68$ [0.44; 1.05]). Species recapture probabilities varied from 0.34 [0.27;

280 0.42] in the white-throated treecreeper, to 0.074 [0.038; 0.12] in the spiny-cheeked honeyeater
281 (Fig. 1).

282 **Effects of number of days of extreme temperatures**

283 The effect of the number of extreme summer days was strongly negative ($\beta=-0.57$ [-1.01; -
284 0.08]), corresponding to a decline in survival probability from 0.86 [0.78;0.95] when there are
285 no days above 38°C to 0.59 [0.45; 0.77] for 30 days above 38°C (Fig. 2). The effect of the num-
286 ber of extreme winter days was marginally negative ($\beta=-0.39$ [-1.01; 0.04]), corresponding to a
287 decline in survival probability from 0.84 [0.76;0.90] for 0 days below 0°C to 0.53 [0.28;0.78]
288 for 44 days below 0°C (Fig. 2; Table S2). The effect of extreme temperatures explained 43%
289 [16%; 70%] of temporal variation in survival among years in summer and 13% [0%; 36%] in
290 winter. The effects of the number of extreme summer and winter days were also apparent when
291 including transients, in Model 6 (summer $\beta=-0.33$ [-0.57; -0.10], winter $\beta=-0.37$ [-0.62; -0.15]),
292 with the effect in summer being a bit weaker and the effect in winter being of similar strength
293 but more precisely estimated (Fig. S8).

294
295 Model 4 revealed that species differed significantly in their responses to extreme summer tem-
296 peratures ($\sigma= 0.14$ [0.02;0.32]) and to extreme winter temperatures ($\sigma= 0.12$ [0.02;0.27]), but
297 those differences were biologically small so that the pattern of survival was qualitatively con-
298 sistent across species (Fig. 2, Fig. S5, Table S8). Moreover, as is often the case in mixed models
299 (Houslay and Wilson, 2017), despite significant variance among species the uncertainty in spe-
300 cies-specific slopes was large so that it is not possible to identify which species responded more
301 or less strongly (Fig. S5). *In particular, those differences were not significantly explained by dif-*
302 *ferences in the mean body size of species (Model 5, Table S9).*

303
304 Guild-specific analyses confirm the consistency of the responses among species. The negative
305 effect of extreme temperatures in summer was independently found in insectivore, nectarivore
306 and omnivore species (Table S3, Fig. S6). On the other hand, the effect of extreme temperatures
307 in winter was present only in nectarivore species, where it was significant and strong ($\beta=-0.66$ [-
308 1.56;-0.43]), with a predicted decline in survival probability from 0.89 [0.78;0.97] with 0 days
309 below 0°C to 0.41 [0.05;0.81] with 44 days below 0°C. For the granivore guild, a small sample
310 size prevented a precise estimation of any parameter for weather effects.

311
312 Winter precipitation had a negative effect on survival ($\beta=-0.52$ [-0.94; -0.17]). The effect was
313 statistically supported in the nectarivore guild model ($\beta=-0.92$ [-1.56;-0.43]) but not found in

314 other guilds (Table S3). Summer precipitation had no clear effect on survival across species ($\beta=-$
315 0.24 [-0.57; -0.57]), or in any of the guilds (Table S3).

316
317 When fitting model 2 to all species together (Table S4), there was no evidence of interactions
318 between number of days beyond extreme temperatures and precipitation, in summer ($\beta=0.04 [-$
319 0.4; 0.52]) or in winter ($\beta=0.13 [-0.44; 0.13]$). In guild models, there was support for an interac-
320 tion only in omnivorous species, for summer, with increased survival to extreme temperatures at
321 higher precipitation ($\beta=0.67 [0.03; 1.42]$) (Table S5).

322
323 Fitting model 3 to all species together allowed us to disentangle the effects of mean tempera-
324 tures from the number of days with extreme temperatures. For summer, there was sufficient
325 evidence that the number of days above 38°C had a negative effect on survival probability after
326 accounting for effects of mean temperature ($\beta=-0.32 [-0.55; -0.03]$) (Table S6). In winter the
327 trend for the effect of the number of days beyond 0°C was marginally negative but the uncer-
328 tainty was large ($\beta=-0.28 [-0.68; 0.04]$).

329
330 In summary, winter extremes had a weak effect on 6-monthly survival, except in the case of
331 nectarivores which are predicted to have low survival (ca 41%) in the coldest winters with > 40
332 days below freezing. In contrast, the negative effect of summer extremes was strong and consis-
333 tent across species (Model 4), showing little variation among species (Fig. S5) and all three
334 guild-models showing similar trends (Fig. S6). Our results are robust to the inclusion of the cor-
335 related effects of mean extreme temperatures (Model 3, Table S6), to the inclusion or exclusion
336 of transient individuals (Model 6, Fig. S8, Table S10), and in accounting for species (Model 4,
337 Fig. S5) and guild differences (Fig. S6).

338

339 **Climate predictions:**

340 At Charcoal the number of winter days below 0°C is projected to decrease from 12.0 in the year
341 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 sum-
342 mer days above 38°C is projected to increase from 13.8 in 2016 to 28.7 (RCP 2.6), 36.4 (RCP
343 4.5) and 67.4 (RCP 8.5) in 2104 (Fig. 3). Based on these climate projections, model predictions
344 for survival to 2104 showed broad-scale declines in annual survival across species (Fig. 4). As-
345 suming median precipitation, in winter, 6-month survival is projected to increase slightly as win-
346 ters warm, whereas summer survival and annual survival were predicted to decline substantially,
347 with the severity of the decline depending on the RCP scenario (Fig. 4).

348

349

350 **DISCUSSION**

351 We quantified patterns of adult survival for two bird communities in semi-arid south-eastern
352 Australia as a function of exposure to temperature extremes in winter and summer, using data
353 from 37 species that have been the subject of continuous ringing programs over 30 years. Sur-
354 vival probability did not differ between summer and winter, but survival declined at a higher
355 rate with increasing exposure to summer days with thermal maxima $>38^{\circ}\text{C}$, than with increasing
356 exposure to winter days with minima $<0^{\circ}\text{C}$. The effect of hot days in summer was consistent
357 across species and guilds whereas the effect of cold days in winter was consistent across species
358 but only statistically clear in nectarivores. Model projections to 2104 suggest that survival may
359 be reduced by a third from current levels; the increase in survival associated with milder, warm-
360 ing winters will be insufficient to offset the negative effects on survival of more frequent ex-
361 treme days above $>38^{\circ}\text{C}$ in summer.

362

363 **Survival**

364

365

366 Our study does not elucidate the causes of temperature-related summer mortality or the specific
367 timeframe over which such mortality occurs, but several mechanisms might be at play. Mortality
368 might be a direct result of hyperthermia or lethal dehydration during heatwave events as previ-
369 ously reported in arid Australia (McKechnie et al., 2012, Saunders et al., 2011). However, in-
370 creasing exposure to high temperatures $>38^{\circ}\text{C}$ is also likely to increase mortality over broader
371 timeframes via increasing the need for evaporative cooling to maintain body temperatures below
372 lethal limits or reducing food intake with consequences for water and energy budgets (Mitchell
373 et al., 2018). Recent work by McKechnie et al. (2017) examined the evaporative cooling capac-
374 ity and heat tolerance of five insectivorous and nectarivorous passerine species in Australia's
375 arid zone, among them the spiny-cheeked honeyeater (*Acanthagenys rufogularis*) included in
376 this study. They confirmed the reliance of these species on evaporative heat loss via panting at
377 high air temperatures. When air temperatures exceeded 38°C , rates of evaporative water loss in-
378 creased rapidly and linearly to at least sevenfold (670–860%) above basal rates under field labo-
379 ratory conditions (McKechnie et al., 2017). Previous work at both Charcoal and Weddin showed
380 that prolonged exposure to days with air temperature $>38^{\circ}\text{C}$ was associated with reductions in

381 body condition of white-plumed honeyeaters (*Ptilotula penicillatus*) (Bailey et al., 2020), and at
382 Charcoal, heat-exposed individuals in poor condition were less likely to be recaptured the fol-
383 lowing spring (Gardner et al., 2016). This apparent mortality may have been a result of ther-
384 moregulatory constraints but could also result from heat-related changes in foraging patterns and
385 microhabitat use (du Plessis et al., 2012; Edwards et al., 2015; Fungi et al., 2019) that lead to a
386 reduction in food intake and loss of body condition, although we have no direct evidence in our
387 study species.

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

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

406 In an attempt to understand the causes of collapse of bird communities in the Mojave Desert
407 USA over the last century (Iknayan & Beissinger, 2018), Riddell et al. (2019) modelled chang-
408 ing water requirements for thermoregulation using biophysical models and found that species
409 declines were associated with increasing water requirements for body cooling in hot conditions.
410 They found that birds inhabiting the hottest, driest sites without surface water had the lowest
411 probability of persistence. Increasing water requirements were correlated with declines in insec-
412 tivores and carnivores (non-drinkers with animal-based diets) but not herbivores and omnivores

413 (drinkers with plant-based diets), in conditions where surface water was present.

414 In contrast to these studies, we found that dietary guilds displayed similar patterns of summer
415 survival with increasing exposure to daily maxima $>38^{\circ}\text{C}$. We found no evidence for an interac-
416 tion between rainfall and increasing exposure to extremes $>38^{\circ}\text{C}$ across species, although the
417 negative effect of summer extremes was reduced in higher rainfall conditions in the omnivorous
418 guild. Despite this result, our study design is unlikely to detect the effects of rainfall-related wa-
419 ter availability on summer survival because we calculated rainfall as the sum of rain for each 6-
420 month period and is not temporally related to the occurrence of extreme days $>38^{\circ}\text{C}$. The struc-
421 ture of our analyses does not permit finer-scale resolution of the co-occurrence of rainfall and
422 temperature $>38^{\circ}\text{C}$, which seems critical for understanding responses to heat. Indeed, previous
423 study of mass loss in white-plumed honeyeaters at Charcoal found that apparent mortality was
424 associated with high summer temperatures but only in low rainfall conditions, characterized as
425 rainfall in the 4 weeks prior to capture (Gardner et al., 2016). This suggests that water availabil-
426 ity in hot conditions may be critical for drinking species, but we have no comparable data for
427 non-drinking species. Although these studies suggest that drinkers might fare worse in the ab-
428 sence of surface water in hot conditions, the broad-scale ecological significance of such findings
429 are unclear. Behavioural field studies are needed to understand the trade-offs individuals make
430 while foraging in the heat in conditions of varying water availability, and the influence dietary
431 guild has on mortality risk, to complement lab-based studies of physiology.

432

433 **Climate Projections and survival**

434 Under all RCP scenarios the number of hot days $>38^{\circ}\text{C}$ is predicted to increase and the number
435 of cold days $<0^{\circ}\text{C}$ is predicted to decrease until the end of the century. Given that increasing ex-
436 posure to cold winter days is associated with decreased survival, warmer winters are projected to
437 increase 6-monthly survival. Conversely, hot summer days are deleterious to survival and pro-
438 jected to become more common reducing 6-monthly survival by 2104. The increase in winter
439 survival will be more than offset by decreasing survival in summer. Indeed, annual survival is
440 projected to decrease from 0.631 to 0.430 at best, 0.11 at worst, by 2104. We note that these cal-
441 culations come with assumptions and should not be taken as a prophecy. First, we predicted sur-
442 vival based only on the predicted changes in extreme temperatures, while ignoring other
443 changes that may affect bird survival in the next 80 years. Second, in the case of hot days the
444 calculation is based on an extrapolation since a summer with more than 25 days above 38°C has

445 never been observed at our study sites, whereas climate models predict yearly averages of 30 to
446 70 days above 38°C. It is possible that the effect of days above 38°C is not consistent for the
447 range of values observed at our study sites and for the larger values in the range predicted by cli-
448 mate models. Third, our calculations assume no significant adaptation of the bird populations to
449 the changing climate (see below).

450 Nevertheless, the prediction of a substantial decrease in annual survival for the bird community
451 currently present in our study sites is likely robust. Indeed, the deleterious effects of temperature
452 extremes we identified statistically are consistent with physiological mechanisms (see next para-
453 graph). Even if the shape of the relationship between survival and number of hot days is not ac-
454 curately represented by our extrapolation (for instance, being optimistic there may be a plateau
455 beyond which survival does not decline), we know of no plausible mechanism that would re-
456 verse the trend of decreasing survival across a broader range of hot days. Therefore, more hot
457 days on average will certainly decrease mean survival compared to the current situation. In addi-
458 tion, cold days are already quite rare in our study sites and are predicted to almost disappear
459 within a few decades under all RCP scenarios, whereas hot days will become more and more
460 common until the end of the century (Fig. 3). Trading very few cold days for a dozen or more
461 hot days logically decreases overall survival.

462
463 Our results add to concerns about the persistence of avian populations in arid and semi-arid re-
464 gions of Australia and on other continents. Modelling avian water requirements for temperatures
465 predicted for the 2080s, McKechnie and Wolf (2010) concluded that desert birds in Australia
466 will experience reduced survival times more frequently during summer due to large increases in
467 thermoregulatory water requirements, regardless of water availability. Similarly, Conradie et al.
468 (2020) modelled the risks of lethal hyperthermia and dehydration for 10 Australian arid zone
469 bird species to 2104 based on thermal physiology data. They concluded that increased water de-
470 mands for evaporative cooling will greatly increase mortality risk and several species will also
471 be vulnerable to lethal hyperthermia, particularly smaller species. In combination, increasing
472 temperatures and unpredictable water availability pose a significant risk to the avifauna of the
473 Australian interior, particularly in the far western parts of the continent (Conradie et al., 2020).
474 Our analyses, based on demographic data, suggest that climate change also poses a threat to
475 birds in semi-arid regions of eastern Australia.

476
477 Elsewhere, Albright et al. (2019) modelled the consequences of 4°C warming to the year 2104
478 for desert passerines in the United States, and concluded warming would greatly increase the ex-

479 tent, frequency and intensity of dehydration risk over large parts of the south-western United
480 States, affecting water balance, daily activity and geographic distribution of desert birds in these
481 regions. Building on that work, simulation models of heat flux showed that observed declines
482 over the last century in the Mojave desert were positively associated with climate-driven in-
483 creases in water requirements for evaporative cooling: predictions suggest an increase in water
484 requirements of 50 to 78% under future climate scenarios, all else held equal (Riddell et al.,
485 2019). Finally, Conradie et al. (2019) synthesized physiological and behavioural data to evaluate
486 the risks of lethal extreme heat events versus sublethal costs of chronic exposure to hot weather
487 for birds in the Kalahari Desert. They concluded that the risk of acute heat exposure will remain
488 relatively low to the end of the century compared with Australia and south-western USA due to
489 lower rates of warming. By contrast, sublethal costs of chronic heat exposure are likely to drive
490 large declines in avian diversity in the southern African arid zone by the end of the century.

491
492 These laboratory-based studies provide a physiological basis for climate-driven local extinctions
493 that are likely to apply to the current study. Birds in our study will inevitably be exposed to
494 greater risk of acute hyperthermia and dehydration as summers warm in these semi-arid environ-
495 ments. Model projections for the region indicate a 50% increase in the frequency of days with
496 air temperatures $>38^{\circ}\text{C}$, a temperature threshold known to affect white-plumed honeyeaters at
497 both sites (Gardner et al., 2014, 2016, Bailey et al., 2020). Moreover, recent heatwaves in semi-
498 arid South Australia, provide some insights into the consequences of a 4°C rise for the survival
499 of small passerines. In January 2019 the *mean* daily maximum temperature was 37.5°C , 4.2°C
500 above average, identical to the temperature increase predicted for that region in 2090. Birds at
501 the site were exposed to up to 10 h per day of air temperatures above body temperature (40°C)
502 (Sharpe et al., 2019), the threshold at which evaporative cooling is required to maintain body
503 temperatures below lethal limits (Boyles et al., 2011; Albright et al., 2017). Apparent mortality
504 among the colour-ringed population of insectivorous jacky winters, *Microeca fascinans*, in-
505 creased almost three-fold during the two-month heatwave period (20% of the population died)
506 and all breeding attempts were abandoned. Birds were never observed to forage, provision
507 nestlings or incubate at air temperatures $> 38^{\circ}\text{C}$ (Sharpe et al., 2021). More recently, in Decem-
508 ber 2019, 30% of the ringed population disappeared, and presumably died, within 24hr of air
509 temperatures reaching 49°C (Sharpe et al., 2021).

510
511 Body size will inevitably affect avian responses to high temperatures, with smaller birds at par-
512 ticular risk of mortality. Balancing energy and water budgets against the risk of fatal hyperther-

513 mia is a challenge for smaller birds because they have smaller energy stores and body water
514 pools but higher rates of heat gain and higher mass-specific rates of evaporative water and en-
515 ergy use (Smit et al., 2016, Albright et al., 2017). Consequently, smaller birds have shorter sur-
516 vival windows during extreme heat events than larger species. Albright et al. (2017) estimate
517 that a 9.7g Lesser Goldfinch (*Spinus psaltria*) will lose body mass at about twice the rate of 71g
518 Curve-billed Thrasher (*Toxostoma curvirostre*) (3.4% versus 1.8% body mass per hour). An in-
519 crease in air temperature from 40 to 44°C will result in a 150% increase in rates of evaporative
520 water loss, but time to death through dehydration differs greatly because of differences in mass-
521 specific rates of evaporative water loss (Albright et al., 2017). However, we found no effect of
522 body size on responses to temperature extremes, although the response to temperatures >38°C
523 was consistent with poorer survival of smaller individuals. Our data may be too limited to detect
524 strong effects, as we analysed only 37 species with a limited range of sizes (from 48 to 133mm).

525 Our study looks at just one component of fitness: longitudinal adult survival. Clearly, estimates
526 of reproduction are necessary to model population viability *per se*, but such data are not avail-
527 able for our study species. Nevertheless, our estimates of survival are likely to correlate with
528 population decline, regardless of recruitment. Even if populations maintain recruitment at cur-
529 rent levels by advancing the start of seasonal breeding as winters warm, increasing exposure to
530 extreme heat represents a clear threat to survival, affecting all individuals, suggesting a down-
531 ward trend in population size is likely. Assuming the decrease in annual survival of around 30%
532 (RCP 2.6), recruitment would have to increase by ca. 40% to offset the decline in survival ($1/(1-$
533 $0.3) = 1.43$), which seems unrealistic. In general, adaptive micro-evolution may be substantial
534 over a few generations (Bonnet et al., 2022), but current evidence suggests that adaptive re-
535 sponses are most likely insufficient to offset the current rate of climate change (Radchuk et al.,
536 2019). Moreover, the potential for genetic adaptation to higher temperatures that could reduce
537 mortality is unclear given the lack of evidence for such effects in birds (Gienapp et al., 2008;
538 Chevin & Hoffmann, 2017). In Australia, there is evidence for microevolution in genes that are
539 associated with heat-related desiccation in *Drosophila melanogaster* (Umina et al., 2005), but we
540 are unaware of similar examples in birds. This reflects the rarity of examples of microevolution
541 in response to climate change in general, and heat tolerance in particular (Gienapp et al., 2008;
542 Chevin & Hoffmann, 2017). In addition to microevolutionary changes in the mean response to
543 extreme temperatures, a genetic response to natural selection may mitigate the negative impact
544 of climate change on survival by reducing the temporal variation of vital rates, via demographic
545 buffering (Hilde et al., 2020).

546 **CONCLUSIONS**

547 Our study highlights the significance of temperature extremes for species' persistence in arid
548 and semi-arid regions, comprising some 70% of the terrestrial land mass of Australia, and about
549 40% globally. We used long-term ringing data and a mark-recapture framework to estimate sur-
550 vival as a function of temperature extremes, rather than make projections based on the physio-
551 logical costs of heat exposure. Despite differences in methodology and approach, our conclu-
552 sions are similar to physiological-based projections, and suggest that rising summer tempera-
553 tures pose a risk to population persistence for birds in arid and semi-arid regions.

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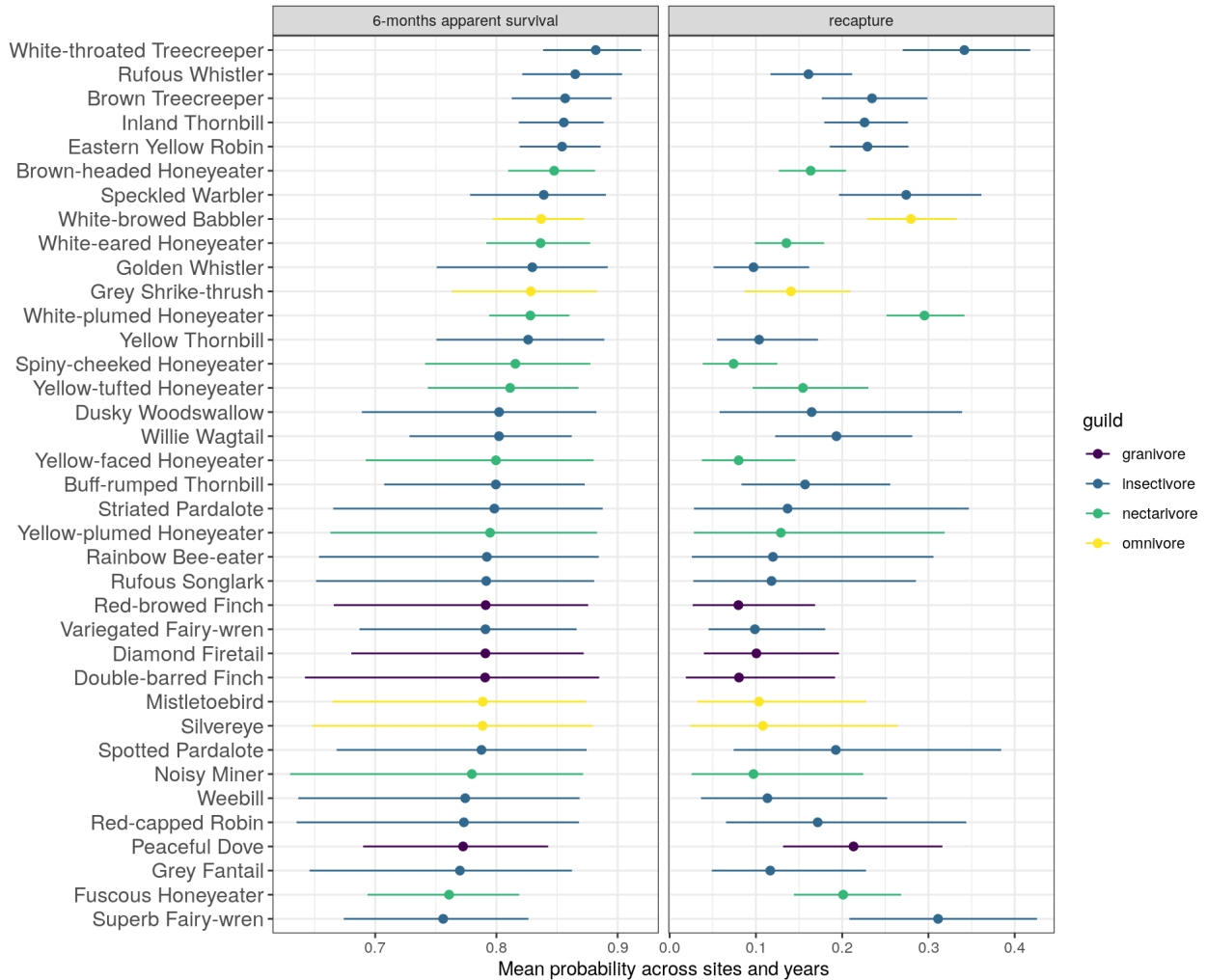
806 **DATA ACCESSIBILITY STATEMENT**

807 Data will be available on Dryad

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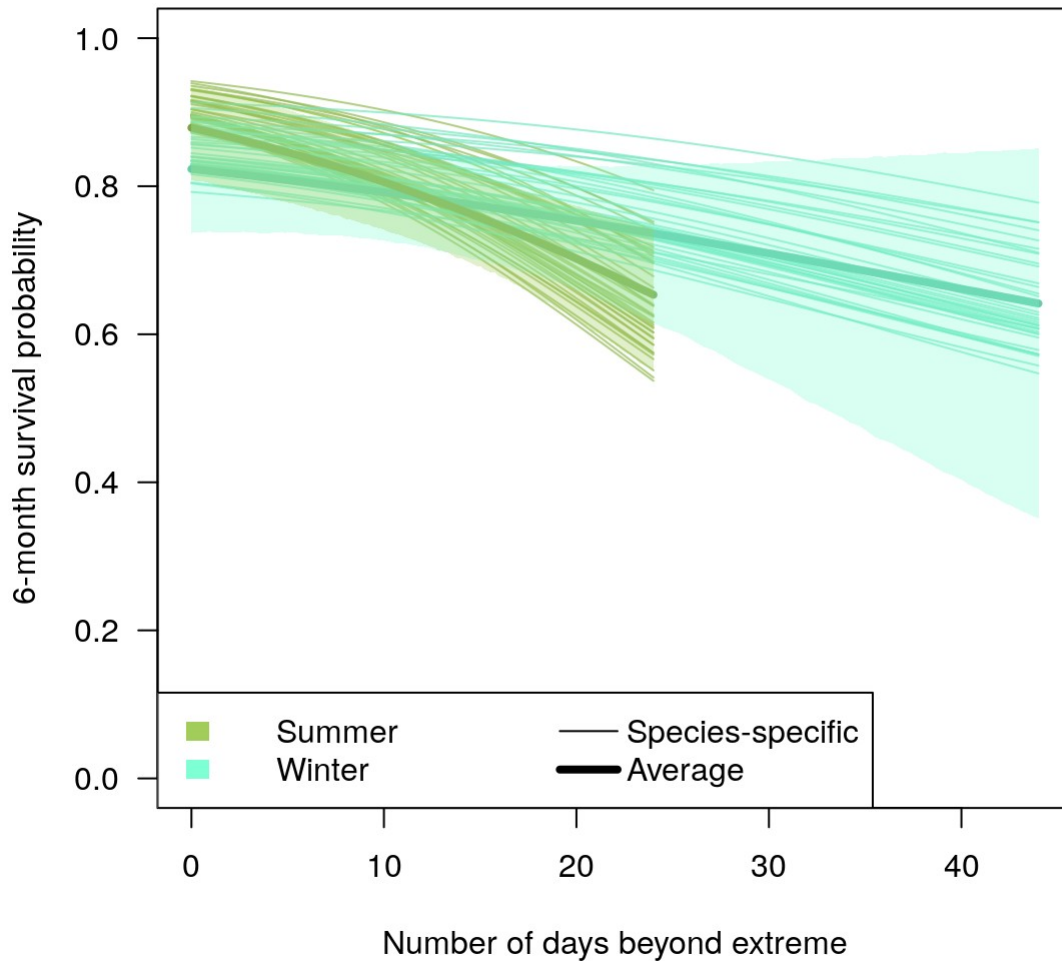
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810 Figure 1. Species-specific 6-monthly mean survival and mean recapture probabilities as esti-
 811 mated from a random intercept model (Model 1). Species are arranged by mean-survival on the
 812 y-axis and color-coded by guild. Survival and recapture probabilities are calculated conditional
 813 on a median number of days with temperature extremes, median rainfall, and integrating sites,
 814 seasons and temporal variance. Points represent posterior means and horizontal bars represent
 815 95% highest posterior density credible intervals.
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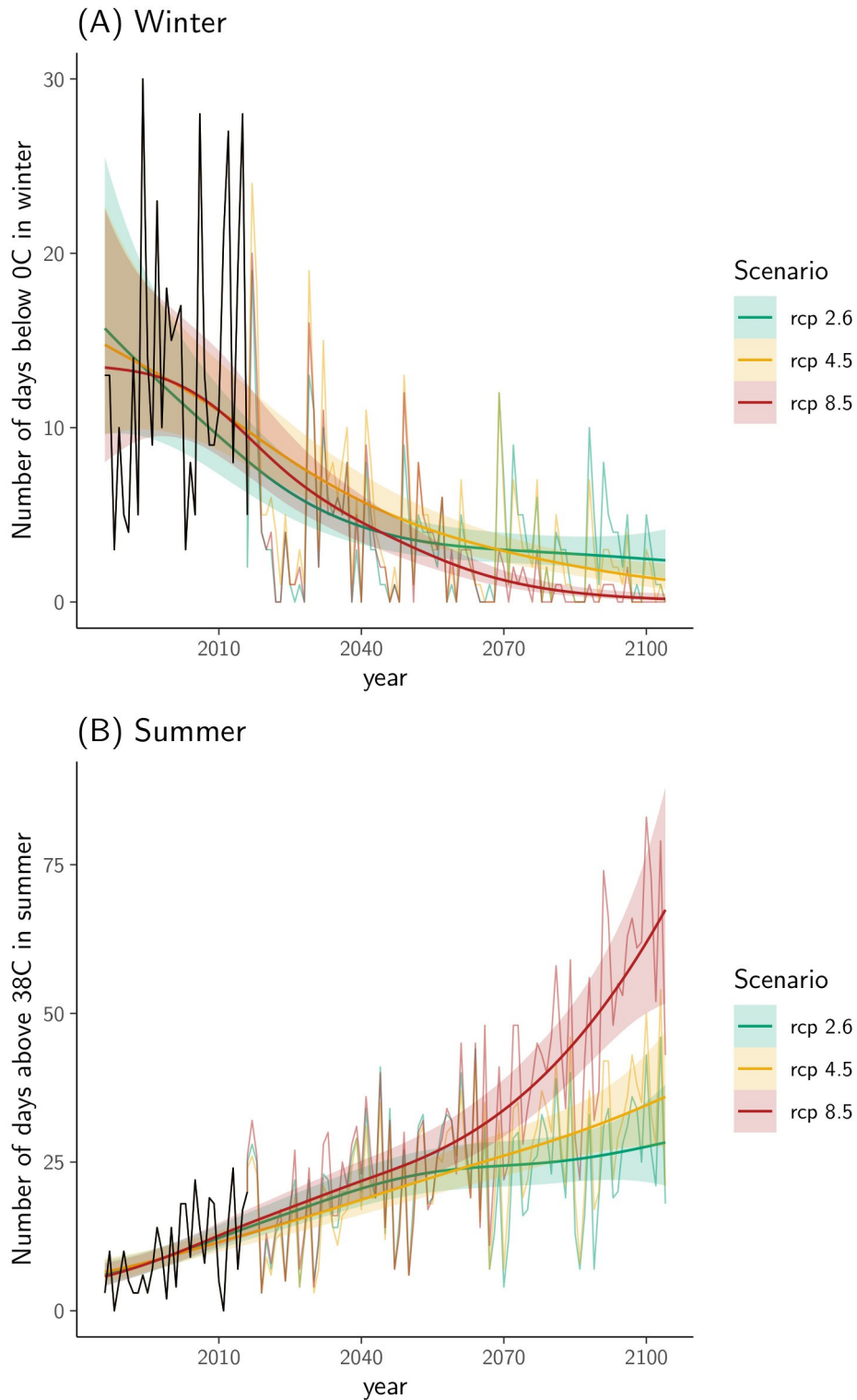
818 Figure 2. Predicted probability of 6-monthly survival as a function of the number of days of ex-
819 treme summer temperatures recording daily maxima $>38^{\circ}\text{C}$ and extreme winter temperatures
820 recording minima $<0^{\circ}\text{C}$. Average predictions, over all species, are shown in thick lines with
821 shaded areas representing 95% credible intervals, and were derived from model 1. Thin lines
822 represent species-specific predictions derived from model 4. Predictions were estimated for a
823 median rainfall and population density, but integrated over temporal variation, and in the case of
824 the average predictions, over species variation.

Apparent 6-month survival and extreme temperatures

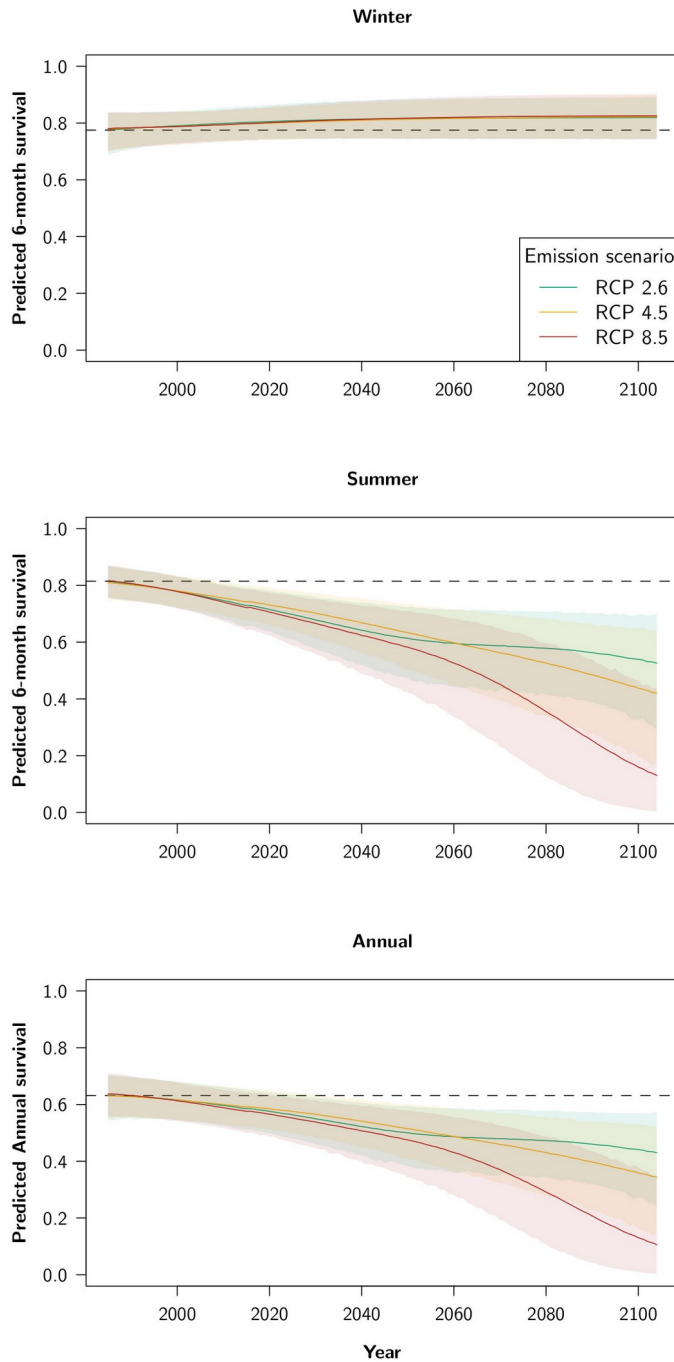


825 Figure 3. Predictions of daily temperature extremes under three emission scenarios from the
826 model CESM1-CAM5. (A) Number of days on which temperatures are below 0°C in winter; (B)
827 Number of days on which temperatures are above 38°C in summer. Numbers are observed from
828 1986 to 2015 (black line) and simulated according to the model from 2016 to 2104. Smoothed
829 lines and 95% confidence intervals are produced with negative-binomial generalised additive
830 models using thin-plate smooths of year from 1986 to 2104.
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834 Figure 4. Projected 6-monthly survival as a function of predicted change in the number of (a)
835 winter and (b) summer days with temperature extremes $>38^{\circ}\text{C}$ or $<0^{\circ}\text{C}$, respectively; (c) an-
836 nual survival to 2104 (averaged over all species, sites and time periods), for three scenarios of
837 emissions and associated climate change. For winter the predictions from the three scenarios
838 largely overlap. Dashed lines indicate the initial predicted survival probability to provide context
839 for trends in predicted survival. Shaded areas represent 95% credible intervals.



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