1   **Title: Hot droughts compromise interannual survival across all group sizes in a**

2   **cooperatively breeding bird**

3   **Running title: Hot droughts compromise interannual survival**

4   Amanda R. Bourne*[1], Susan J. Cunningham[1], Claire N. Spottiswoode[1,2], Amanda R. Ridley[1,3]

5   [1] FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Private

6   Bag X3, Rondebosch 7701, South Africa

7   [2] Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

8   [3] Centre for Evolutionary Biology, School of Biological Sciences, University of Western Australia, Crawley 6009,

9   Australia

10   Author contacts: ARB (abourne.uct@gmail.com), SJC (susie.j.c@gmail.com), CNS (cns26@cam.ac.uk),

11   ARR (amanda.ridley@uwa.edu.au)

12   *Corresponding author: Amanda Ruth Bourne; 0027 (83) 440 2081; abourne.uct@gmail.com

13   FitzPatrick Institute of African Ornithology, Room 2.18, John Day Zoology Building, University Avenue,

14   University of Cape Town, 7701, South Africa

15   **Keywords:** Sociality, unpredictable environments, cooperative breeding, climate change,

16   southern pied babbler, hot drought, group size

17   **Statement of authorship**

18   ARR, SJC, ARB, and CNS conceived the study and secured funding. ARR started habituation of

19   the study animals and collection of life history data in 2003 and has maintained it ever since; this

20   was central to making the study possible. ARB undertook all fieldwork from 2016 onwards.

21   ARB and ARR analysed the data. ARB drafted the manuscript. All authors contributed

22   substantially to revisions, and gave final approval for publication.

23   **Data accessibility statement**

24   The data underlying all analyses presented here will be archived at the University of Cape

25   Town's open-access institutional data respository, ZivaHub (a figshare platform), where it will

26   be publicly available.

27 **<u>Abstract</u>**

28 Increasingly harsh and unpredictable climate regimes are affecting animal populations around

29 the world as climate change advances. One relatively unexplored aspect of species vulnerability

30 to climate change is whether and to what extent responses to environmental stressors might be

31 mitigated by variation in group size in social species. We used a 15-year dataset for a

32 cooperatively-breeding bird, the southern pied babbler *Turdoides bicolor*, to determine the

33 impact of temperature, rainfall, and group size on body mass change and interannual survival in

34 both juveniles and adults. Hot and dry conditions were associated with reduced juvenile growth,

35 mass loss in adults, and compromised survival between years in both juveniles (-86%) and adults

36 (-60%). Individuals across all group sizes experienced similar effects of climatic conditions.

37 Larger group sizes may not buffer individual group members against the impacts of hot and dry

38 conditions, which are expected to increase in frequency and severity in future.

39 **<u>Introduction</u>**

40 Anthropogenic climate change is affecting population dynamics across taxa (du Plessis *et al.*

41 2012; Allen *et al.* 2015; Rey *et al.* 2017; Spooner *et al.* 2018). Understanding life history

42 responses to current environmental conditions is increasingly important for predicting

43 vulnerability to future climate change (Camacho *et al.* 2018; Conradie *et al.* 2019). Species

44 living in arid and semi-arid environments are useful models for studying such responses, because

45 these environments are characterised by extremes in temperature and rainfall (McKechnie *et al.*

46 2012), and are experiencing rapid increases in temperature and interannual rainfall variability as

47 a result of anthropogenic climate change (Feng & Fu 2013; Mayaud *et al.* 2017). Despite

48 evidence that arid-zone species are well adapted to harsh and unpredictable environments

49 (McKechnie *et al.* 2016; O'Connor *et al.* 2017), increasing temperatures and decreasing rainfall

50 measurably affect behaviour, body condition, growth, and survival in arid-zone birds

51 (McKechnie & Wolf 2010; Cunningham *et al.* 2013; Sunday *et al.* 2014; Iknayan & Beissinger

52 2018). While droughts are a natural feature of arid and semi-arid ecosystems (MacKellar *et al.*

53 2014; Tokura *et al.* 2018), an increase in the frequency of 'hot droughts' – when above-average

54 temperatures and below-average rainfall co-occur (Overpeck 2013) – is likely (New *et al.* 2006;

55 Kruger & Sekele 2013), with the potential to compromise population persistence in many

56 wildlife species (Walther *et al.* 2002; Sinervo *et al.* 2010; Cruz-McDonnell & Wolf 2016; Paniw

57 *et al.* 2019).

58   Life-history traits with the potential to mitigate the impacts of high temperatures and

59 drought are of significant interest. Global comparative studies show that the distribution of

60 cooperatively-breeding (Rubenstein & Lovette 2007; Jetz & Rubenstein 2011; Lukas & Clutton-

61 Brock 2017; Shen *et al.* 2017) and group-living (Griesser *et al.* 2017) birds and mammals is

62   associated with harsh and highly variable environments, suggesting that the presence of helpers

63   buffers against environmental uncertainty (Jetz & Rubenstein 2011; Russell 2016; Cornwallis *et*

64   *al.* 2017), at least up to an optimal number (Markham *et al.* 2015; Ridley 2016). It has been

65   hypothesised that cooperative breeding either evolved in such enviroments (Rubenstein &

66   Lovette 2007; Lukas & Clutton-Brock 2017), enabled species to colonise such environments

67   (Cornwallis *et al.* 2017), or prevented extinction under increasingly harsh conditions (Russell

68   2016; Griesser *et al.* 2017). One prominent explanation for the occurrence of cooperative

69   breeding in birds is that it represents a 'bet-hedging' strategy (Rubenstein 2011): breeding

70   individuals share the costs of reproduction with helpers, enabling them to breed successfully

71   even when conditions are poor (Rubenstein & Lovette 2007). Cooperation may therefore

72   moderate impacts of climate change via task-partitioning (Clutton-Brock *et al.* 2004; Ridley &

73   Raihani 2008), improved access to resources (Golabek *et al.* 2012; Ebensperger *et al.* 2016), or

74   load-lightening (reductions in individual workload in response to the presence of helpers; Crick

75   1992; Hatchwell 1999; Meade *et al.* 2010; Mumme *et al.* 2015; Langmore *et al.* 2016).

76   A small number of recent studies empirically test the reproductive benefits of cooperation

77   across varying environmental conditions (Langmore *et al.* 2016; Guindre□Parker & Rubenstein

78   2018; van de Ven *et al.* 2020), and one further considers adult survival (Guindre□Parker &

79   Rubenstein 2020). These empirical tests primarily consider reproduction and survival in response

80   to variation in rainfall. Temperature is rarely included despite the fact that thermoregulatory

81   benefits of group living have been demonstrated (Paquet *et al.* 2016). Behavioural

82   thermoregulation (investing time and energy in self-maintenance, including seeking shade or

83   increasing rest) provides a potential mechanism through which load-lightening may buffer group

84   members against the costs of climate variation. Individuals in larger groups may be able to

85   allocate more time to self-maintenance and therefore suffer fewer consequences of trade-offs

86   between self-maintenance and other essential activities during adverse weather. This may allow

87   higher reproductive success under challenging environmental conditions, and also better mass

88   maintenance and improved survival probabilities.

89   Long-term monitoring of a population of *Turdoides bicolor* (southern pied babblers,

90   hereafter 'pied babblers') provides an opportunity to empirically test the impact of environmental

91   conditions on body mass change (ΔM_b) and survival between groups of different sizes in a

92   cooperatively breeding species (Ridley 2016). Larger mass is likely to be beneficial in pied

93   babblers because heavier individuals disperse more successfully into breeding positions (Ridley

94   *et al.* 2008). Mass loss occurs when pied babblers provision young (Wiley & Ridley 2016),

95   defend contested territories (Humphries 2013), are evicted from their groups (Ridley *et al.* 2008),

96   or experience high temperatures (du Plessis *et al.* 2012). High temperature extremes have

97   increased in frequency and severity at the study site over the last two decades (van de Ven 2017)

98   and rainfall is extremely variable from year to year (MacKellar *et al.* 2014). In pied babblers,

99   high temperatures and/or drought increase the risk of local extinction (Wiley 2017), reduce

100   offspring provisioning rates (resulting in smaller nestlings; Wiley & Ridley 2016), limit foraging

101   efficiency (du Plessis *et al.* 2012), lower daily energy expenditure (Bourne *et al.* 2019), and

102   decrease investment in territorial defence (Golabek *et al.* 2012).

103   Here, we examine how within-season ΔM_b and interannual survival in pied babblers

104   varies with temperature, rainfall, and group size. We expected negative effects of high

105   temperatures, and positive effects of high rainfall and larger group sizes, on 1) ΔM_b in juveniles

106   and in breeding adults, 2) survival of juvenile birds from nutritional independence at 90 days of

107   age to recruitment into the adult population at one year of age, and 3) survival of breeding adults

108   from one breeding season to the next. Analyses do not include subordinate adults because

109   subordinate adults (both sexes) often disperse (Ridley *et al.* 2008; Raihani *et al.* 2010) and

110   dispersal is easily confounded with mortality (Layton-Matthews, Ozgul, & Griesser, 2018). We

111   further predicted that larger group sizes would buffer against climatic effects due to load-

112   lightening allowing individuals to invest more in self-directed behaviours during periods of harsh

113   weather. Specifically, we predicted that individuals in larger groups would experience

114   disproportionately fewer negative effects of high temperatures and drought on both ΔM_b and

115   survival.

Materials and methods

Study site and system

118   Pied babblers are medium-sized (60–90 g), cooperatively-breeding passerines endemic to

119   the Kalahari Desert in southern Africa (Hockey *et al.* 2005). Fieldwork was undertaken at the 33

120   km^2 Kuruman River Reserve (KRR; 26°58'S, 21°49'E). Mean summer daily maximum

121   temperature in the region averages 34.7 ± 9.7°C, and mean annual precipitation averages 186.2 ±

122   87.5mm (1995–2015, van de Ven, McKechnie & Cunningham 2019). Rainfall has been

123   declining and high temperature extremes increasing in both frequency and severity over the last

124   20 years (Kruger & Sekele 2013; van Wilgen *et al.* 2016; van de Ven 2017).

125   Pied babbler group sizes range between 3–15 adults (Ridley 2016). Groups consist of a

126   single breeding pair, one or more subordinate adult helpers, and immature offspring (Nelson-

127   Flower *et al.* 2011). All adult group members cooperate, participating in territorial defence,

128   sentinel behaviour, and caring for young (Ridley 2016). Pied babblers are considered

129   nutritionally independent (receiving < 1 feed per hour; referred to as 'juveniles') by 90 days of

130   age (Ridley & Raihani 2007), and are defined as sexually mature adults one year after hatching

131   (Ridley 2016).

132   Birds in the study population are habituated to observation at distances of 1–5 m (Ridley

133   & Raihani 2007). Group composition and life history checks are conducted weekly with

134   habituated groups throughout each summer breeding season (September to March). Groups are

135   territorial and can be reliably located by visits to each territory. Birds in the study population are

136   marked with a unique combination of metal and colour rings for individual identification.

137   **Data collection**

138   Data were collected for each breeding season between September 2005 and 2019. Pied

139   babblers are sexually monomorphic (Ridley 2016; Bourne *et al.* 2018) and molecular sexing was

140   used to determine sex of individuals (following Fridolfsson & Ellegren, 1999). Blood samples

141   for sexing were collected by brachial venipuncture.

142   *Body mass measurements*

143   Nestlings were weighed to 0.1 g on a top-pan scale 11 days post-hatching ($Mass_{11}$). Body

144   mass data were collected from 90 ($\pm$ 15) day-old birds ($Mass_{90}$; $n = 323$ mass measurements

145   from 124 individuals) by enticing individuals to stand on a top-pan balance in exchange for a

146   small food reward (Ridley 2016). Most measurements (74%) were collected within 7 days of the

147   90 day mark. Mean mass was calcultated where multiple measurements per individual were

148   available (52% of juveniles). The sampling period is justified because pied babblers are

149   approximately fully-grown by 90 days of age (Raihani & Ridley 2007; Thompson et al. 2013;

150   Ridley 2016). This was confirmed by data from 16 individuals from whom we collected ≥ 5

151   mass measurements between 75 and 105 days of age [1 (6%) maintained mass over the period, 7

152   (44%) lost mass, and 8 (50%) gained mass, with an average change in mass between earliest and

153   latest measurement of ~1 g].

154   Body mass data were collected from adult breeding birds from the beginning (September

155   or October, $Mass_{Oct}$) and end (February or March, $Mass_{Mar}$) of each breeding season in the same

156   way as for juveniles. Variation in exact sampling periods for each mass measure reflect annual

157   variation in the timing of the breeding season. We chose the difference between $Mass_{Oct}$ and

158    $Mass_{Mar}$ as a biologically relevant measure because this time period encompasses a) the hottest

159   months at the study site (December, average $T_{max} = 35.71°C$; and January, average $T_{max} =$

160    $35.69°C$), b) the wettest months at the study site (72% of annual rain falls December-February),

161   and c) the core breeding season (68% of breeding occurs October-December). We collected

162   multiple $Mass_{Oct}$ and $Mass_{Mar}$ measurements for 63% and 52% of the birds respectively, and used

163   the average of all mass measurements per individual where available.

164   All body mass measurements from juveniles and adults were collected at dawn,

165   representing pre-foraging body mass. Body mass change (ΔM_b) was calculated in grams as

166   follows: ΔM_b between 11 days and 90 days of age for juveniles ($\Delta M_{b.Juv}$) = $Mass_{90}$ - $Mass_{11}$; and

167   ΔM_b from the start to the end of the breeding season for breeding adults ($\Delta M_{b.Adults}$) = $Mass_{Mar}$ -

168    $Mass_{Oct}$.

169   *Life history data*

170   *(i) Juvenile birds*

171   All nests initiated in the study population during each breeding season were monitored to

172   determine hatching dates. Each brood was checked daily from 14 days post-hatching onwards, to

173   determine the date on which nestlings fledged. Natal group size ($G.Size_{Brood}$; the number of

174   adults present in each individual's natal group between hatching and fledging; constant during

175   the chick rearing period for all but five of 147 nests), average group size for the period between

176   fledging and independence ($G.Size_{90}$; variations in group size due to older juveniles reaching 1

177   year of age, or dispersal of subordinate adults, were observed in 58 of 147 breeding attempts),

178   and brood size (number of nestlings in the brood 11 days post-hatch) were recorded for each

179   brood. Presence/absence of fledglings was noted during weekly visits within each breeding

180   season and presence/absence of juvenile pied babblers was recorded at one year (±15 days) post

181   hatching. Presence/absence in the population at one year of age represents a 'disappearance rate'

182   likely to be driven primarily by mortality. Dispersal typically occurs after individuals have

183   reached sexual maturity and the mean age at first dispersal is 565 days (Nelson-Flower *et al.*

184   2018). Individuals that dispersed before one year of age ($n = 1$) were excluded from the analysis.

185   *(ii) Adult breeding birds*

186   Dominant individuals can be identified unambiguously through incubation behaviour

187   (Ridley 2016) and distinctive duets (Wiley & Ridley 2018). Presence/absence of dominant

188   individuals was recorded at the beginning of each breeding season during an annual census, at

189   which point we could determine whether breeding adults had survived over the most recent

190   winter putting them in the position to breed again. For breeding adults, territory and pair fidelity

191   is high between years and voluntary dispersal is unusual (Raihani *et al.* 2010; Wiley & Ridley

192   2018). Overwinter disappearance is therefore likely to be driven primarily by mortality. Data for

193   individuals who were dominant for only part of a breeding season due to death ($n = 47$) or

194   dispersal ($n = 9$) were excluded from analyses of interannual survival. We calculated average

195   group size during each breeding season ($G.Size_{BrSeas}$; variations in group size were observed in

196   62 of 177 group-seasons).

197   *Temperature and rainfall*

198   Daily maximum temperature (°C) and rainfall (mm) data were collected from an on-site

199   weather station (Vantage Pro2, Davis Instruments, Hayward, USA; see van de Ven, McKechnie,

200   & Cunningham, 2019). Missing data from 2009, 2010, and 2011 were sourced from a nearby

201   South Africa Weather Services (SAWS) weather station (Van Zylsrus, 28 km), which recorded

202   significantly repeatable temperature measurements (Lin's concordance correlation coefficient r_c

203    $= 0.957$, 95 % CI: 0.951–0.962), and moderately repeatable rainfall measurements ($r_c = 0.517$, 95

204   % CI: 0.465–0.566) in comparison with the on-site weather station. Differences in rainfall were

205   small (average difference $= 0.045 \pm 3.075$ mm, 95 % CI $= -5.981$–6.072 mm), suggesting that

206   both weather stations adequately detected wet vs. dry periods.

207   For analyses relating to juveniles, daily maximum temperatures were averaged for the

208   offspring developmental periods between hatching and fledging (mean $T_{maxBrood}$) and between

209   fledging and independence (mean T_{max90}). Rainfall was summed for the 60 days prior to initiation

210   of incubation at the nest from which each individual fledged ($Rain_{60}$; to allow for delays between

211   rainfall and invertebrate emergence; Cumming & Bernard, 1997; Ridley & Child, 2009) and for

212   the period between fledging and independence ($Rain_{90}$). For analyses relating to adults, daily

213   maximum temperatures were averaged, and rainfall was summed, over the whole breeding

214   season (Sept – Mar, Mean $T_{maxBrSeas}$; $Rain_{BrSeas}$). Long term rainfall data for the region was used

215   to determine the presence or absence of a meteorological drought within a breeding season

216   ($Drought_{BrSeas}$). These data were obtained from a SAWS weather station at Twee Rivieren (~120

217   km from the study site; available until 2013). Following Mayaud et al (2017), meteorological

218   drought was defined as $\leq 75\%$ of average precipitation between September and March (≤ 137.75

219   mm), using long term data for the 30-year period 1984–2013 to determine average precipitation

220   in the region.

Box 1: Glossary of terms

Brood size	Number of nestlings per brood
$G.Size_{Brood}$	Number of adults in the natal group at initiation of incubation
$G.Size_{90}$	Average number of adults in the natal group between fledge and nutritional independence at 90 days of age
$G.Size_{BrSeas}$	Average number of adults in the natal group over the breeding season
$Mass_{11}$	Nestling body mass (0.1 g) collected 11 days after hatching
$Mass_{90}$	(Average) body mass data (0.1 g) collected from 90 ($\pm$ 15) day-old birds
$\Delta M_{b.Juv}$	Change in juvenile body mass (g), calculated as $Mass_{90}$ - $Mass_{11}$
$Mass_{Oct}$	(Average) body mass data (0.1 g) collected from adults at the beginning of the breeding season (September and October)
$Mass_{Mar}$	(Average) body data (0.1 g) collected from adults at the end of the breeding season (February and March)
$\Delta M_{b.Adults}$	Change in adult body mass (g), calculated as $Mass_{Mar}$ - $Mass_{Oct}$
Mean $T_{maxBrood}$	Average daily maximum temperatures between hatching and fledging
Mean T_{max90}	Average daily maximum temperatures between fledging and nutritional independence at 90 days of age
Mean $T_{maxBrSeas}$	Average daily maximum temperatures between the start (September) and the end (March) of the breeding season
$Rain_{60}$	Total rainfall in the 60 days prior to initiation of incubation at the nest from which each individual fledged
$Rain_{90}$	Total rainfall between fledging and nutritional independence at 90 days of age
$Rain_{BrSeas}$	Total rainfall between the start (September) and the end (March) of the breeding season
$Drought_{BrSeas}$	Occurrence of a meteorological drought (rainfall < 135.75 mm) within the breeding season

Caption: The grey boxes below show the breeding seasons within which data were collected. All the climate-related predictor variables were collected during Breeding Season$_{(t)}$ and used in models testing variation in body mass change within the same Breeding Season$_{(t)}$ and interannual survival into the following Breeding Season$_{(t+1)}$.

Statistical analyses

221
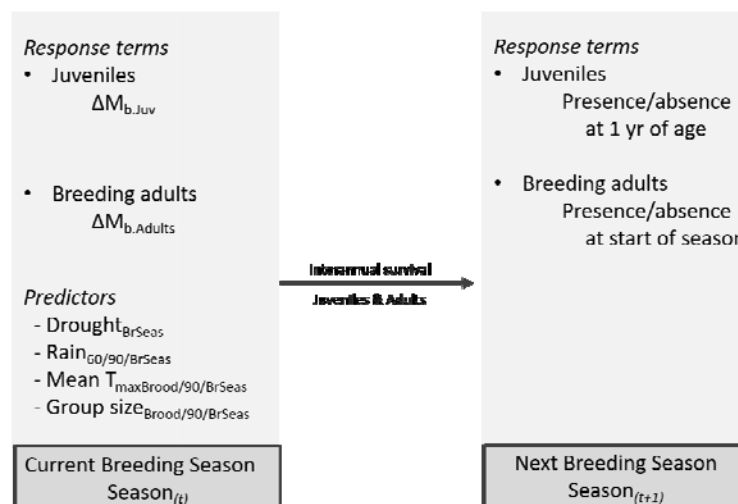
222   Statistical analyses were conducted in R v 3.4.1 (R Core Team 2017). Mixed effects

223 models, using the package *lme4* (Bates *et al.* 2015), were used for all analyses, see Box 1. Model

224 selection with Akaike's information criterion corrected for small sample size (AICc) was used to

225 explore a series of models to determine which parameters best explained patterns of variation in

226 the data (Symonds & Moussalli 2011; Harrison *et al.* 2018). Where multiple models were within

227 5 AICc of the top model, top model sets were averaged using the package *MuMin* (Barton 2015)

228 and we present parameter estimates for interpretation after model averaging (Burnham &

229 Anderson 2002; Grueber *et al.* 2011). All continuous explanatory variables were scaled by

230 centering and standardising by the mean (Schielzeth 2010; Harrison *et al.* 2018). All explanatory

231 variables were tested for correlation with one another (all VIF < 2 for pairs of continuous

232 predictors, Fox & Monette 1992). Rainfall measures were always highly correlated with drought

233 ($F_{1,247\text{-}350} > 37.611$, $p < 0.001$), and therefore rainfall and drought were not included in the same

234 additive models (Harrison *et al.* 2018). Linear model fits were checked using normal Q-Q plots

235 and histograms of residuals. Binomial model fits were checked for overdispersion in the

236 *RVAideMemoire* package (Herve 2019) and for zero-inflation in the *DHARMa* package (Hartig

237 2020). Model terms with confidence intervals not intersecting zero were considered to explain

238 significant patterns in the data (Grueber, Nakagawa, Laws, & Jamieson, 2011). Sample sizes

239 reflect datasets after removing records containing missing values. Unless otherwise indicated,

240 summary statistics are presented as mean ± one standard deviation.

241   Interactions between group size and climatic effects on ΔM_b and survival would be

242 consistent with a buffering effect of group size. We conducted sensitivity power analyses to

243 identify the minimum determinable effect of two-way interactions given our sample sizes (Cohen

244   1988; Greenland *et al.* 2016). Assuming a fourfold increase in required sample size to adequately

245   detect interactions in mixed-effects linear regression models (Leon & Heo 2009), we confirmed

246   sufficient sample size to detect 1) small to moderate main effects in all analyses (Cohen's $f^2 \leq$

247   0.12 in all cases), 2) moderate to very large effects of two-way interactions in ΔM_b analyses ($f^2 =$

248   0.28 for fledglings, $f^2 = 0.54$ for adults), and 3) small to moderate effects of two-way interactions

249   in interannual survival analyses ($f^2 \leq 0.14$ for juveniles, $f^2 = 0.09$ for breeding adults).

250   Where interannual survival probabilities for juveniles and breeding adults were

251   influenced by interactions, we used the package *lsmeans* (Lenth 2016) to predict survival

252   probabilities based on different values of the interacting factors.

253   *Body mass change:* To determine which variables explained $\Delta M_{b.Juv}$ and $\Delta M_{b.Adults}$, we used

254   maximum likelihood linear mixed-effects models (LMMs). For $\Delta M_{b.Juv}$ ($n = 124$), we considered

255   the influence of G.Size$_{90}$, Drought$_{BrSeas}$, Rain$_{60}$, Rain$_{90}$, mean T$_{max90}$, sex, brood size, and the

256   interactions among climate variables and group size. Brood identity nested within group identity

257   were included as random terms to account for repeated measures. For $\Delta M_{b.Adults}$ ($n = 82$

258   measurements from 53 different individuals), we considered the influence G.Size$_{BrSeas}$,

259   Drought$_{BrSeas}$, Rain$_{BrSeas}$, mean T$_{maxBrSeas}$, age (in days since hatching), sex, and the interactions

260   among climate variables and group size. Individual identity nested within group identity were

261   included as random terms.

262   *Survival:* Non-monitoring periods over winter prevented detailed time-step survival analyses,

263   such as Cox proportional hazards models (Cox 1972; Austin 2017; Guindre☐Parker &

264   Rubenstein 2020), for both juveniles and adults. Therefore, to determine which variables

265   explained interannual survival of known individuals in the study population, we used generalised

266   linear mixed-effects models (GLMMs) with a binomial distribution (survival to next breeding

267   season = yes/no) and a logit link function.

268   *Juveniles:* For juvenile birds, interannual survival was measured as survival from

269   nutritional independence to one year of age ($\pm$ 15 days; recorded in the following

270   breeding season – see Box 1). The factors that influence pied babbler survival

271   probabilities are not constant across time during early development (Bourne *et al.* n.d.;

272   Ridley 2016), and conditions experienced in the nest can carry over to influence survival

273   probabilities later (Harrison *et al.* 2011; Auer & Martin 2017; Moore & Martin 2019).

274   We therefore conducted separate analyses specifically considering climate and social

275   factors experienced in the nest and after fledging. For survival to one year, we considered

276   the influence of (a) $G.Size_{Brood}$, $Rain_{60}$, $Drought_{BrSeas}$, mean $T_{maxBrood}$, sex, $Mass_{11}$, brood

277   size, and the two way interactions amongst all group size and climate variables (i.e

278   conditions between hatching and fledging; $n = 247$ individuals); and (b) $G.Size_{90}$, $Rain_{90}$,

279        $Drought_{BrSeas}$, mean T_{max90}, sex, $Mass_{11}$, brood size, and the two way interactions among

280   all group size and climate variables (i.e. conditions between fledging and nutritional

281   independence; $n = 229$ individuals). Brood identity nested within natal group identity

282   were included as random terms in both analyses.

283   *Breeding adults:* For breeding adults, interannual survival was measured from the end of

284   a breeding season in which they attempted to breed to the beginning of the subsequent

285   breeding season (see Box 1). For interannual survival ($n = 352$ records from 136

286   different adults), we considered the influence of $G.Size_{BrSeas}$, $Drought_{BrSeas}$, $Rain_{BrSeas}$,

287   Mean $T_{maxBrSeas}$, age, sex, and the two way interactions among all group size and climate

288   variables. Individual identity nested within group identity were included as random

289   terms.

290   We tested for the influence of ΔM_b on interannual survival probabilities for both age

291   classes separately, using univariate binomial GLMMs with a logit link function, due to much

292   smaller sample sizes for body mass than for presence/absence data.

293   **<u>Results</u>**

294   Annual average summer maximum temperature at the study site from 2005–2019 was

295   34.2 ± 0.9 °C (range: 32.4–36.5 °C), summer rainfall averaged 185.4 ± 86.2 mm (range: 64.4–

296   352.1 mm), and droughts occurred in 5 of 14 breeding seasons studied (Fig. 1A). Group size

297   varied between groups and breeding seasons, averaging 4.2 ± 1.4 adults per group across all

298   breeding seasons (range: 2–9 adults; Fig. 1B), but did not differ significantly between drought

299   and not-drought years ($F_{1,164} = 0.754$, $p = 0.387$). Between 2005 and 2019, the largest group

300   averaged 5.4 ± 2.3 adult group members (range across 11 breeding seasons: 2.3–9), while the

301   smallest group averaged 3.3 ± 0.9 members (range across 12 breeding seasons: 2–5).

302   *Change in body mass*

303   Fledglings that survived to 90 days were heavier as nestlings (mean $Mass_{11} = 40.0 ± 5.5$

304   g, $n = 270$) than those that did not survive (37.4 ± 7.3 g, $n = 295$; LMM with brood identity as

305   the random term: Est = 2.403 ± 0.526, $t = 4.566$, *95% CI* 1.371, 3.437). Individuals gained

306   significantly more mass between fledging and independence during wetter periods, and when

307   they were raised in larger broods (Table 1A, Fig. 2A, Fig. 2B). $\Delta M_{b.Juv}$ did not vary significantly

308   with sex, group size or temperature between fledging and independence, nor did we find

309   evidence of significant interactions among climate and group size variables (Table S1).

310   High temperatures and low rainfall during the breeding season were associated with body

311   mass loss between the start and the end of the breeding season in breeding adults (Table 1B; Fig.

312   2C, Fig. 2D). $\Delta M_{b.Adults}$ did not vary significantly with sex or group size, after model averaging,

313   and nor did we find evidence of significant interactions among climate and group size variables

314   (Table S2). Age was not associated with variation in $\Delta M_{b.Adults}$ in a subset of 36 individuals of

315   known age (Table S3) and we therefore excluded age from the models analysing our full dataset

316   presented here.

317   *Survival: juveniles*

318   Of 596 nestlings of known $Mass_{11}$, 254 (42.6%) survived to nutritional independence. Of

319   these, 173 (68.1%) were present in the study population one year post-hatching. Natal group size

320   ranged from 2–9 adults (mean = 4.4 ± 1.5). The likelihood of a juvenile surviving to one year of

321   age increased as $Rain_{60}$ increased (Table 1C, Fig. 3A). However, juveniles that experienced high

322   mean $T_{maxBrood}$ were less likely to survive to one year of age (Table 1C, Fig. 3B; see Table S4 for

323   full model selection output).

324   Juveniles were also less likely to survive to one year of age when they were exposed to

325   high mean T_{max90} and $Drought_{BrSeas}$. The effect of $Drought_{BrSeas}$ on juvenile survival to one year

326   of age was influenced by temperature: mean probability of survival was high (0.90 ± 0.05) when

327   juvenile birds experienced both $Drought_{BrSeas}$ and relatively cool mean T_{max90}, whereas mean

328   probability of survival was very low (0.12 ± 0.08) when juvenile birds experienced both

329    $Drought_{BrSeas}$ and high mean T_{max90} (Table 1D, Fig. 3C). This represents a more than seven-fold

330   decrease in survival when individuals experienced both drought and high temperatures as

331   dependent fledglings, compared to when drought occurred but temperatures were mild. Survival

332   to one year of age did not vary significantly with $Mass_{11}$, sex, brood size, or group size in either

333   analysis. Survival to one year of age was also not significantly influenced by interactions

334   between group size and environmental conditions (see Tables S4–S5 for full model selection

335   output). Survival to one year of age was not associated with $\Delta M_{b.Juv}$ (GLMM: Est = 0.041 $\pm$

336   0.037, z = 1.106, 95% CI: -0.039, 0.081).

337   *Survival: breeding adults*

338   In 264 out of 352 records of interannual survival (75%; from 136 different individuals),

339   breeding adults were still present at the start of the next breeding season. Breeding adults were

340   less likely to be present at the start of the next breeding season when they had experienced

341   Drought$_{BrSeas}$ (Table 1E). The effect of Drought$_{BrSeas}$ on the survival of breeding adults was

342   influenced by temperature: mean probability of survival was high (0.81 $\pm$ 0.06) when individuals

343   had experienced Drought$_{BrSeas}$ alongside relatively cool mean T$_{maxBrSeas}$. However, mean

344   probability of survival was low (0.32 $\pm$ 0.09; Table 1E, Fig. 4) when individuals experienced

345   both drought conditions alongside high mean T$_{maxBrSeas}$, representing a more than 50% decrease

346   in survival of breeding adults from one year to the next compared to when drought occurred but

347   temperatures were mild. Interannual survival of breeding adults did not vary significantly with

348   sex or group size, nor did we find evidence of significant interactions among climate and group

349   size variables (see Table S6 for full model selection output). Age was not associated with

350   variation in survival in a subset of 58 individuals of known age (Table S7) and we therefore

351   excluded age from the models analysing our full dataset presented here. The probability of

352   breeding adults surviving to the start of the next breeding season was not associated with

353    $\Delta M_{b.Adults}$ (GLMM, Est = 0.031 $\pm$ 0.071, z = 0.436, 95% CI: -0.111, 0.171).

Discussion

354

355   We investigated the potential for group size to buffer against the impacts of climatic

356   factors on ΔM_b and interannual survival in a cooperatively breeding bird. We found that

357   measures of ΔM_b and survival for individuals in larger groups were not affected differently by

358   high temperatures and drought compared to those in smaller groups. Environmental conditions

359   significantly affected ΔM_b and interannual survival in both juveniles and breeding adults across

360   all group sizes, a finding that contributes to a rapidly growing body of literature (Overpeck 2013;

361   Allen *et al.* 2015; Cruz-McDonnell & Wolf 2016) demonstrating that high temperatures and

362   prolonged periods of low rainfall negatively impact on survival in a range of species.

363   Exposure to high temperatures and low rainfall was strongly associated with reduced

364   growth in juvenile pied babblers and body mass loss in breeding adults. Body mass performs

365   well as an index of condition (Labocha & Hayes 2012), particularly when change *within*

366   individuals is measured over time, and poor body condition has been linked to reduced survival

367   in both adult birds (e.g. Gardner *et al.* 2018) and nestlings (e.g. Todd *et al.* 2003; Schwagmeyer

368   & Mock 2008). In our study population, in a simple univariate assessment, the within-individual

369   ΔM_b we recorded did not appear to be significantly associated with interannual survival in either

370   juvenile or breeding adult pied babblers, at least over our measurement windows, suggesting that

371   reduced survival is not a consequence of body mass loss/reduced growth.

372   In pied babblers, exposure to chronic, sublethal effects of high temperatures and low

373   rainfall within the same breeding season are associated with increased risk of overwinter

374   mortality. Hot and dry conditions experienced by juvenile pied babblers between fledging and

375   independence were associated with lower probability of survival to one year of age. Lower

376   survival probabilities result in reduced recruitment into the adult population. Hot and dry

377   conditions were also associated with strongly reduced likelihood of interannual survival in

378   breeding adults. Together these processes likely contribute to the overall trend for population

379   decline in below-average rainfall years in this species (Wiley 2017). Negative effects of adverse

380   climate conditions on the interannual survival of breeding adults are particularly concerning

381   because interannual survival rates of breeding adults (compared to non-breeding adult helpers)

382   have the greatest impact on population growth rates in this species (Wiley 2017), and hence the

383   probability of population persistence through time (Layton-Matthews *et al.* 2018).

384   Droughts are currently a regular, natural feature of the local climate (Tokura *et al.* 2018).

385   Temperatures in the region have increased in recent decades (van Wilgen *et al.* 2016) and will

386   continue to do so (IPCC 2013), and therefore an increase in the frequency of hot droughts can be

387   expected. If this occurs, pied babbler populations are likely to decline as altered drought regimes

388   reduce opportunities for population recovery following hot drought events. Consecutive years

389   characterised by exceptionally hot and dry conditions could lead to failed recruitment and

390   population crashes, as has been observed in *Athene cunicularia* burrowing owls (Cruz-

391   McDonnell & Wolf 2016) and is predicted for pied babblers (Wiley 2017; Conradie *et al.* 2019).

392   Group size did not buffer the impacts of hot, dry weather on individual body mass

393   change or survival in juveniles or breeding adults, since birds across all group sizes were

394   similarly affected. This is consistent with the findings of two concurrent studies on a

395   cooperatively-breeding mammal (van de Ven *et al.* 2019a) and a cooperatively breeding bird

396   (Guindre-Parker & Rubenstein 2020). Adverse effects of climatic conditions on ΔM_b and

397   survival are therefore likely driven primarily by physiological tolerance limits (Smit *et al.* 2018)

398   and resource constraints (Nowakowski *et al.* 2018) acting on individuals, irrespective of the

399   number of individuals present in their social group. Benefits of group living and cooperation,

400   including load-lightening and the production of more surviving young by larger groups, have

401   been observed in pied babblers previously (Ridley 2016; Wiley & Ridley 2016; Bourne *et al.*

402   2020). Yet we show here that larger group sizes did not moderate the influence of high

403   temperatures and drought on body mass change or survival. While it is possible that the benefits

404   of larger group sizes and the presence of helpers may have previously helped to mitigate the

405   effects of adverse environmental conditions (Jetz & Rubenstein 2011; Russell 2016; Cornwallis

406   *et al.* 2017), it appears that any such advantage is no longer detectible given current extreme

407   conditions and a rapidly changing climate. Buffering effects of group size may be detectable in

408   reproductive outputs rather than measures of mass change and survival, although see Bourne et

409   al. (n.d.) which suggests that this is not the case in pied babblers.

410   The Intergovernmental Panel on Climate Change predicts that the incidence of hot and

411   dry extremes will continue to become more frequent over most land masses (IPCC 2013). In arid

412   and semi-arid regions already affected by both decreased precipitation and increased warming,

413   interannual survival and recruitment in resident avian species (such as this population of pied

414   babblers) may be insufficient to allow for population recovery between hot droughts. Taken

415   together with our finding that larger group sizes did not buffer pied babblers against adverse

416   climatic conditions, our data raise concerns for the long-term persistence of arid-zone species in

417   the face of changing climatic conditions. The adaptive benefits of cooperative life history

418   strategies in highly variable environments are unlikely to be sufficient to counteract the impacts

419   of rapidly changing climatic conditions, in particular the increased frequency of climate extremes

420   such as heat waves and drought.

Acknowledgements

References

439   Allen, C.D., Breshears, D.D. & McDowell, N.G. (2015). On underestimation of global

440   vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene.

441   *Ecosphere*, 6, 1–55.

442   Auer, S.K. & Martin, T.E. (2017). Parental care mitigates carry-over effects of poor early

443   conditions on offspring growth. *Behav. Ecol.*, 28, 1176–1182.

444   Austin, P.C. (2017). A tutorial on multilevel survival analysis: methods, models and applications.

445   *Int. Stat. Rev.*, 85, 185–203.

446   Barton, K. (2015). *MuMIn: Multi-model inference*. Available at: https://cran.r-

447   project.org/package=MuMin. Last accessed 1 June 2020.

448   Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed effects models

449   using lme4. *J. Stat. Softw.*, 67, 1–48.

450   Bourne, A.R., Cunningham, S.J., Nupen, L.J., McKechnie, A.E. & Ridley, A.R. (2018). *Male*

451   *and female Southern Pied Babbler* Turdoides bicolor *nestlings respond similarly to heat*

452   *stress*. Available at: https://www.bou.org.uk/wp-content/uploads/2019/08/bou-funded-

453   project-report-bourne.pdf. Last accessed 1 June 2020.

454   Bourne, A.R., Cunningham, S.J., Spottiswoode, C.N. & Ridley, A.R. (2020). Compensatory

455   breeding in years following drought in a desert-dwelling cooperative breeder. *Front. Ecol.*

456   *Evol. DOI: 10.3389/fevo.2020.00190*

457   Bourne, A.R., Cunningham, S.J., Spottiswoode, C.N. & Ridley, A.R. (under review). High

458   temperatures drive offspring mortality in a cooperatively breeding bird. *Proc. R. Soc.*

459   *London Biol. Sci.*

460   Bourne, A.R., McKechnie, A.E., Cunningham, S.J., Ridley, A.R., Woodborne, S.M. & Karasov,

461   W.H. (2019). Non☐invasive measurement of metabolic rates in wild, free☐living birds

462   using doubly labelled water. *Funct. Ecol.*, 33, 162–174.

463   Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical*

464   *information-theoretic approach*. Springer Verlag, New York.

465   Camacho, A., Rusch, T., Ray, G., Telemeco, R.S., Rodrigues, M.T. & Angilletta, M.J. (2018).

466   Measuring behavioral thermal tolerance to address hot topics in ecology, evolution, and

467   conservation. *J. Therm. Biol.*, 73, 71–79.

468   Clutton-Brock, T.H., Russell, A.F. & Sharpe, L.L. (2004). Behavioural tactics of breeders in

469   cooperative meerkats. *Anim. Behav.*, 68, 1029–1040.

470   Cohen, J. (1988). *Statistical power analysis for the behavioral sciences*. 2nd Editio. Lawrence

471   Erlbam Associates, New York.

472   Conradie, S., Woodborne, S.M., Cunningham, S.J. & McKechnie, A.E. (2019). Chronic,

473   sublethal effects of high temperatures will cause severe declines in southern African arid-

474   zone birds during the 21st century. *Proc. Natl. Acad. Sci.*, 116, 14065–14070.

475   Cornwallis, C.K., Botero, C.A., Rubenstein, D.R., Downing, P.A., West, S.A. & Griffin, A.S.

476   (2017). Cooperation facilitates the colonization of harsh environments. *Nat. Ecol. Evol.*, 1,

477   0057.

478   Cox, D.R. (1972). Regression models and life-tables. *J. R. Stat. Soc.*, 34, 187–220.

479   Crick, H.P. (1992). Load-lightening in cooperatively breeding birds and the cost of reproduction.

480   *Ibis (Lond. 1859).*, 1, 56–61.

481   Cruz-McDonnell, K.K. & Wolf, B.O. (2016). Rapid warming and drought negatively impact

482   population size and reproductive dynamics of an avian predator in the arid southwest. *Glob.*

483   *Chang. Biol.*, 22, 237–253.

484   Cumming, G.S. & Bernard, R.T.F. (1997). Rainfall, food abundance and timing of parturition in

485   African bats. *Oecologia*, 111, 309–317.

486   Cunningham, S.J., Martin, R.O., Hojem, C.L. & Hockey, P.A.R. (2013). Temperatures in excess

487   of critical thresholds threaten nestling growth and survival in a rapidly-warming arid

488   savanna: a study of common fiscals. *PLoS One*, 8, e74613.

489   Ebensperger, L.A., Correa, L.A., León, C., Ramírez-Estrada, J., Abades, S., Villegas, Á., *et al.*

490   (2016). The modulating role of group stability on fitness effects of group size is different in

491   females and males of a communally rearing rodent. *J. Anim. Ecol.*, 85, 1502–1515.

492   Feng, S. & Fu, Q. (2013). Expansion of global drylands under a warming climate. *Atmos. Chem.*

493   *Phys.*, 13, 10081–10094.

494   Fox, J. & Monette, G. (1992). Generalised collinearity diagnostics. *J. Am. Stat. Assoc.*, 87, 178–

495   183.

496   Fridolfsson, A.-K. & Ellegren, H. (1999). A simple and universal method for molecular sexing of

497   non-ratite birds. *J. Avian Biol.*, 30, 116–121.

498   Gardner, J.L., Rowley, E., Rebeira, P. De, Rebeira, A. De & Brouwer, L. (2018). Associations

499   between changing climate and body condition over decades in two southern hemisphere

500   passerine birds. *Clim. Chang. Responses*, 5, 1–14.

501   Golabek, K., Ridley, A.R. & Radford, A. (2012). Food availability affects strength of seasonal

502   territorial behaviour in a cooperatively breeding bird. *Anim. Behav.*, 83, 613–619.

503   Greenland, S., Senn, S.J., Rothman, K.J., Carlin, J.B., Poole, C., Goodman, S.N., *et al.* (2016).

504   Statistical tests, P values, confidence intervals, and power: a guide to misinterpretations.

505   *Eur. J. Epidemiol.*, 31, 337–350.

506 Griesser, M., Drobniak, S.M., Nakagawa, S. & Botero, C.A. (2017). Family living sets the stage

507   for cooperative breeding and ecological resilience in birds. *PLOS Biol.*, 15, e2000483.

508 Grueber, C.E., Nakagawa, S., Laws, R.S. & Jamieson, I.G. (2011). Multimodal inference in

509   ecology and evolution: challenges and solution. *J. Evol. Biol.*, 24, 699–711.

510 Guindre☐Parker, S. & Rubenstein, D.R. (2018). The oxidative costs of parental care in

511   cooperative and pair☐breeding African starlings. *Oecologia*, 188, 53–63.

512 Guindre☐Parker, S. & Rubenstein, D.R. (2020). Survival benefits of group living in a fluctuating

513   environment. *Am. Nat.*, In press.

514 Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R. & Bearhop, S. (2011). Carry-over effects as

515   drivers of fitness differences in animals. *J. Anim. Ecol.*, 80, 4–18.

516 Harrison, X.A., Donaldson, L., Correa-cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D., *et*

517   *al.* (2018). A brief introduction to mixed effects modelling and multi-model inference in

518   ecology. *Peer J*, 6, 1–32.

519 Hartig, F. (2020). *DHARMa: residual diagnostics for hierarchical (multi-level / mixed)*

520   *regression model*. *cran.R-project.org*. Available at: https://cran.r-

521   project.org/package=DHARMa. Last accessed 4 March 2020.

522 Hatchwell, B.J. (1999). Investment strategies of breeders in avian cooperative breeding systems.

523   *Am. Nat.*, 154, 205–219.

524 Herve, M. (2019). *RVAideMemoire: testing and plotting procedures for biostatistics*. *cran.R-*

525   *project.org*. Available at: https://cran.r-project.org/package=RVAideMemoire. Last

526   accessed 4 March 2020.

527   Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (2005). *Roberts' Birds of Southern Africa, 7th*

528   *Edition*. 7th edn. John Voleker Bird Book Fund, Cape Town.

529   Humphries, D.J. (2013). The mechanisms and function of social recognition in the cooperatively

530   breeding Southern pied babbler, Turdoides bicolor. PhD Thesis, MacQuarie University.

531   Iknayan, K.J. & Beissinger, S.R. (2018). Collapse of a desert bird community over the past

532   century driven by climate change. *Proc. Natl. Acad. Sci.*, 115, 8597–8602.

533   IPCC. (2013). *Climate Change 2013: The Intergovernmental Panel on Climate Change fifth*

534   *assessment report*. Cambridge University Press, Cambridge.

535   Jetz, W. & Rubenstein, D.R. (2011). Environmental uncertainty and the biogeography of

536   cooperative breeding in birds. *Curr. Biol.*, 21, 72–78.

537   Kruger, A.C. & Sekele, S.S. (2013). Trends in extreme temperature indices in South Africa:

538   1962-2009. *Int. J. Climatol.*, 33, 661–676.

539   Labocha, M.K. & Hayes, J.P. (2012). Morphometric indices of body condition in birds: a review.

540   *J. Ornithol.*, 153, 1–22.

541   Langmore, N.E., Bailey, L.D., Heinsohn, R.G., Russell, A.F. & Kilner, R.M. (2016). Egg size

542   investment in superb fairy-wrens: helper effects are modulated by climate. *Proc. R. Soc. B*,

543   283, 10–12.

544   Layton-Matthews, K., Ozgul, A. & Griesser, M. (2018). The interacting effects of forestry and

545   climate change on the demography of a group-living bird population. *Oecologia*, 186, 907–

546   918.

547   Lenth, R. V. (2016). Least-squares means: the R package lsmeans. *J. Stat. Softw.*, 69, 1–33.

548   Leon, A.C. & Heo, M. (2009). Sample sizes required to detect interactions between two binary

549   fixed-effects in a mixed-effects linear regression model. *Comput. Stat. Data Anal.*, 53, 603–

550   608.

551   Lukas, D. & Clutton-Brock, T. (2017). Climate and the distribution of cooperative breeding in

552   mammals. *R. Soc. Open Sci.*, 4, 160897.

553   MacKellar, N., New, M. & Jack, C. (2014). Observed and modelled trends in rainfall and

554   temperature for South Africa: 1960-2010. *S. Afr. J. Sci.*, 110, 1–13.

555   Markham, A.C., Gesquiere, L.R., Alberts, S.C. & Altmann, J. (2015). Optimal group size in a

556   highly social mammal. *Proc. Natl. Acad. Sci.*, 112, 4882–4887.

557   Mayaud, J.R., Bailey, R.M. & Wiggs, G.F.S. (2017). Modelled responses of the Kalahari Desert

558   to 21st century climate and land use change. *Sci. Rep.*, 7, 3887–3898.

559   McKechnie, A.E., Hockey, P.A.R. & Wolf, B.O. (2012). Feeling the heat: Australian landbirds

560   and climate change. *Emu*, 112, i–vii.

561   McKechnie, A.E., Smit, B., Whitfield, M.C., Noakes, M.J., Talbot, W.A., Garcia, M., *et al.*

562   (2016). Avian thermoregulation in the heat: evaporative cooling capacity in an archetypal

563   desert specialist, Burchell's sandgrouse (*Pterocles burchelli*). *J. Exp. Biol.*, 219, 2137–2144.

564   McKechnie, A.E. & Wolf, B.O. (2010). Climate change increases the likelihood of catastrophic

565   avian mortality events during extreme heat waves. *Biol. Lett.*, 6, 253–6.

566   Meade, J., Nam, K.B., Beckerman, A.P. & Hatchwell, B.J. (2010). Consequences of "load-

567   lightening" for future indirect fitness gains by helpers in a cooperatively breeding bird. *J.*

568   *Anim. Ecol.*, 79, 529–537.

569   Moore, M.P. & Martin, R.A. (2019). On the evolution of carry□over effects. *J. Anim. Ecol.*, 88,

570   1832–1844.

571   Mumme, R.L., Bowman, R., Pruett, M.S. & Fitzpatrick, J.W. (2015). Natal territory size, group

572   size, and body mass affect lifetime fitness in the cooperatively breeding Florida scrubjay.

573   *Auk*, 132, 634–646.

574   Nelson-Flower, M.J., Hockey, P.A.R., O'Ryan, C., Raihani, N.J., Du Plessis, M.A. & Ridley,

575   A.R. (2011). Monogamous dominant pairs monopolize reproduction in the cooperatively

576   breeding pied babbler. *Behav. Ecol.*, 22, 559–565.

577   Nelson-Flower, M.J., Wiley, E.M., Flower, T.P. & Ridley, A.R. (2018). Individual dispersal

578   delays in a cooperative breeder: ecological constraints, the benefits of philopatry and the

579   social queue for dominance. *J. Anim. Ecol.*, 87, 1227–1238.

580   New, M., Hewitson, B., Stephenson, D.B., Tsiga, A., Kruger, A., Manhique, A., *et al.* (2006).

581   Evidence in trends in daily climate extremes over southern and west Africa. *J. Geophys.*

582   *Res.*, 111, D14102.

583   Nowakowski, A.J., Frishkoff, L.O., Agha, M., Todd, B.D. & Scheffers, B.R. (2018). Changing

584   thermal landscapes: merging climate science and landscape ecology through thermal

585   biology. *Curr. Landsc. Ecol. Reports*, 3, 57–72.

586   O'Connor, R.S., Wolf, B.O., Brigham, R.M. & McKechnie, A.E. (2017). Avian

587   thermoregulation in the heat: efficient evaporative cooling in two southern African

588   nightjars. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.*, 187, 477–491.

589   Overpeck, J. (2013). The challenge of hot droughts. *Nature*, 503, 350–351.

590   Paniw, M., Maag, N., Cozzi, G., Clutton-Brock, T. & Ozgul, A. (2019). Life history responses of

591   meerkats to seasonal changes in extreme environments. *Science (80-.).*, 363, 631–635.

592   Paquet, M., Doutrelant, C., Loubon, M., Theron, F., Rat, M. & Covas, R. (2016). Communal

593   roosting, thermoregulatory benefits and breeding group size predictability in cooperatively

594   breeding sociable weavers. *J. Avian Biol.*, 47, 749–755.

595   du Plessis, K.L., Martin, R.O., Hockey, P.A.R., Cunningham, S.J. & Ridley, A.R. (2012). The

596   costs of keeping cool in a warming world: Implications of high temperatures for foraging,

597   thermoregulation and body condition of an arid-zone bird. *Glob. Chang. Biol.*, 18, 3063–

598   3070.

599   R Core Team. (2017). *R: a language and environment for statistical computing. R Found. Stat.*

600   *Comput.* R Foundation for Statistical Computing, Vienna.

601   Raihani, N.J., Nelson-Flower, M.J., Golabek, K.A. & Ridley, A.R. (2010). Routes to breeding in

602   cooperatively breeding pied babblers *Turdoides bicolor*. *J. Avian Biol.*, 41, 681–686.

603   Raihani, N.J. & Ridley, A.R. (2007). Variable fledging age according to group size: trade-offs in

604   a cooperatively breeding bird. *Biol. Lett.*, 3, 624–627.

605   Rey, B., Fuller, A., Mitchell, D., Meyer, L.C.R. & Hetem, R.S. (2017). Drought-induced

606   starvation of aardvarks in the Kalahari: an indirect effect of climate change. *Biol. Lett.*, 13,

607   20170301.

608   Ridley, A.R. (2016). Southern pied babblers: The dynamics of conflict and cooperation in a

609   group-living society. In: *Cooperative Breeding in Vertebrates: Studies of Ecology,*

610   *Evolution, and Behavior* (eds. Dickinson, J.L. & Koenig, W.). Cambridge University Press,

611   Cambridge, pp. 115–132.

612   Ridley, A.R. & Child, M.F. (2009). Specific targeting of host individuals by a kleptoparasitic

613   bird. *Behav. Ecol. Sociobiol.*, 63, 1119–1126.

614   Ridley, A.R. & Raihani, N.J. (2007). Variable postfledging care in a cooperative bird: causes and

615   consequences. *Behav. Ecol.*, 18, 994–1000.

616   Ridley, A.R. & Raihani, N.J. (2008). Task partitioning increases reproductive output in a

617   cooperative bird. *Behav. Ecol.*, 19, 1136–1142.

618   Ridley, A.R., Raihani, N.J. & Nelson-Flower, M.J. (2008). The cost of being alone: the fate of

619   floaters in a population of cooperatively breeding pied babblers. *J. Avian Biol.*, 39, 389–

620   392.

621   Rubenstein, D.R. (2011). Spatiotemporal environmental variation, risk aversion, and the

622   evolution of cooperative breeding as a bet-hedging strategy. *Proc. Natl. Acad. Sci.*, 108,

623   10816–10822.

624   Rubenstein, D.R. & Lovette, I.J. (2007). Temporal environmental variability drives the evolution

625   of cooperative breeding in birds. *Curr. Biol.*, 17, 1414–1419.

626   Russell, A.F. (2016). Chestnut-crowned babblers: dealing with climatic adversity and uncertainty

627   in the Australian arid zone. In: *Cooperative Breeding in Vertebrates* (eds. Koenig, W.D. &

628   Dickinson, J.L.). Cornell University, New York.

629   Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients.

630   *Methods Ecol. Evol.*, 1, 103–113.

631   Schwagmeyer, P.L. & Mock, D.W. (2008). Parental provisioning and offspring fitness: size

matters. *Anim. Behav.*, 75, 291–298.

Shen, S.-F., Emlen, S.T., Koenig, W.D. & Rubenstein, D.R. (2017). The ecology of cooperative breeding behaviour. *Ecol. Lett.*, 20, 708–720.

Sinervo, B., Méndez-de-la-Cruz, F., Miles, D., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., *et al.* (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science (80-.).*, 328, 894–899.

Smit, B., Whitfield, M.C., Talbot, W.A., Gerson, A.R., McKechnie, A.E. & Wolf, B.O. (2018). Avian thermoregulation in the heat: phylogenetic variation among avian orders in evaporative cooling capacity and heat tolerance. *J. Exp. Biol.*, 221, jeb174870.

Spooner, F.E.B., Pearson, R.G. & Freeman, R. (2018). Rapid warming is associated with population decline among terrestrial birds and mammals globally. *Glob. Chang. Biol.*, 24, 4521–4531.

Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T., *et al.* (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc. Natl. Acad. Sci.*, 111, 5610–5615.

Symonds, M.R.E. & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.*, 65, 13–21.

Thompson, A.M., Raihani, N.J., Hockey, P.A.R., Britton, A., Finch, F.M. & Ridley, A.R. (2013). The influence of fledgling location on adult provisioning: a test of the blackmail hypothesis. *Proc. Biol. Sci.*, 280, 20130558.

653   Todd, L.D., Poulin, R.G., Wellicome, T.I. & Brigham, R.M. (2003). Post-fledging survival of

654   burrowing owls in Saskatchewan. *J. Wildl. Manage.*, 67, 512–519.

655   Tokura, W., Jack, S.L., Anderson, T. & Hoffman, M.T. (2018). Long-term variability in

656   vegetation productivity in relation to rainfall, herbivory, and fire in Tswalu Kalahari

657   Reserve. *Koedoe*, 60, 1–18.

658   van de Ven, T.M.F.N. (2017). Implications of climate change on the reproductive success of the

659   southern yellow-billed hornbill *Tockus leucomelas*. PhD thesis, University of Cape Town.

660   van de Ven, T.M.F.N., Fuller, A. & Clutton☐Brock, T. (2020). Effects of climate change on pup

661   growth and survival in a cooperative mammal, the meerkat. *Funct. Ecol.*, 34, 194–202.

662   van de Ven, T.M.F.N., McKechnie, A.E. & Cunningham, S.J. (2019). The costs of keeping cool:

663   behavioural trade-offs between foraging and thermoregulation are associated with

664   significant mass losses in an arid-zone bird. *Oecologia*, 191, 205–215.

665   Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., *et al.* (2002).

666   Ecological responses to recent climate change. *Nature*, 416, 389–95.

667   Wiley, E.M. (2017). Examining how multilevel population dynamics and climate influence

668   breeding behaviour, within-group stability and demography in a cooperatively breeding

669   bird. PhD thesis, University of Western Australia.

670   Wiley, E.M. & Ridley, A.R. (2016). The effects of temperature on offspring provisioning in a

671   cooperative breeder. *Anim. Behav.*, 117, 187–195.

672   Wiley, E.M. & Ridley, A.R. (2018). The benefits of pair bond tenure in the cooperatively

673   breeding pied babbler (*Turdoides bicolor*). *Ecol. Evol.*, 8, 7178–7185.

674 van Wilgen, N.J., Goodall, V., Holness, S., Chown, S.L. & McGeoch, M.A. (2016). Rising

675 temperatures and changing rainfall patterns in South Africa's national parks. *Int. J.*

676 *Climatol.*, 36, 706–721.

677

678 **<u>Table 1</u>**

679 *Table 1: Top GLMM model sets for all analyses. Model averaging was implemented on all models with $\Delta AICc < 5$. Significant*

680 *terms after model averaging are shown in bold. Null models shown for comparison with top model sets. For full model sets, see*

681 *Supporting Information.*

Table 1A: Factors influencing body mass change in fledglings (n = 124 individuals from 74 nests by 25 different groups over 14 breeding seasons)			
	AICc	ΔAICc	ω
Null model	788.50	16.32	0.00
Top model set:			
$Rain_{60}$ + $Rain_{90}$ + Brood size	772.18	0.00	0.39
$Rain_{90}$ + Brood size	773.35	1.17	0.22
$Rain_{60}$ + $Rain_{90}$ + Brood size + $G.Size_{BrSeas}$	773.38	1.20	0.21
Brood size **+ Sex**	774.35	2.17	0.13
$Rain_{60}$ + Brood size	776.27	4.09	0.05
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*
Intercept	29.423	0.808	27.825/31.021
Brood size	**1.778**	**0.639**	**0.513/3.044**
$G.Size_{BrSeas}$	-0.002	0.318	-0.632/0.629
$Rain_{60}$	0.636	0.674	-0.692/1.964
$Rain_{90}$	**1.166**	**0.776**	**0.223/2.695**
Sex	0.229	0.671	-1.088/1.548

Table 1B: Factors influencing body mass change in adults (n = 82 measures from 53 different individuals at 21 different groups over 11 breeding seasons)			
	AICc	ΔAICc	ω
Null model	453.30	16.09	0.00
Top model set:			
Mean $T_{MaxBrSeas}$ + $Rain_{BrSeas}$	437.21	0.00	0.46
Mean $T_{MaxBrSeas}$ + $Rain_{BrSeas}$ + Mean $T_{MaxBrSeas}$ * $Rain_{BrSeas}$	437.47	0.26	0.40
Mean $T_{MaxBrSeas}$ + $Rain_{BrSeas}$ + $G.Size_{BrSeas}$	439.54	2.33	0.14
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*
Intercept	0.210	0.439	-0.663/1.084
Mean $T_{MaxBrSeas}$	**-1.189**	**0.518**	**-2.218/-0.160**

	Effect	SE	95% CI
Rain$_{BrSeas}$	**1.695**	**0.452**	**0.797/2.594**
G.Size$_{BrSeas}$	0.008	0.156	-0.304/0.320
Mean T$_{MaxBrSeas}$ * Rain$_{BrSeas}$	-0.282	0.543	-1.357/0.793

Table 1C: Effect of conditions experienced between hatching and fledging on interannual survival of juvenile birds
(*n* = 247 different individuals from 143 broods by 30 different groups over 14 breeding seasons)

	AICc	ΔAICc	ω$_i$
Null model	315.50	10.17	0.00
Top model set:			
Rain$_{60}$ + Mean T$_{maxBrood}$ + Rain$_{60}$ * Mean T$_{maxBrood}$	305.33	0.00	0.52
Rain$_{60}$ + Mean T$_{maxBrood}$ + G.Size$_{Brood}$ + Rain$_{60}$ * Mean T$_{maxBrood}$	307.44	2.11	0.18
Rain$_{60}$ + Mean T$_{maxBrood}$	307.78	2.45	0.15
Rain$_{60}$ + Mean T$_{maxBrood}$ + G.Size$_{Brood}$	309.84	4.52	0.05
Rain$_{60}$	310.10	4.77	0.05
Rain$_{60}$ + Sex	310.31	4.98	0.04
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*
Intercept	0.901	0.209	0.489/1.314
G.Size$_{Brood}$	0.004	0.082	-0.157/0.165
Mean T$_{maxBrood}$	**-0.334**	**0.191**	**-0.710/-0.043**
Rain$_{60}$	**0.495**	**0.192**	**0.117/0.872**
Sex	-0.017	0.101	-0.216/0.182
Rain$_{60}$ + Mean T$_{maxBrood}$ + Rain$_{60}$ * Mean T$_{maxBrood}$	-0.293	0.259	-0.803/0.218

*Residual deviance: 277.56 on 241 degrees of freedom (ratio: 1.147)

Table 1D: Effect of conditions experienced between fledging and independence on interannual survival of juvenile birds
(*n* = 233 different individuals from 135 broods by 30 different groups over 14 breeding seasons)

	AICc	ΔAICc	ω$_i$
Null model	303.30	17.79	0.00
Top model set:			
Drought$_{BrSeas}$ + Mean T$_{max90}$ + Drought$_{BrSeas}$ * Mean T$_{max90}$	286.28	0.00	0.54
Drought$_{BrSeas}$ + Mean T$_{max90}$ + G.Size$_{90}$ + Drought$_{BrSeas}$ * Mean T$_{max90}$	286.57	0.29	0.46
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*
Intercept	0.709	0.167	0.379/1.038
Drought$_{BrSeas}$ (drought = YES)	**1.862**	**0.676**	**0.531/3.194**
G.Size$_{90}$	0.099	0.152	-0.199/0.397
Mean T$_{max90}$	**-0.363**	**0.175**	**-0.708/-0.018**
Drought$_{BrSeas}$ + Mean T$_{max90}$ + Drought$_{BrSeas}$ (drought = YES) * Mean T$_{max90}$	**-2.845**	**0.868**	**-4.555/-1.136**

*Residual deviance: 272.911 on 227 degrees of freedom (ratio: 1.202)

Table 1E: Effect of conditions experienced during the breeding season on interannual survival of breeding adults
(n = 352 measurements of interannual survival from 136 different individuals in 37 different groups over 14 breeding seasons)

	AICc	ΔAICc	ω$_i$
Null model	391.00	33.78	0.00
Top model set:			
Drought$_{BrSeas}$ + Mean T$_{maxBrSeas}$ + Drought$_{BrSeas}$ * Mean T$_{maxBrSeas}$	357.22	0.00	0.58
Drought$_{BrSeas}$ + Mean T$_{maxBrSeas}$ + **G.Size$_{BrSeas}$** + Drought$_{BrSeas}$ * Mean T$_{maxBrSeas}$	357.84	0.62	0.42
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*

Intercept	1.763	0.199	1.371/2.154
Drought$_{BrSeas}$ (drought = YES)	**-1.240**	**0.230**	**-1.693/-0.787**
G.Size$_{BrSeas}$	0.092	0.159	-0.219/0.404
Mean T$_{maxBrSeas}$	0.404	0.161	-0.086/0.721
Drought$_{BrSeast}$ + Mean T$_{maxBrSeas}$ + Drought$_{BrSeas}$ (drought = YES) * Mean $_{TmaxBrSeas}$	**-1.184**	**0.216**	**-1.609/-0.758**

*Residual deviance: 288.145 on 346 degrees of freedom (ratio: 0.833)

682

683

684 **Figures**

685 *Fig. 1: (A) Average maximum temperature (black dashes ± 1 SD) and total rainfall (vertical bars: no colour = no drought, hatched*

686 *= drought) for each austral summer breeding season studied from 2005 to 2019. Dashed horizontal line represents rainfall =*

687 *137.75 mm; years with rainfall < 137.75 mm were classified as drought years. (B) Boxplots show median (black line), first and*

688 *third quartiles (box), and interquartile range (whiskers) for the distribution of average group size across each breeding season.*

689 *Open circles represent data points (jittered for improved visibility) and lines present the study-wide average group size (solid*

690 *horizontal line) ± 1 SD (dashed horizontal lines).*

691 *Fig. 2: Change in body mass in southern pied babbler* Turdoides bicolor *fledglings between the fledging and nutritional*

692 *independence in relation to (A) brood size and (B) rainfall (mm) between the fledging and nutritional independence and in adults*

693 *between the start and end of the breeding season in relation to (C) average daily maximum temperatures and (D) total rainfall*

694 *(mm) during the breeding season . Data points in (A) are jittered for improved visibility. Juvenile pied babblers from larger*

695 *broods gained more mass between 11- and 90-days-of-age. This is likely explained by nestlings from larger broods fledgling at a*

696 *smaller body mass, and hence growing more once they had left the nest, than those which fledged from smaller broods and may*

697 *have attained larger mass while still in the nest.*

698 *Fig. 3: Interannual survival (0 = not present, 1 = present) in juvenile southern pied babblers* Turdoides bicolor *in relation to (A)*

699 *rainfall prior to hatching; (B) mean daily maximum temperature between hatching and fledging; and (C) the interaction between*

700 *temperature and drought between fledge and independence (non-drought breeding seasons: open circles, dashed confidence*

701 *intervals, black colour; drought breeding seasons: open triangles, dotted confidence intervals, gray colour). Data points are*

702 *integers (0,1) jittered for improved visibility. Individuals in the study population are uniquely identifiable by their colour and*

703 *metal ring combinations (D; photograph by Nicholas B. Pattinson).*

704 *Fig. 4: Survival of breeding adult southern pied babblers* Turdoides bicolor *from one breeding season to the next in relation to*

705 *temperature and drought conditions during the initial breeding season (non-drought years: open circles, dashed confidence*

706 *intervals, black colour; drought years: open triangles, dotted confidence intervals, gray colour). Data points are integers (0,1)*
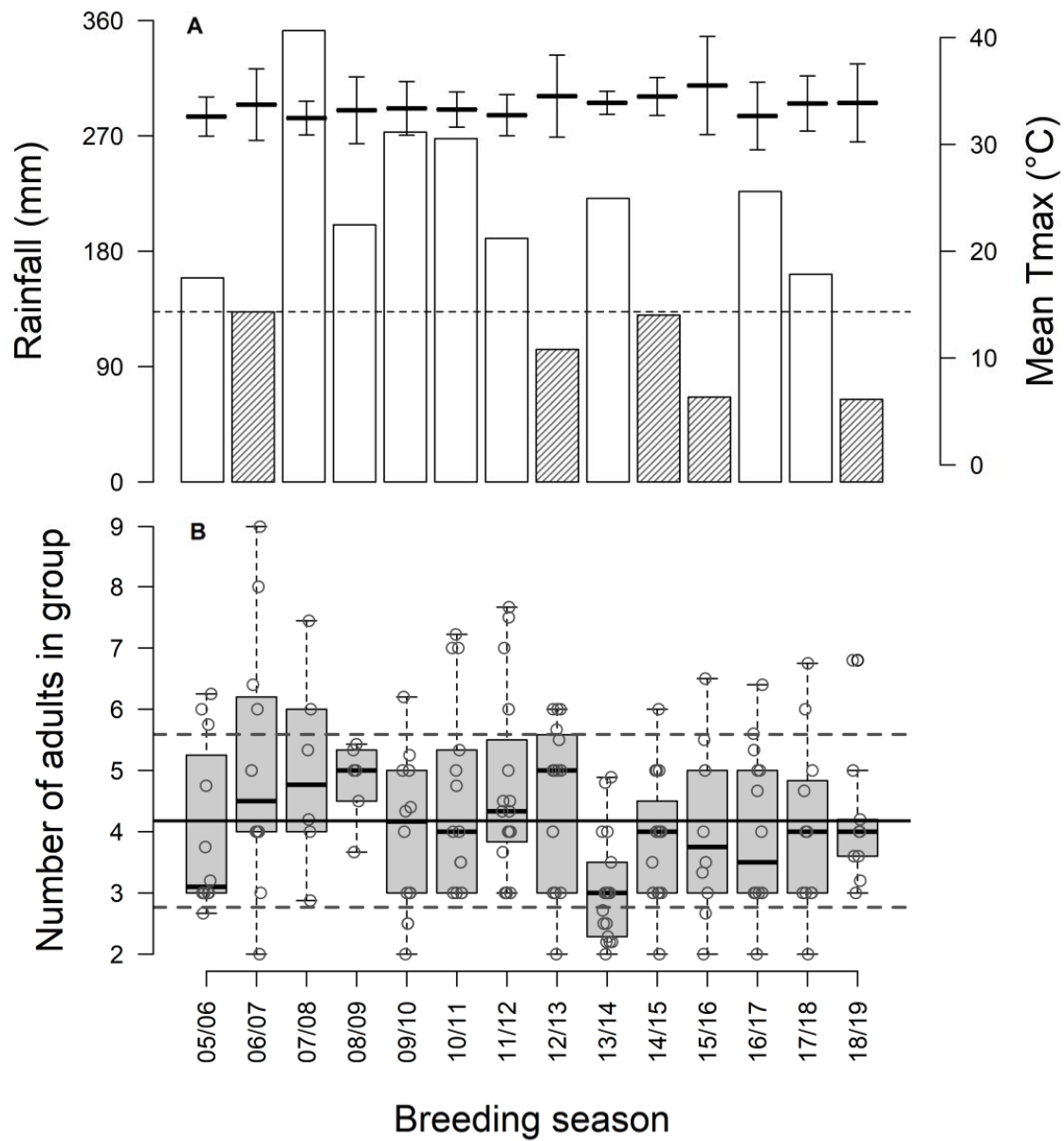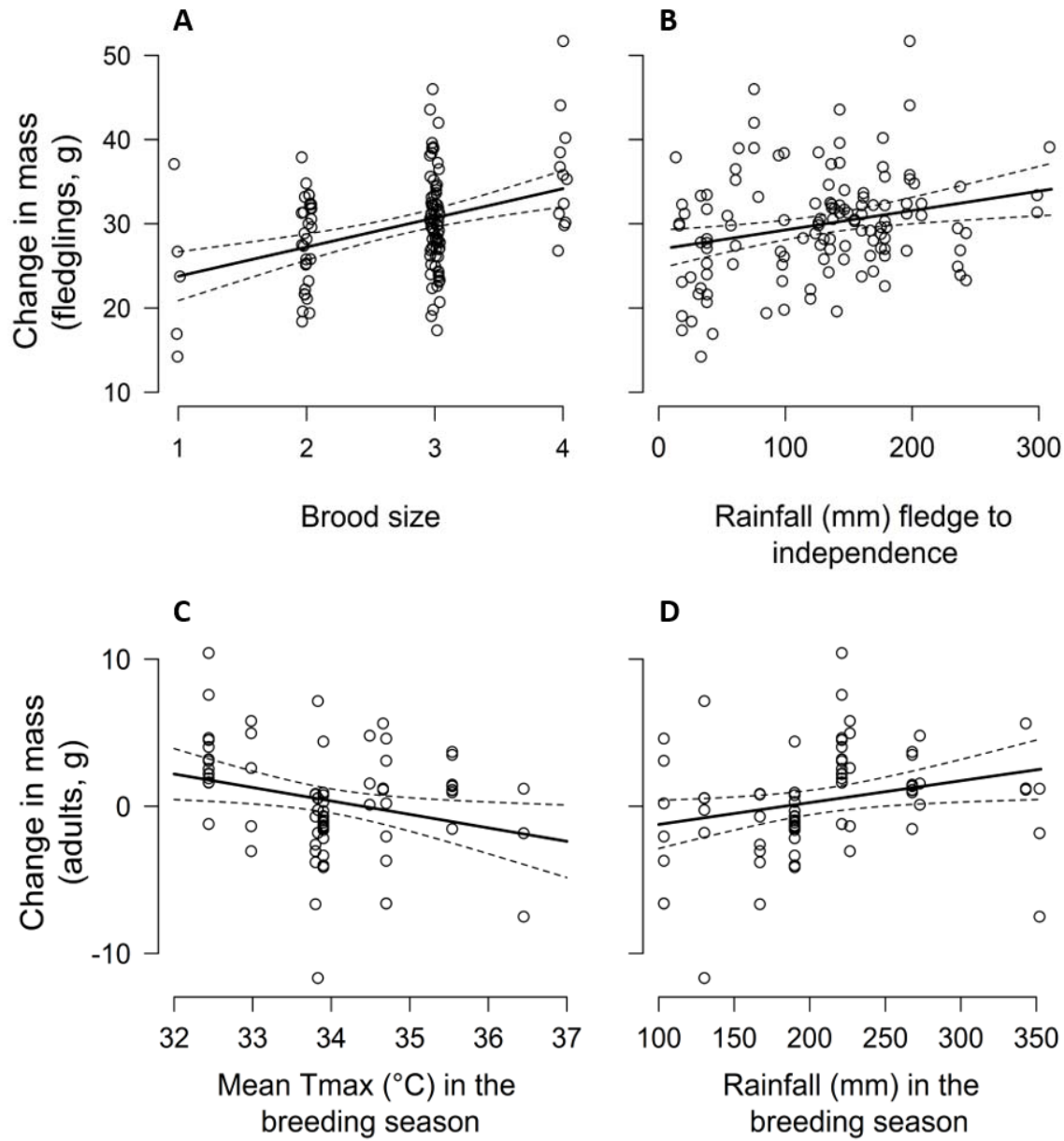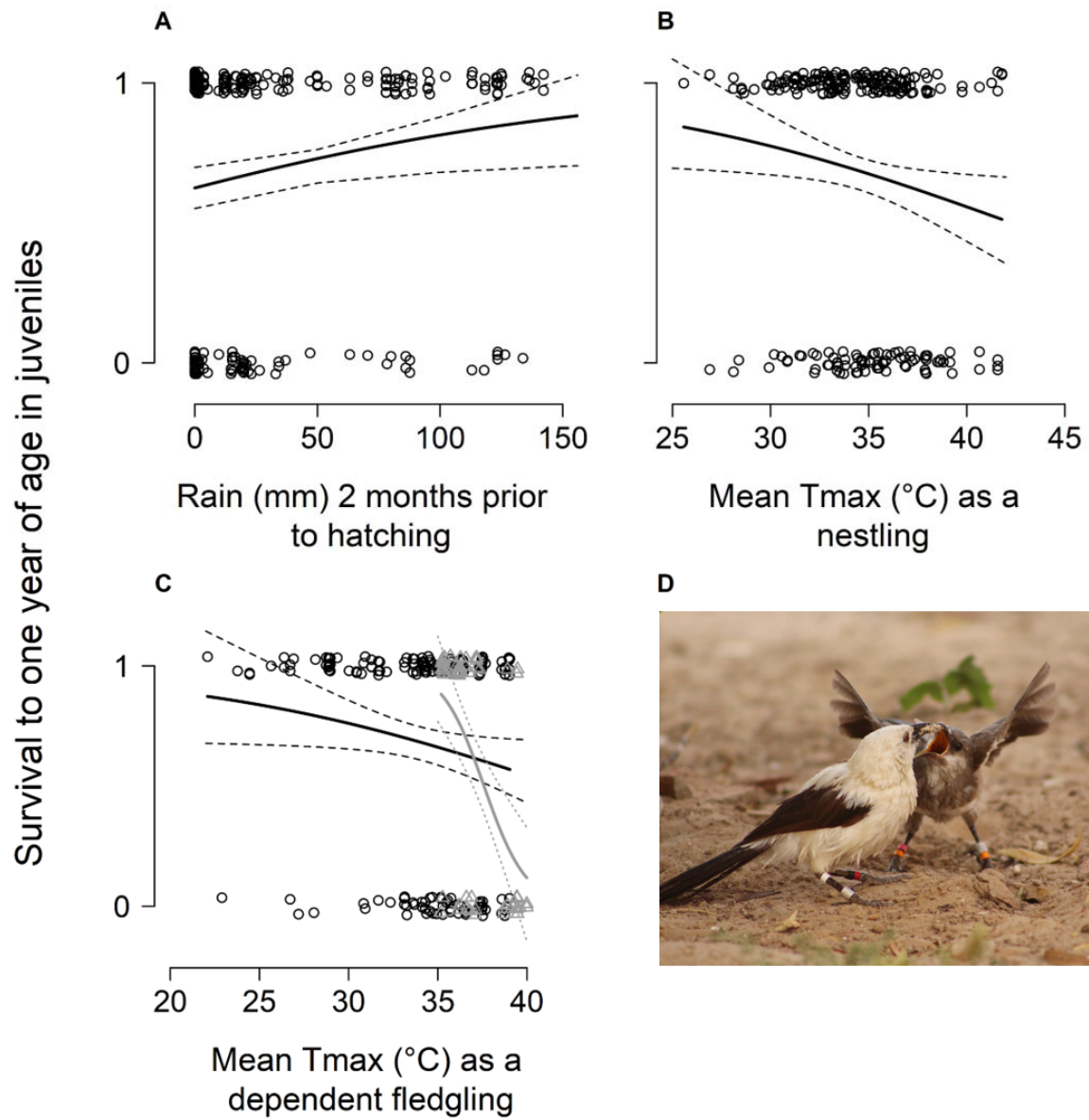
707 *jittered for improved visibility.*

708

709

710   **Figure 1**

711

712

713 **Figure 2**

714

715

716

717   **Figure 3**

718

719

720 **Figure 4**

721