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1 **Individual and demographic consequences of reduced body condition following**  
2 **repeated exposure to high temperatures**

3

4 *Running head:* Climate-driven changes in body condition

5

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18 **Abstract**

19 Although the lethal consequences of extreme heat are increasingly reported in the literature,  
20 the fitness costs of exposure to sub-lethal high air temperatures, typically identified in the 30-  
21 40°C range, are poorly understood. We examine the effect of high ( $\geq 35^\circ\text{C}$ ) daily maxima on  
22 body condition of a semi-arid population of white-plumed honeyeaters *Ptilotula penicillatus*  
23 monitored between 1986 and 2012. During this 26 year period temperature has risen, on  
24 average, by  $0.06^\circ\text{C}$  each year at the site, the frequency of days with thermal maxima  $\geq 35^\circ\text{C}$   
25 has increased and rainfall has declined. Exposure to high temperatures affected body  
26 condition of white-plumed honeyeaters, but only in low rainfall conditions. There was no  
27 effect of a single day of exposure to temperatures  $\geq 35^\circ\text{C}$  but repeated exposure was  
28 associated with reduced body condition: 3.0% reduction in body mass per day of exposure.  
29 Rainfall in the previous 30 days ameliorated these effects, with reduced condition evident  
30 only in dry conditions. Heat-exposed males with reduced body condition were less likely to  
31 be recaptured at the start of the following spring; they presumably died. Heat-exposed  
32 females, regardless of body condition, showed lower survival than exposed males, possibly  
33 due to their smaller body mass. The higher mortality of females and smaller males exposed to  
34 temperatures  $\geq 35^\circ\text{C}$  may have contributed to the increase in mean body size of this  
35 population over 23 years. Annual survival declined across time concomitant with increasing  
36 frequency of days  $\geq 35^\circ\text{C}$  and decreasing rainfall. Our study is one of few to identify a  
37 proximate cause of climate change related mortality, and associated long-term demographic  
38 consequence. Our results have broad implications for avian communities living in arid and  
39 semi-arid regions of Australia, and other mid-latitudes regions where daily maximum  
40 temperatures already approach physiological limits in regions affected by both decreased  
41 precipitation and warming.

42

43 *Keywords:* body condition, climate change, demographic change, mechanism, mortality,

44 Meliphagidae, temperature extremes, white-plumed honeyeater, semi-arid, sub-lethal

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47 **INTRODUCTION**

48 Despite numerous studies providing correlative evidence for the effects of climate change on  
 49 the distributions, phenology and morphology of species, few identify proximate causes of  
 50 demographic change (Cahill et al. *et al.* 2013, Ockendon et al. 2014, Selwood et al. 2014).  
 51 The consequences for demography of exposure to extreme temperatures is gaining increasing  
 52 attention in the literature given forecasts of global increases in the frequency and intensity of  
 53 extreme climatic events (Boyles et al. 2011, Easterling et al. 2011, McKechnie and Wolf  
 54 2012). Much research has focused on the lethal consequences of extreme heat. Exposure to  
 55 high temperatures, above critical thresholds, has been shown to cause mass mortalities in a  
 56 range of taxa including endotherms and ectotherms (Cerrano et al. 2000, Easterling et al.  
 57 2000, Welbergen et al. 2008, McKechnie and Wolf 2012, Saunders et al. 2011).

58 Birds may be particularly vulnerable to the effects of extreme temperatures due to  
 59 their relatively high body temperatures, small body sizes, and predominantly diurnal habits  
 60 (Scholander et al. 1950, Boyles et al. 2011, McKechnie and Wolf 2012). In birds, lethal  
 61 hyperthermia occurs when body temperatures exceed about 45°C (Boyles et al. 2011,  
 62 McKechnie and Wolf 2010). McKechnie and Wolf (2010) modelled the effects of increasing  
 63 maximum temperatures on avian water balance during extremely hot conditions and argued  
 64 that mortality events for birds inhabiting hot deserts will become increasingly frequent under  
 65 future climate scenarios. Smaller individuals and species are particularly vulnerable because  
 66 the relatively larger surface area to volume ratios that characterize smaller individuals, and  
 67 allow more effective dumping of heat loads in warmer conditions, may become  
 68 disadvantageous under short-term exposure to extreme heat; larger surface areas result in  
 69 disproportionate rates of evaporative water loss, with smaller birds more vulnerable to acute  
 70 dehydration and mortality (McKechnie and Wolf 2012).

71 Less well understood are the fitness costs of exposure to sub-lethal air temperatures,  
 72 typically identified as temperatures in the 30-40°C range (McKechnie et al. 2012). High  
 73 temperatures have been shown to affect nestling development and foraging ecology with  
 74 negative consequences for body condition and fitness. For example, for southern fiscals  
 75 *Lanius collaris* in the Kalahari increasing exposure to high temperatures (33-37°C) during the  
 76 nestling period affected chick development, reducing fledgling body mass and tarsus length  
 77 and delaying fledging date, all of which have negative effects on survival (Cunningham et al.  
 78 2013a). Similarly, adult southern pied babblers *Turdoides bicolor* were unable to maintain  
 79 body mass when daily air temperatures exceeded 35.5°C, because individuals did not gain  
 80 sufficient mass during the day to compensate for normal overnight weight loss that occurs  
 81 due to fasting (du Plessis et al. 2012). Because reduced body condition can compromise  
 82 survival and reproductive success, du Plessis et al. (2012) concluded that short-term exposure  
 83 to extreme heat might be harmless but repeated exposure is likely to compromise ability to  
 84 maintain body condition, with negative consequences for fitness.

85 Body condition may also be involved in driving changes in structural body size that  
 86 have been correlated with recent rapid climate change (Gardner et al. 2011). Gardner et al.  
 87 (2014) found that the mean body size of a population of white-plumed honeyeaters *Ptilotula*  
 88 *penicillatus* had increased over 23 years; this was mainly associated with increases in  
 89 ambient temperature at the site. Two mechanisms may have been involved. First, as  
 90 considerable energy is required for the maintenance of high avian body temperatures  
 91 (Gillooly et al. 2001), a warming climate may reduce the costs of keeping warm leading to  
 92 improved body condition, and the subsequent production of larger offspring (Gardner et al.  
 93 2014). Second, exposure to daily maxima  $\geq 35^\circ\text{C}$  was associated with larger body size, an  
 94 effect attributed to size-dependent mortality. Gardner et al. (2014) suggested that the average  
 95 body size of the population might have increased following mortality of smaller individuals,

96 which are more vulnerable to acute dehydration in heatwave conditions, in accordance with  
 97 the predictions of McKechnie and Wolf (2010). Despite this possibility, lethal temperatures  
 98  $>45^{\circ}\text{C}$  are rare at the site (3 days in 23 years), so the consequences for fitness of increasing  
 99 exposure to high temperatures may be mediated via cumulative effects on body condition as  
 100 proposed by du Pleissis et al. (2012), rather than result from immediate mortality from heat  
 101 stress (McKechnie and Wolf 2010).

102 Here, we assess this hypothesis by testing the effect of high daily maximum  
 103 temperatures on the body mass of the white-plumed honeyeaters over the period 1986-2012  
 104 as studied by Gardner et al. (2014). We predicted that:

- 105 (1) repeated exposure to temperatures  $\geq 35^{\circ}\text{C}$  will have a negative effect on body condition  
 106 and will be associated with lower survival;  
 107 (2) repeated exposure to daily maxima  $\geq 35^{\circ}\text{C}$  will have a disproportionate effect on smaller  
 108 individuals.  
 109 (3) rainfall will ameliorate the effects of high temperatures via the provision of free water that  
 110 can reduce dehydration in hot conditions (McKechnie and Wolf 2012).  
 111 (4) long-term trends in survival will be negative, in accordance with temporal increases in  
 112 temperature and decreasing rainfall at the site (Gardner et al. 2014).

113

## 114 **METHODS**

### 115 *Study site and study species*

116 We studied a population of white-plumed honeyeaters over a 26 year period (1986–2012) at  
 117 The Charcoal Tank Nature Reserve, near West Wyalong, in central western New South  
 118 Wales ( $-33.9831^{\circ}\text{S}$ ,  $147.1575^{\circ}\text{E}$ ). Details of the site and population are given in Gardner *et*  
 119 *al.* (2014). In brief, the Reserve comprises an 86 ha remnant of *Eucalyptus* and *Melaleuca*  
 120 woodland, surrounded by wheat fields on all sides, and has three dams providing semi-



121 permanent water. The climate has become hotter and drier over the last 26 years at Wyalong.  
 122 Since 1985, total annual rainfall has declined significantly, temperature has increased by  
 123 0.06°C on average each year, and the annual frequency of hot days recording maxima  $\geq 35^{\circ}\text{C}$   
 124 has increased, particularly since 1995 (Gardner et al. 2014).

125 White-plumed honeyeaters are a small (14-22g this study) widespread Australian  
 126 passerine species belonging to the large and diverse Meliphagidae (Joseph et al. 2014). Males  
 127 are larger than females: 18.8g (n=397) versus 16.9g (n = 315) this study. The species is  
 128 primarily nectarivorous, but invertebrate prey forms an important part of the diet, especially  
 129 for growing young (Ford and Paton 1976). White-plumed honeyeaters are considered resident  
 130 or sedentary at the site, although some local movements may occur (Gardner et al. 2014). The  
 131 annual breeding season usually extends from July to the end of November, with free flying  
 132 juveniles captured between October and March each season; late breeding occurs very rarely  
 133 at the site, with only 2 of 140 juveniles captured outside this period in May. Adults undertake  
 134 an annual flight feather moult, usually starting in December or January following breeding,  
 135 with birds undertaking their first flight feather moult at the end of their first year of life.

136 Birds were captured in mist-nets 2-7 times each year as part of a long-term banding  
 137 (ringing) program at this site. One of us (MC) personally directed and supervised data  
 138 collection over the 26 years of the project and methods were consistent over time. Birds were  
 139 weighed with a Pesola balance to an accuracy of 0.5 g and the primaries were scored for  
 140 moult. Wing length, an index of structural body size, was measured as the length of the  
 141 flattened wing chord to the nearest 1.0 mm using a butt-ended ruler. Among passerines, wing  
 142 length is the best single linear predictor of structural size, and accordingly may be used as an  
 143 index of body size (Gosler et al. 1998).

144 Birds in their first three months of life and first year birds can be distinguished from  
 145 adults on the basis of plumage (Gardner et al. 2014); we only included adults in this study.



146 The sexes could be separated on differences in head-bill lengths with males larger than  
 147 females (Gardner et al. 2014).

148

149 *Statistical analysis*

150 *(i) Data*

151 We selected data for adults captured between October and March inclusive (1986 – 2010) to  
 152 eliminate the effect of cold winter days (those below 0°C; May-August) that can affect body  
 153 size (Krams et al. 2012). We excluded any bird in flight feather moult. We calculated  
 154 environmental variables from climate data, based on standardised daily records from the  
 155 Wyalong (Station 073054, West Wyalong Post office 33.93° S 147.24° E) weather station  
 156 (Bureau of Meteorology), located 10.5 km from the study site. We extracted the maximum  
 157 temperature on the day before capture for each individual, hereafter called initial exposure.  
 158 To assess the effect of repeated exposure to high temperatures, we calculated the number of  
 159 days with maxima  $\geq 35^{\circ}\text{C}$  to which each bird had been exposed in the 7 days prior to initial  
 160 exposure. We also extracted the amount of rainfall that fell on the day before capture for each  
 161 individual as well as that recorded in the 30 days prior to capture; we used a 30 day period  
 162 based on evidence of a one month lag between rainfall and food availability that affected  
 163 reproduction in a semi-arid bird (Illera and Díaz 2006).

164

165 *(ii) Models*

166 *Effects of climate on body condition.* We investigated the effect of maximum daily  
 167 temperature on body mass by constructing linear mixed models with body mass as the  
 168 response variable. We fitted both linear and quadratic terms for maximum temperature on the  
 169 day before capture (initial exposure) as explanatory variables because we predicted that  
 170 increasing body mass will be associated with increasing daily maximum temperature, up to

171 about 35°C, due to reductions in the thermoregulatory costs of keeping warm (introduction),  
 172 but the positive effect on body mass will be reversed with exposure to temperatures  $\geq 35^\circ\text{C}$ .  
 173 We also tested for the effects of repeated exposure to high temperatures by fitting the number  
 174 of days with maxima  $\geq 35^\circ\text{C}$  to which each bird had been exposed in the 7 days prior to initial  
 175 exposure. As the provision of free water can reduce dehydration in hot conditions, we fitted  
 176 rainfall recorded on the day of initial exposure as an additional variable (McKechnie and  
 177 Wolf 2010). Rainfall is also associated with increased food availability, particularly in arid  
 178 climates, so birds exposed to high temperatures following periods of high rainfall may be in  
 179 better condition, and therefore cope better with high temperatures (Brown and Sherry 2006).  
 180 Hence, we also fitted total rainfall recorded in the 30 days prior to initial exposure. Because  
 181 the distribution of rainfall was bimodal in our data set we fitted the term as a categorical  
 182 variable, high ( $\geq 35\text{mm}$ ) versus low ( $< 35\text{ mm}$ ) (Appendix: Fig. A1). Finally, as the response  
 183 of body mass to high temperatures is predicted to be affected by  $T_{\text{max}}$  (maximum temperature  
 184 on the day before capture), plus cumulative effects of exposure to high temperatures in the  
 185 preceding days (number days  $\geq 35^\circ\text{C}$ ) as well as recent rainfall (rain 30 last days), we fitted a  
 186 three-way interaction between these terms, as well as appropriate two-way interactions.

187 We fitted the identity of individuals as a random term to account for the recaptures of  
 188 the same individuals over multiple years. We controlled for structural body size using  
 189 residual wing length, which we calculated from a regression between wing length, abrasion  
 190 score, sex and age to account for changes in wing length due to age and feather abrasion. We  
 191 assigned an index of feather wear to account for abrasion of the tips of primary feathers,  
 192 which occurs between successive moults and affects wing length (Gardner et al. 2014). We  
 193 also controlled for month and time (24h) of capture, both of which are known to affect body  
 194 mass, and included minimum age, based on recapture information, because effects on body  
 195 mass may vary with age and experience (Monaghan 2008). Finally we included year of

196 capture to control for factors additional to climate that may affect body mass. All continuous,  
 197 explanatory variables were centered on their means.

198

199 *Fitness costs of reduced body condition following exposure to high temperatures.*

200 We predicted that individuals with reduced body condition following exposure to high  
 201 temperatures would have lower survival through the following winter. Based on recapture  
 202 information we identified whether individuals survived until the following spring/summer,  
 203 nominally October 1 (binomial response: yes/no). We used recapture as a proxy for survival  
 204 because adults known to be alive had a 78% chance of recapture in each year (Gardner et al.  
 205 2014). For each individual we assessed survival using recapture information, based on a  
 206 minimum period of two years from the date of capture. We tested whether survival  
 207 (recapture) was affected by body condition for exposed (experienced  $\geq 1$  day with  
 208 temperature  $\geq 35^{\circ}\text{C}$  on the day of initial exposure or in the preceding week) and non-exposed  
 209 (experienced no temperatures  $\geq 35^{\circ}\text{C}$  on the day of initial exposure or in the preceding week)  
 210 individuals using generalised linear models with binomial distributions. Because we lacked  
 211 data on the proportion of mass lost for each individual we could not directly link exposure,  
 212 mass loss and body size. So instead we used residual body condition, which estimates energy  
 213 reserves using size-corrected body mass, calculated by fitting mass as the response variable  
 214 against residual wing, sex and time of day. Because the probability of survival may vary with  
 215 age, sex, body size (residual wing), month, and year of capture we fitted these terms as  
 216 additional explanatory variables. We also tested whether patterns of survival due to body  
 217 condition differed between the sexes and with body size by fitting two interaction terms  
 218 (body condition  $\times$  sex, body condition  $\times$  residual wing). We selected, at random, one record  
 219 per individual, and ran separate analyses for individuals that were exposed to daily maxima  
 220  $\geq 35^{\circ}\text{C}$  and those that were not. We used separate analyses because the structure of our data

221 did not allow us to control for differences in the effect of body condition on survival due to  
 222 age, sex and size for exposed versus non-exposed individuals which would require fitting a  
 223 prohibitive number of 3-way interaction terms between condition, exposure (yes/no) and each  
 224 variable, given our sample size.

225

226 *Changes in survival over 26 years.* We predicted that the survival of individuals would have  
 227 declined across time given annual increases in the frequency of days recording temperatures  
 228  $\geq 35^{\circ}\text{C}$  and decline in rainfall at the site (Gardner et al. 2014). We fitted recapture as a proxy  
 229 for survival as the response variable (as defined above), and year as an explanatory variable.

230 We controlled for differences in survival due to age and sex. We also fitted an interaction  
 231 between year  $\times$  sex to test whether the temporal pattern of survival differed between the  
 232 sexes.

233

234 *(iii) Model fitting*

235 To avoid multicollinearity among the explanatory variables, we first estimated pair-wise  
 236 Pearson's correlation coefficients between the explanatory variables (Appendix: Table A1)  
 237 and confirmed that correlations were not high for all the combinations ( $|r| < 0.28$ ). We also  
 238 calculated variance inflation factors (VIF) which in all cases were  $< 3$  which is below the  
 239 threshold recommended by Zuur *et al.* (2010). To account for model selection uncertainty,  
 240 we adopted a multi-model inference approach based on the Akaike information criteria  
 241 (AICc) (Burnham and Anderson, 2002). We first generated a candidate set of models with all  
 242 possible parameter subsets, which were then fitted to the data and ranked by  $\Delta\text{AICc}$  values  
 243 (the difference between each model's AICc and  $\text{AICc}_{\min}$ , that of the "best" model). We  
 244 reported the top 10 models for each analysis. In each case, the top 10 models include all  
 245 models with  $\Delta\text{AICc}$  values  $< 2$ , as well as some models with  $\Delta\text{AICc} > 2$ . All analyses were

246 conducted in R 2.15.3 (R Development Core Team 2012), linear mixed models were fitted  
 247 using the package lme4 (Bates et al. 2012), generalised linear models were fitted using the  
 248 MASS package (Venables and Ripley 2002).

249

250 **RESULTS**

251 *Factors affecting body condition*

252 Body mass was affected by temperature and rainfall after controlling for structural size  
 253 (residual wing length), sex, relative age, time of day, month and year of capture. There was  
 254 no detectable effect on body mass of maximum temperature on the day before capture in the  
 255 range 12-41°C, as this variable was not included in any top models (Table 1). Similarly,  
 256 rainfall on the day prior to capture had no detectable effect on body mass as this variable was  
 257 not included in the best model (Table 1). Rather, the effects of temperature and rainfall  
 258 appeared to be cumulative.

259 Repeated exposure to days with temperatures  $\geq 35^{\circ}\text{C}$  in the 7 days prior to initial  
 260 exposure was included in the best model and most of the following top models and the 95%  
 261 confidence intervals (CIs) of the estimated coefficient for the best model did not overlap  
 262 zero; it was associated with reductions in body mass in all cases (Table 1, Fig. 1). However,  
 263 the effect differed with rainfall conditions (N days  $\geq 35^{\circ}\text{C} \times \text{rain } 30\text{d}$  was included in the best  
 264 model and most of the following top models and 95% CIs did not overlap zero in the best  
 265 model; Table 1, Fig. 1). In the best model, body mass declined by 0.53g with each day of  
 266 exposure to daily maxima  $\geq 35^{\circ}\text{C}$  when low rainfall conditions prevailed in the 30 day prior  
 267 to capture (Table 1, Fig. 1). In high rainfall conditions there was no effect on body mass of  
 268 repeated exposure to temperatures  $\geq 35^{\circ}\text{C}$  (Table 1, Fig. 1).

269

270 *Effects of body condition on survival*

271 The probability of survival (recapture) differed for exposed and non-exposed individuals. For  
 272 adults exposed to temperatures  $\geq 35^{\circ}\text{C}$  on the day before capture or during the preceding  
 273 week, those in poorer condition were less likely to be recaptured in the following spring  
 274 (nominally from October 1) (Table 2a, Fig. 2); body condition was included in all top models  
 275 (Table 2a). The effect of body condition on recapture did not vary with body size (residual  
 276 condition  $\times$  residual wing was not included in the best model or in most top models), but  
 277 differed between the sexes (residual condition  $\times$  sex was included in all top models and 95%  
 278 CIs for the coefficient in best model did not overlap zero) (Table 2a, Fig.2). For males,  
 279 recapture increased with body condition (coefficient in the top model = 0.69), but there was  
 280 no effect of body condition on the recapture of females (coefficient in the top model = -0.06)  
 281 (Table 2a, Fig. 2). Overall, females were less likely to be recaptured than males (sex effect  
 282 was negative in all top models and the 95% CIs for the coefficient in best model did not  
 283 overlap zero (Table 2a).

284 For adults not exposed to temperatures  $\geq 35^{\circ}\text{C}$  on the day before capture or during the  
 285 preceding week, the probability of recapture in the following spring did not vary with body  
 286 condition (residual condition effect), nor did the effect of condition vary with sex (residual  
 287 condition  $\times$  sex) or body size (residual condition  $\times$  residual wing) as neither of these  
 288 variables was included in any top model (Table 2b, Fig. 2). Body condition was not included  
 289 in the best model or in most top models. Further, these two models had larger AICc values  
 290 than the corresponding models without body condition (Appendix Table A3b). Overall,  
 291 females had a lower chance of recapture than males (sex effect included in all top models and  
 292 the 95% CIs for the coefficient in best model did not overlap zero), and the probability of  
 293 recapture declined across years (year effect included in all top models; the 95% CIs for the  
 294 coefficient in best model did not overlap zero) (Table 2b, Fig. 2).

295



296 *Long-term survival over 26 years*

297 The probability of survival (recapture) declined over time (year effect was negative in the  
 298 best model and in all top models in which the term was included; 95% CIs did not overlap  
 299 zero in the best model (Table 3). Overall, females had lower survival than males (sex effect  
 300 for females was negative in the best model and in all top models in which the term was  
 301 included; 95% CIs did not overlap zero in the best model; Table 3), but the temporal pattern  
 302 of survival did not differ between the sexes and there was no effect of minimum age on  
 303 survival, as these variables were not included in the best model or in the majority of top  
 304 models (Table 3).

305

306 **DISCUSSION**

307 Exposure to high temperatures had strong effects on the body condition of white-plumed  
 308 honeyeaters, with repeated exposure to temperatures  $\geq 35^{\circ}\text{C}$  driving reductions in body mass  
 309 in low rainfall conditions. There was no effect of a single day of exposure to daily maxima  
 310  $\geq 35^{\circ}\text{C}$  but repeated exposure in low rainfall conditions was associated with loss of condition.  
 311 Rainfall in the 30d prior to exposure ameliorated the effects of high temperatures, with mass  
 312 loss associated only with low rainfall conditions. Heat-exposed (i.e. those that had  
 313 experienced at least one hot day) males in poorer condition were less likely to be recaptured  
 314 at the start of the following spring (nominally October 1) and presumably died. Overall,  
 315 survival declined over the 26 years of the study.

316

317 *Body condition, rainfall and heat waves*

318 Our top model estimates mass losses of 3.0% of body weight per day of exposure to high (35-  
 319  $41^{\circ}\text{C}$ ) temperatures in low rainfall conditions. Similar rates of mass loss were recorded for  
 320 semi-arid babblers: overnight mass loss averaged 3.82% following days with maxima  $>30^{\circ}\text{C}$ ,



321 in low rainfall conditions toward the end of the dry season (Du Plessis et al. 2012). In that  
 322 case, mass loss was associated with a reduction in foraging efficiency such that birds could  
 323 not gain sufficient energy during hot days to counteract normal overnight weight loss. This  
 324 study (Du Plessis et al. 2012) identified 35.5°C as a critical temperature beyond which net  
 325 mass losses were incurred. Similarly, Cunningham et al. (2013a) recorded changes in body  
 326 mass and growth in nestling southern fiscals when temperatures reached 33-37°C. Our results  
 327 are consistent with these studies but definition of threshold temperatures at which fitness  
 328 costs are incurred requires further study, since critical temperatures are likely to vary among  
 329 species as well as within, and several thresholds may exist within a single species, each  
 330 affecting a different correlate of fitness (Cunningham et al. 2013).

331 Our results provide a rare demonstration of the importance of rainfall in ameliorating  
 332 individual responses to high temperatures (Bolger et al. 2005, Cahill et al. 2013, Cunningham  
 333 et al. 2013). Mass loss following repeated exposure to temperatures  $\geq 35^\circ\text{C}$  occurred only  
 334 when rainfall in the 30 days prior to capture was low (Fig. 1). This mass loss could simply  
 335 represent dehydration: at temperatures above about 30°C, cooling is achieved via panting and  
 336 involves evaporative water loss. Birds, such as white-plumed honeyeaters, that are lighter  
 337 than about 25g are particularly vulnerable due to their relatively large surface area to volume  
 338 ratios (Wolf 2000, McKechnie and Wolf 2010). However, only when environmental  
 339 temperatures exceed body temperature (about 40°C in birds) do rates of evaporative water loss  
 340 and dehydration increase dramatically, particularly for small individuals (Dawson and  
 341 Whittow 2000, Wolf 2000), and in our study, we recorded relatively few days of  
 342 temperatures above 40°C (115d in 26 years). Moreover, rainfall on the day of exposure to  
 343 high temperatures had no detectable effect on body mass suggesting that dehydration was not  
 344 the primary factor involved, although several dams at the site that provide semi-permanent  
 345 water may have masked any direct effect of rainfall if birds had access to free water at the

346 time of exposure. Accordingly, we have limited evidence that dehydration was the primary  
 347 factor driving the negative effects of low rainfall on body condition.

348 Effects of rainfall on body condition may also be mediated via influence on primary  
 349 productivity and the resulting quality and quantity of food available with consequences for  
 350 energy budgets (Albright et al. 2010, Mackey et al. 2012). Body condition can be strongly  
 351 affected by rainfall-induced variation in food supply with reduced food availability resulting  
 352 in loss of condition via catabolizing muscle and fat tissue (Brown and Sherry, 2006). Indeed,  
 353 previous analyses showed negative effects of lower rainfall on juvenile growth in this  
 354 population (Gardner et al. 2014).

355 High temperatures may also compromise energy budgets by reducing rates of prey  
 356 capture during the hottest parts of the day or by forcing individuals to reduce or cease  
 357 foraging altogether to reduce environmental heat loads; such forms of behavioural  
 358 thermoregulation are almost universal among desert birds (Austin 1976, Wolf 2000, Huey et  
 359 al. 2012, du Plessis et al. 2012, McKechnie and Wolf 2012; Cunningham et al. 2013). Thus,  
 360 in low rainfall conditions, the negative effects of high temperatures on energy budgets are  
 361 likely to be exacerbated because body condition will already be reduced (Brown and Sherry  
 362 2006). Whether mass loss in our study was primarily due to failure to balance energy or water  
 363 budgets or both requires further investigation.

364

365 *Survival of individuals following exposure to daily maxima  $>35^{\circ}\text{C}$*

366 For individuals exposed to high temperatures, those in poorer condition were less likely to be  
 367 recaptured and presumably died (Table 2). It is unlikely that these individuals left the study  
 368 site as birds in this population are sedentary (Gardner et al. 2014). We estimate mass losses  
 369 of up to 18% of body mass, given that some individuals were exposed to six consecutive days  
 370 with daily maxima  $\geq 35^{\circ}\text{C}$ , and mass declined by 0.53 g with each day of exposure.

371 Presumably, our study underestimates effects of exposure to hot days on body condition  
 372 because banders (ringers) avoid working through extended periods of hot weather due to the  
 373 risk of bird mortality during capture. Weather records indicate that heatwaves with up to 16  
 374 consecutive days of temperatures  $\geq 35^{\circ}\text{C}$  were recorded during our study period. Such  
 375 conditions would result in much higher mass loss (theoretically 48%, excluding time for  
 376 recovery between episodes), which would likely result in direct mortality (Wolf and  
 377 Walsberg 1996, Wolf 2000). Understanding the physiological consequences of repeated,  
 378 rather than acute, exposure to high temperatures and its effects on water and energy budgets  
 379 is an urgent priority.

380         Despite immediate survival following repeated exposure to high temperatures, heat-  
 381 exposed white-plumed honeyeaters in poorer condition were less likely to be recaptured in  
 382 the following spring. We suggest that the timing of exposure to heatwaves, during or just  
 383 prior to moult, may be of critical importance for fitness, magnifying the probability of  
 384 mortality via delayed, condition-dependent costs on feather moult. It has recently been shown  
 385 experimentally that the quality of feathers produced during moult can be condition-  
 386 dependent, with poor condition associated with slower moult rate and reduced feather quality,  
 387 leading to the suggestion that feather quality might be a major mediator of life history trade-  
 388 offs (Dawson et al. 2000, Vágási et al. 2012). Indeed, birds in poor condition due to climate-  
 389 driven, food deprivation suffered carry-over costs on feather growth (Brown and Sherry  
 390 2006). Because poor quality plumage impairs insulation and increases thermoregulatory costs  
 391 it can lead to lower survival during winter and reduced reproduction in the following year  
 392 (Nilsson and Svensson 1996, Dawson et al. 2000, Vágási et al. 2012). In white-plumed  
 393 honeyeaters, wing moult occurs between December and April each year, immediately after  
 394 breeding, and increasingly co-occurs with exposure to high temperatures (November to  
 395 March) (Gardner et al. 2014). Energetic constraints are highest during this period of the

396 annual routine, and additional costs on condition imposed by increasing exposure to  
 397 heatwaves might subsequently affect moult quality with delayed consequences for survival  
 398 over winter.

399 Overall, female white-plumed honeyeaters were less likely to be recaptured than  
 400 males, regardless of whether they were exposed to high temperatures. In contrast, the survival  
 401 of heat-exposed males was affected by body condition. That condition-dependent mortality  
 402 was detected only in males may relate to sex differences in body mass. Females are smaller  
 403 than males and may be below a critical mass threshold that reduces their capacity to endure  
 404 the costs of exposure, and only larger males are able to survive. Nevertheless, the higher  
 405 mortality of (smaller) heat-exposed males and females overall, may have contributed to the  
 406 temporal increase in mean body size of this population over 23 years (Gardner et al. 2014).

407  
 408 *Population-level trends in survival*

409 At the population level, survival has declined across time, concomitant with the temporal  
 410 decline in rainfall and increase in temperature at the site (see Gardner et al. 2014). Given our  
 411 demonstration of the effects of temperature and rainfall on body condition and its effect on  
 412 survival we suggest that climate-driven effects on body condition are a contributing factor in  
 413 the declining survival of this population. Our study thus provides a rare example of a  
 414 proximate cause of climate-related variation in individual survival and associated long-term  
 415 (demographic) consequence (see reviews by Cahill et al. 2013, Ockendon et al. 2014,  
 416 Selwood et al. 2014). It suggests that selection on heat tolerance may involve exposure to  
 417 sub-lethal temperatures with effects on fitness mediated via body condition with  
 418 consequences for demography and population persistence.

419 Our results indicate complex, climate-driven changes in demographic rates rather than  
 420 a direct relationship between mortality and limited tolerance to high temperatures as

421 highlighted by recent studies (Ozgul et al. 2009, Cahill et al. 2013, Ockendon et al. 2014,  
 422 Selwood et al. 2014). Nevertheless, as the severity of heatwaves increase in the coming years,  
 423 consistent with the long-term trend at the site (Gardner et al. 2014), direct mortality via acute  
 424 exposure to extreme heat is also likely, particularly given the trend for declining rainfall.  
 425 Finally, our study has broad implications for avian communities living in arid and semi-arid  
 426 regions of Australia and other mid-latitude regions characterized by daily maximum  
 427 temperatures that are already close to known physiological limits in regions that are most  
 428 affected by decreased precipitation, as well as by warming (e.g. South Africa; see du Plessis  
 429 et al. 2012, Cunningham et al. 2013a) (IPCC 2013).

430

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441

442 **LITERATURE CITED**

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577

**SUPPLEMENTAL MATERIAL**

578

**Ecological Archives**

579 Appendix A: Supplementary information for variables included in analyses.

Table 1. Factors affecting the body mass of adult white-plumed honeyeaters captured during the spring and summer months (October-March) between 1986 and 2012. Shown are coefficients and their standard errors (SE) for variables included in the top 10 models following model selection based on Akaike information criteria (AICc). Models were ranked by  $\Delta AICc$  values (the difference between each model's AICc and  $AICc_{min}$ , that of the "best" model). Variables identified as important in the best model have 95% confidence intervals (CI) of estimated coefficients that do not overlap zero and are shown in bold. Residual wing was calculated from a regression with wing length as the response variable and abrasion score, age and sex as the explanatory variables. N= 642 adults. Terms not included in the top 10 models are: Year, TempMaxDB4Capt, TempMaxDB4Capt<sup>2</sup>, TempMaxDB4Capt x RainDB4CaptYN, TempMaxDB4Capt x Rain30d, TempMaxDB4Capt x N days  $\geq 35^\circ C$ , TempMaxDB4Capt x N days  $\geq 35^\circ C$  x Rain30d. See Appendix A1 explanation of terms.

Model	Intercept	Rain30D (high)	RainDB4Capt (yes)	Year	Age	Month	N days $\geq 35^\circ C$	Residual wing	Time	Sex (female)	Rain30D x N days $\geq 35^\circ C$	AIC	delta
3706	18.643	<b>0.292</b> $\pm 0.090$	NA	NA	0.074 $\pm 0.025$	0.092 $\pm 0.028$	<b>-0.552</b> $\pm 0.113$	<b>0.167</b> $\pm 0.016$	0.001 $\pm 0.001$	<b>-1.914</b> $\pm 0.095$	<b>0.534</b> $\pm 0.129$	1989.019	0.000
3698	18.653	0.292 $\pm 0.090$	NA	NA	NA	0.092 $\pm 0.028$	-0.478 $\pm 0.113$	0.167 $\pm 0.018$	0.001 $\pm 0.001$	-1.914 $\pm 0.129$	0.482 $\pm 0.129$	1990.550	1.531
3690	18.680	0.187 $\pm 0.085$	NA	NA	0.074 $\pm 0.025$	NA	-0.506 $\pm 0.114$	0.166 $\pm 0.016$	0.001 $\pm 0.001$	-1.912 $\pm 0.096$	0.575 $\pm 0.130$	1992.456	3.438
3708	18.728	0.282 $\pm 0.090$	-0.107 $\pm 0.107$	NA	0.075 $\pm 0.025$	0.095 $\pm 0.028$	-0.520 $\pm 0.113$	0.167 $\pm 0.016$	0.001 $\pm 0.001$	-1.907 $\pm 0.095$	0.530 $\pm 0.129$	1992.656	3.638
3682	18.690	0.185 $\pm 0.085$	NA	NA	NA	NA	-0.462 $\pm 0.113$	0.165 $\pm 0.016$	0.001 $\pm 0.001$	-1.942 $\pm 0.096$	0.523 $\pm 0.130$	1993.788	4.770
3700	18.729	0.280	-0.096	NA	NA	0.095	-0.476	0.166	0.001	-1.938	0.477	1994.380	5.361

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		±0.091	±0.107			±0.028	±0.113	±0.016	±0.001	±0.096	±0.129		
3692	18.731	0.178	-0.063	NA	0.075	NA	-0.504	0.165	0.001	-1.908	0.574	1996.741	7.722
		±0.086	±0.108		±0.025		±0.114	±0.016	±0.001	±0.096	±0.130		
3684	18.732	0.178	-0.051	NA	NA	NA	-0.560	0.165	0.001	-1.939	0.571	1998.173	9.155
		±0.087	±0.108				±0.113	±0.016	±0.001	±0.096	±0.130		
1618	18.706	0.230	NA	NA	NA	0.088	NA	0.174	0.001	-1.938	NA	1998.246	9.227
		±0.088				±0.027		±0.016	±0.001	±0.097			
3710	18.644	0.294	NA	-0.003	-0.075	0.093	-0.052	0.167	0.001	-1.915	0.533	1998.364	9.346
		±0.090		±0.010	±0.025	±0.030	±0.113	±0.016	±0.001	±0.095	±0.130		

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preprint

Table 2. The effect of body condition on survival (recapture: yes/no) for adult white-plumed honeyeaters (a) exposed or (b) not exposed to temperatures  $\geq 35^\circ\text{C}$  in the 7 days prior to initial exposure between 1986 and 2012. Shown are coefficients and their standard errors (SE) for variables included in the top 10 models following model selection based on Akaike information criteria (AICc). Variables identified as important in the best model have 95% confidence intervals (CI) of estimated coefficients that do not overlap zero and are shown in bold. Models were ranked by  $\Delta\text{AICc}$  values (the difference between each model's AICc and  $\text{AICc}_{\text{min}}$ , that of the "best" model). Body condition was calculated as the residuals from a regression with body mass as the response variable and residual wing length, time of capture and sex as the explanatory variables.

(a)

Model	(Intercept)	Year	Month	Age	Residual wing	Body condition	Sex (female)	Body condition x residual wing	Body condition x sex (female)	AIC	delta
178	-0.436	-0.066	NA	NA	NA	<b>0.695</b>	<b>-1.158</b>	NA	<b>-0.750</b>	126.349	0.000
	$\pm 0.288$	$\pm 0.041$				<b><math>\pm 0.261</math></b>	<b><math>\pm 0.488</math></b>		<b><math>\pm 0.370</math></b>		
177	-0.479	NA	NA	NA	NA	0.650	-1.009	NA	-0.793	127.018	0.669
	$\pm 0.284$					$\pm 0.252$	$\pm 0.472$		$\pm 0.377$		
186	-0.452	-0.062	NA	NA	0.105	0.767	-1.171	NA	-0.864	127.127	0.779
	$\pm 0.292$	$\pm 0.042$			$\pm 0.080$	$\pm 0.275$	$\pm 0.488$		$\pm 0.391$		
249	-0.590	NA	NA	NA	0.118	0.661	-0.896	-0.094	-0.795	127.327	0.978
	$\pm 0.305$				$\pm 0.076$	$\pm 0.278$	$\pm 0.490$	$\pm 0.417$	$\pm 0.417$		
185	-0.481	NA	NA	NA	0.095	0.729	-1.004	NA	-0.915	127.407	1.059
	$\pm 0.288$				$\pm 0.076$	$\pm 0.267$	$\pm 0.437$		$\pm 0.397$		



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250	-0.553	-0.056	NA	NA	0.096	0.711	-1.003	-0.083	-0.774	127.543	1.194
	±0.310	±0.043			±0.081	±0.287	±0.503	±0.064	±0.408		
182	-0.438	-0.068	NA	0.054	NA	0.698	-1.162	NA	-0.750	128.103	1.754
	±0.288	±0.042		±0.107		±0.262	±0.490		±0.372		
180	-0.438	-0.069	-0.002	NA	NA	0.689	-1.155	NA	-0.736	128.261	1.912
	±0.288	±0.043	±0.005			±0.261	±0.488		±0.372		
50	-0.396	-0.067	NA	NA	NA	0.348	-1.203	NA	NA	128.776	2.427
	±0.274	±0.039				±0.173	±0.477				
190	-0.455	-0.064	NA	0.061	0.086	0.767	-1.170	NA	-0.862	128.835	2.487
	±0.293	±0.042		±0.111	±0.076	±0.275	±0.489		±0.392		

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(b)

Model	(Intercept)	Year	Month	Age	Residual wing	Body condition	Sex (female)	Body condition x residual wing	Body condition x sex (female)	AIC	delta
34	-0.735	<b>-0.087</b>	NA	NA	NA	NA	<b>-0.748</b>	NA	NA	452.514	0.000
	±0.155	<b>±0.030</b>					<b>±0.234</b>				
42	-0.735	-0.087	NA	NA	0.049	NA	-0.754	NA	NA	453.030	0.516
	±0.155	±0.030			±0.041		±0.235				
50	-0.735	-0.086	NA	NA	NA	0.085	-0.753	NA	NA	453.882	1.368
	±0.155	±0.030				±0.106	±0.235				
58	-0.735	-0.086	NA	NA	0.049	0.086	-0.760	NA	NA	454.380	1.866
	±0.156	±0.030			±0.041	±0.107	±0.235				
38	-0.741	-0.087	NA	0.026	NA	NA	-0.737	NA	NA	454.389	1.876
	±0.156	±0.030		±0.074			±0.236				
36	-0.734	-0.088	0.001	NA	NA	NA	-0.751	NA	NA	454.491	1.977
	±0.155	±0.030	±0.002				±0.235				
46	-0.740	-0.087	NA	0.021	0.048	NA	-0.745	NA	NA	454.950	2.436
	±0.157	±0.030		±0.075	±0.041		±0.237				
44	-0.734	-0.088	0.001	NA	0.049	NA	-0.758	NA	NA	455.002	2.488
	±0.156	±0.030	±0.002		±0.041		±0.236				

54	-0.739	-0.086	NA	0.019	NA	0.081	-0.745	NA	NA	455.814	3.301
	±0.156	±0.030		±0.075		±0.107	±0.237				
52	-0.734	-0.086	0.001	NA	NA	0.084	-0.754	NA	NA	455.875	3.361
	±0.155	±0.030	±0.002			±0.107	±0.236				

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Table 3. Temporal change in survival (recapture: yes/no) for adult white-plumed honeyeaters captured between 1986 and 2012. Shown are coefficients and their standard errors (SE) for variables included in the top 10 models following model selection based on Akaike information criteria (AICc). Variables identified as important in the best model have 95% confidence intervals (CI) of estimated coefficients that do not overlap zero and are shown in bold. Models were ranked by  $\Delta AICc$  values (the difference between each model's AICc and  $AICc_{min}$ , that of the “best” model).

Model	(Intercept)	Year	Age	Sex (female)	Year x sex (female)	AIC	delta
6	-0.638 ±0.133	<b>-0.065 ±0.023</b>	NA	<b>-0.851 ±0.208</b>	NA	581.127	0.000
8	-0.646 ±0.134	-0.066 ±0.023	0.038 ±0.059	-0.838 ±0.209	NA	582.733	1.606
14	-0.637 ±0.133	-0.057 ±0.028	NA	-0.872 ±0.214	-0.024 ±0.048	582.879	1.752
16	-0.644 ±0.133	-0.058 ±0.028	0.036 ±0.059	-0.859 ±0.215	-0.022 ±0.048	584.518	3.391
5	-0.647 ±0.132	NA	NA	-0.789 ±0.205	NA	588.035	6.907
7	-0.653 ±0.132	NA	0.028 ±0.057	-0.777 ±0.206	NA	589.792	8.665
2	-1.025 ±0.101	-0.056 ±0.022	NA	NA	NA	596.445	15.318
4	-1.028 ±0.101	-0.057 ±0.022	0.062 ±0.058	NA	NA	597.326	16.199
1	-1.025 ±0.103	NA	NA	NA	NA	601.280	20.153
3	-1.009 ±0.100	NA	0.053 ±0.056	NA	NA	602.402	21.274

**Figure legends**

Figure 1. The effect on body condition of repeated exposure to temperatures  $\geq 35^{\circ}\text{C}$  in high (circles, solid line) and low (triangle, dashed line) rainfall conditions. Body condition was calculated as the residuals from a regression with body mass as the response variable and residual wing length, time of capture and sex as the explanatory variables. N= 642 adults.

Figure 2. The effect of body condition on the probability of recapture at the start of the following spring (nominally October 1) for male and female white-plumed honeyeaters exposed, or not, to daily maxima  $\geq 35^{\circ}\text{C}$ : grey bars = not recaptured; white bars= recaptured. Body condition was calculated as the residuals from a regression with body mass as the response variable and residual wing length, time of capture and sex as the explanatory variables.



