UNIVERSITY OF CAPE TOWN
DEPARTMENT OF STATISTICAL SCIENCES
MSc - Data Science Speacialisation 2021

STA5092Z - Exploratory Data Analysis Assignment 1 - 15%

<u>Due date:</u> Tuesday, 6 April 2021 at 6:00pm
Late submissions will be penalised at 10% per day (pro rata)

GENERAL INSTRUCTIONS:

- Prepare a report that answers the questions. All analyses to be conducted via R and if you wish to use Python, be aware of the fact that exam language is in R. All code must be submitted both as an appendix and on Vula, and should include comments that clearly explain the purpose of the code.

- **NB:** The length of your report (excluding appendices) is limited to a maximum of **10 pages**. Any information beyond the 10ᵗʰ page will be ignored.

- You need to prepare your report in R Markdown format and submit both your final pdf as well as the .Rmd file. It would be nice if you could create the pdf in scientific writing format (ie. article).

- The submissions will be done on VULA under the assignments tab.

- Please attach a plagiarism declaration to your report. Plagiarism of any form will be reported to the university court.

THE SOUTHERN PIED BABBLER (TURDOIDES BICOLOR) DATASET

This problem dataset comes from the UCT's Zivahub:

`https://zivahub.uct.ac.za/articles/dataset/Southern_Pied_Babbler_nestling_mass_tarsus_length_and_survival/12441899`.

Data were collected for each austral summer breeding season from September 2005February 2019 (14 breeding seasons in total). For details of the research, please refer to the paper attached to the assignment here.

PART I - Data Wrangling

For this part, please use head(x, 5) to show your generated dataframes. Explain every step of your actions in detail.

1. Download the data from the following link:
   https://zivahub.uct.ac.za/articles/dataset/Southern_Pied_Babbler_nestling_mass_tarsus_length_and_survival/12441899

2. After unzipping the downloaded file, you will notice that there are 6 .csv files, and 3 of them are metadata, which describes the variables. Extract the data .csv files into R, convert them into tibble format.

3. Merge the two files on fledlings nd nestlings into one single file called Spiedbabbler. Hints:

   (i) You need to convert the date column into a proper date format.

   (ii) Check the names of the variables in each datasets. Rename, select the variables where applicable.

   (iii) Check the types of the variables in each file. Record any changes that are necessary to make sure that all variables are coded correctly and why?

PART II - Data Summaries and Visualizations

Use the merged dataset and attempt the following:

1. What is your total sample size for each year in the Spiedbabbler dataframe (tibble) you created in Part I?

2. Are there any missing values and outliers in the following variables? What is your definition of an outlier?

   - GrpSizeAd
   - GrpSizeTotal
   - Broodsize
   - Mass
   - TmaxMeas
   - No.ChicksFledge
   - Rain
   - Drought

3. Create a table for Mass and Date per nest.

4. Determine the differences between seasons. Hint: Use the temperature variable(s) for this.

5. Plot the Mass over time per nest, with the season variable being a factor grid. Colour code your points with different seasons. Hint: Axis scales.

6. Calculate the yearly average of Mass, Broodsize, GrpSizeTotal, No.ChicksFledge, Rain. Plot this information on a seasonal and/or Drought grid.

7. Finally create a plot that you think would be a useful information given this dataset.

2 **Title: High temperatures drive offspring mortality in a cooperatively breeding bird**

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10 **Abstract**

11   An improved understanding of life history responses to current environmental variability is

12 required to predict species-specific responses to anthopogenic climate change. Previous research

13 has suggested that cooperation in social groups may buffer individuals against some of the negative

14 effects of unpredictable climates. We use a 15-year dataset on a cooperative-breeding arid-zone

15 bird, the southern pied babbler *Turdoides bicolor*, to test i) whether environmental conditions and

16 group size correlate with survival of young during three development stages (egg, nestling,

17 fledgling), and ii) whether group size mitigates the impacts of adverse environmental conditions

18 on survival of young. Exposure to high mean daily maximum temperatures (mean T_{max}) during

19 early development was associated with reduced survival probabilities of young in all three

20 development stages. No young survived when mean $T_{max} > 38°C$, across all group sizes. Low

21 survival of young at high temperatures has broad implications for recruitment and population

22 persistence in avian communities given the rapid pace of advancing climate change. Impacts of

23 high temperatures on survival of young were not moderated by group size, suggesting that the

24 availability of more helpers in a group is unlikely to buffer against compromised offspring survival

25 as average and maximum temperatures increase with rapid anthropogenic climate change.

26 **Keywords:** climate change, cooperative breeding, dryland ecology, environmental variability,
27 survival of young, southern pied babbler

Introduction

29 Anthropogenic climate change has altered weather patterns in every ecosystem on Earth [1,2],

30 with far-reaching consequences for population dynamics across taxa [3]. An improved

31 understanding of life history responses to current environmental variability is required to predict

32 species-specific responses to climate change [4]. While cooperative breeders occur in diverse

33 habitats [5,6], comparative research has demonstrated that both cooperatively-breeding birds [7]

34 and mammals [8] occur with disproportionate frequency in regions characterised by high spatial

35 and temporal variability in environmental conditions. This implies that group living enhances

36 the ability to persist in challenging environments [9]. To date, however, there are few empirical

37 studies that explicitly test the extent to which group-living mitigates the effects of climate

38 variability on reproduction [10–13]. Of these studies, only Langmore *et al.* (2016) and van de

39 Ven *et al.* (2019) explore impacts of temperature alongside variation in group size, despite

40 evidence of thermoregulatory benefits of group living [14], and only Covas *et al.* [13] consider

41 offspring survival across more than one development stage. This latter point is important,

42 because specific drivers of survival can differ substantially between development stages [15–17].

43   Temperature and rainfall patterns are important measures of climate variability, playing a

44 critical role in offspring survival rates observed in vertebrates [18], and recent changes in

45 temperature and rainfall patterns have led to adjustments to the timing and success of breeding in

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some bird species [19,20]. For birds in arid environments, higher rainfall is often associated with improved offspring survival [21,22], droughts are associated with reduced offspring survival [23,24] and periods of very hot weather are typically associated with lower nest survival rates [15,25] and nestling growth rates [26–28]. Therefore, it is reasonable to expect that offspring survival and population persistence of birds in arid environments will be impacted as regions become hotter and drier under climate change [29,30].

Cooperative breeding, where more than two individuals rear a single brood [31], occurs in ~9% of bird species [32]. Reproductive benefits of cooperation include earlier fledging age and more broods raised per season [33], reduced costs of breeding for females [11,34], enhanced egg investment [35], increased fledgling recruitment [17,36], and the ability to raise overlapping broods [12,37]. Global comparative studies suggest that cooperative breeding evolved in unpredictable environments [38], facilitated the colonisation of such environments [39], or prevented extinction under increasingly harsh conditions [40]. One prominent explanation for the occurrence of cooperative breeding in birds in variable environments is that it represents a 'bet-hedging' strategy [38], whereby breeding individuals share the costs of reproduction with helpers and are thus able to reduce interannual variation in offspring survival in response to unpredictable rainfall and food availability [9]. This implies that cooperation might buffer breeding attempts from failure during adverse environmental conditions [13,41].

A likely mechanism underlying such benefits of cooperation is load-lightening [42], which refers to individual reductions in workload in response to the presence of additional group members. Load-lightening has been observed in a number of cooperatively-breeding species [11,16,43], and may operate via task-partitioning [37,44] or by improved access to resources [45,46]. In larger groups, there are more individuals available to assist with breeding attempts,

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69   which can either lead to load-lightening amongst individual group members [11,37], or to

70   cumulatively greater investment in young [36,47]. Both are potential benefits of group living that

71   may be particularly advantageous when unfavourable rainfall or temperature conditions are

72   experienced. Specifically, these effects could mean that larger groups are better able to maintain

73   adequate levels of parental care to eggs, nestlings, and/or fledglings at high temperatures or

74   during periods of low rainfall, despite individual declines in investment in parental care

75   behaviours.

76   We use a comprehensive 15-year dataset on southern pied babblers *Turdoides bicolor*

77   (hereafter 'pied babblers'), a cooperatively-breeding passerine endemic to the Kalahari in

78   southern Africa, to explore the impacts of temperature, rainfall, and group size (the number of

79   adults in the group, indicating the potential for the breeding pair to receive help) on the survival

80   of young, including fledgling survival. Specifically, we test for effects of these parameters on

81   survival of young from i) initiation of incubation to hatching; ii) hatching to fledging; and iii)

82   fledging to nutritional independence at 90 days of age. We expected high temperatures to reduce

83   survival, and high rainfall and larger group sizes to enhance survival during each development

84   stage. If the presence of helpers buffers the effect of environmental variation on reproduction, as

85   proposed by the temporal variability hypothesis [9], then we would expect an interaction

86   between environmental factors and group size, such that weaker impacts of adverse climatic

87   conditions on reproduction are observed in larger groups.

4

Materials and methods

Study site and system

Fieldwork was conducted at the Kuruman River Reserve (33 km^2, KRR; 26°58'S, 21°49'E) in the southern Kalahari. Mean summer daily maximum temperatures at the study site, from 1995-2015, averaged 34.7 ± 9.7°C and mean annual precipitation averaged 186.2 ± 87.5mm [48]. The Kalahari region is characterised by hot summers and periodic droughts [49], with extremely variable rainfall between years [50] and increases in both the frequency and severity of high temperature extremes over the last 20 years [51]. Pied babblers are medium-sized (60–90 g), cooperatively-breeding passerines endemic to the Kalahari where they live in territorial groups ranging in size from 3–15 adults [52]. They breed during the austral summer, from September to March [53]. Pied babbler groups consist of a single breeding pair with subordinate helpers [54], and all adult group members (individuals > 1 year old) engage in cooperative behaviours, including territory defence and parental care [53,55]. Previous research has shown that high temperatures and drought negatively affect many aspects of this species' ecology, including foraging efficiency, body mass maintenance, interannual survival, and provisioning of young [56–59].

Birds in the study population are marked as nestlings with a metal band (engraved with a unique number) and a unique combination of up to three colour rings for individual identification, and are habituated to observation at distances of 1–5 m [55]. Habituated groups are visited weekly during the breeding season to check group composition and record life history events, including breeding activity.

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109 **Data collection**

110 Data were collected for each austral summer breeding season from September 2005–February

111 2019 (14 breeding seasons in total).

112 *Nest life history data*

113 Nest monitoring (location of nests, determination of incubation, hatch, and fledge or failure

114 dates, records of group size and brood size) followed Ridley & van den Heuvel [33]. Nests were

115 located by observing nest-building, and incubation start, hatch and fledge dates were determined

116 by checking nests every 2-3 days. Breeding attempts were considered to have failed when nests

117 were no longer attended, or when dependent fledglings were not seen on two consecutive visits.

118 Failure dates were calculated as the midpoint between the date of the last pre-fail nest/group

119 check and the date when the nest was no longer attended or the fledgling was missing. In most

120 cases, it was not possible to determine the proximate cause of nest failure or death, although

121 common causes of nest failure in this species include predation, abandonment, and nestling

122 starvation [52,60].

123 Group size (mean = 4.2 ± 1.5, range: 2–10 adults) was recorded for each nest incubated.

124 Brood size was recorded 11 days after hatching (mean = 2.7 ± 0.8, range: 1–5 nestlings), when

125 nestlings were ringed. We defined early development as the period between initiation of

126 incubation and nutritional independence at 90 days of age [55]. Average time from initiation of

127 incubation to hatching is 14 ± 1.2 days. Average time between hatching and fledging is $15.4 \pm$

128 1.7 days. Pied babblers are nutrionally independent (receiving < 1 feed per hour) by 90 days of

129 age [55].

Sexing & nestling mass

131   Pied babblers are sexually monomorphic (Ridley, 2016) and molecular sexing was used to

132   determine the sex of individuals (*sensu* Fridolfsson & Ellegren 1999). Blood samples were

133   collected by brachial venipuncture and stored in Longmire's lysis buffer. Nestlings were ringed,

134   blood sampled, and weighed to 0.1 g ($Mass_{11}$) on a top-pan scale 11 days post-hatching.

135   *Temperature and rainfall*

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

137   station (Vantage Pro2, Davis Instruments, Hayward, USA). Missing weather data from 2009,

138   2010, and 2011 were sourced from a nearby South African Weather Services weather station

139   (Van Zylsrus, 28 km away), which produces significantly repeatable temperature measurements

140   and moderately repeatable rainfall measurements, adequately detecting detecting wet vs. dry

141   periods, in comparison with the on-site weather station [63].

142   Daily minimum (T_{min}) and maxium (T_{max}) temperatures, and daily temperature variation

143   (T_{max} - T_{min}), were averaged for each development stage: incubation (mean T_{minInc}, mean T_{maxInc},

144   mean T_{varInc}), nestling (mean $T_{minBrood}$, mean $T_{maxBrood}$, mean $T_{varBrood}$), and fledgling (mean

145   T_{min90}, mean T_{max90}, mean T_{var90}). Rainfall was summed for the 60 days prior to initiation of

146   incubation ($Rain_{60}$), and for the period between fledging and independence ($Rain_{90}$).

147   **Statistical analyses**

148   Statistical analyses were conducted in R version 3.6.0 [64]. All continuous explanatory variables

149   were scaled by centering and standardising by the mean [65,66]. All explanatory variables were

150   tested for correlation with one another [67]. Mean T_{max90} and mean T_{min90} were correlated (VIF =

151   2.8,correlation coefficient = 0.77) and all other explanatory variables were not correlated with

152   each other (all VIF < 1.3, correlation coefficient < 0.30). Correlated variables were not included

153   in the same additive models. Unless otherwise indicated, summary statistics are presented as

154   mean ± one standard deviation. Analyses exclude groups > 8 due to small sample sizes for

155   groups of 9 ($n = 5$) and 10 ($n = 1$) over 15 years of records. A quadratic term for temperature was

156   included as a predictor variable only when no main linear effect of temperature was found and

157   visual inspection of the data suggested a non-linear relationship. Sensitivity power analyses,

158   using the package *pwr* [68], indicated that we had sufficient statistical power to detect effects of

159   two-way interactions given our sample sizes [69,70], see Table S1. We tested for temporal trends

160   in environmental (temperature and rainfall) and reproductive (nest success, fledgling survival)

161   parameters using univariate linear models with breeding season as the only predictor. Covariates

162   exhibiting temporal trends were detrended prior to inclusion in our models using the *detrend*

163   function in the package *pracma* [71].

164   *Survival probabilities during each development stage*

165   Pied babbler survival probabilities are not constant across time during early development [53],

166   see Fig. S1, and covariates are unlikely to have the same relationship with survival during all

167   three early development stages. We used generalised linear mixed-effects models (GLMMs) with

168   a binomial distribution and a logit link function in the package *lme4* [72] to determine which

169   variables best predicted survival probabilities during each development stage. These analyses

170   were undertaken at the level of the breeding attempt (i.e. clutch or brood) because individual

171   offspring were only ringed for individual identification from the 11th day after hatching, by

172   which time ~60% of monitored breeding attempts had failed. Model selection using Akaike's

173   information criterion corrected for small sample size (AICc), with maximum likelihood

174   estimation was used to test a series of models to determine which model/s best explained patterns

175   of variation in the data [65]. Where several models were within 5 AICc of the top model, top

176   model sets were averaged using the package *MuMIn* [73]. Model terms with confidence intervals

177   not intersecting zero were considered to explain significant patterns in our data (Grueber,

178   Nakagawa, Laws, & Jamieson, 2011). Binomial model fits were tested against the dispersion

179   parameter in the package *RVAideMemoire* [75].

180   We considered the influence of the following parameters on (i) the probability of at least

181   one egg per clutch surviving to hatch, (ii) the probability of at least one nestling per brood

182   surviving to fledge, and (iii) the probability of at least one fledgling per brood surviving to

183   nutritional independence: for (i) group size, $Rain_{60}$, mean T_{minInc}, mean T_{maxInc}, and mean T_{varInc},

184   for (ii) group size, $Rain_{60}$, mean $T_{minBrood}$, mean $T_{varBrood}$, mean $T_{maxBrood}$, and mean $T_{maxBrood}^{2}$,

185   and for (iii) group size, $Rain_{90}$, mean T_{min90}, mean T_{var90}, mean T_{max90}, and mean T_{max90}^{2}. We tested

186   two-way interactions between rainfall, T_{max}, and group size variables in each analysis, and, in

187   order to account for non-independence of data, we included group identity as a random term in

188   all three analyses.

189   In order to contribute data that can be incorporated into mechanistic modelling of the

190   effects of climate change on avian populations [4], we further sought to identify the threshold

191   T_{max} ('breakpoints') above which survival was compromised during each development stage. We

192   used the package *segmented* [76] to apply a Davies' test for a non-zero difference-in-slope and,

193   when the regression parameter in the linear predictor was non-constant, to identify a point

194   estimate and 95% confidence interval for the breakpoint. We then fitted simple linear regression

195   models for the data above and below the identified breakpoints with temperature (mean T_{maxInc},

196   mean $T_{maxBrood}$, and mean T_{max90} respectively) as the only predictor, and survival per breeding

197   attempt as the response. In the segmented regressions, we used a continuous form of the survival

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198 response, specifically (i) the number of days between initiation of incubation and either the

199 hatching of at least one egg or failure of the breeding attempt before hatching (age at hatch/fail),

200 (ii) the number of days between hatching and fledging at least one nestling from a brood or

201 failure (age at fledge/fail), and (iii) the number of days between fledging and at least one

202 fledgling surviving to nutritional independence or failure (age at survival/fail).

203 *Influence of nestling mass on fledgling survival*

204 In addition to survival data at the scale of the breeding attempt, we have detailed individual-level

205 survival data for 372 fledglings weighed and banded as 11-day-old nestlings. Larger nestling

206 mass is commonly associated with higher survival probabilities in birds [16,77]. Prior research

207 on pied babblers has shown that nestling mass is influenced by environmental factors such as

208 temperature and rainfall [57]. We therefore used a confirmatory path analysis [78,79] to test for

209 indirect effects of environmental and group size factors on survival to nutritional independence

210 in known individual fledglings mediated via their mass as a nestling ($Mass_{11}$). We computed the

211 path analysis using the R package *piecewiseSEM* [80], which can accommodate multiple error

212 structures. This capacity is important because the response terms of our component models have

213 different distributions (see below). While model selection processes can be applied to multiple

214 path analyses [81], our goal was not to choose between competing hypotheses, and but rather to

215 construct a single model testing the relative importance of direct effects of environmental and

216 group size factors vs. effects mediated via nestling mass. Path analysis allowed us to specify and

217 simultaneously quantify all hypothesised relationships of interest, including the indirect effects

218 of weather and group size on survival via nestling mass. Path coefficients are partial regression

219 coefficients and can be interpreted similarly to simple and multiple regression outputs. Statistical

220 significance was taken as $p < 0.05$. We hypothesised that:

10

221   Survival would be negatively affected by i) high temperatures during the nestling and

222 fledgling stages, ii) low rainfall between fledging and independence, iii) smaller group size, and

223 iv) low nestling body mass (model with binomial error structure).

224   Nestling body mass would be negatively affected by i) high mean temperatures during the

225 nestling period, ii) low rainfall prior to the nestling period, and iii) smaller group size (model

226 with Gaussian error structure).

227 **Results**

228 *Temporal patterns in temperature, rainfall and reproduction*

229 Most rain falls between Dec and Feb (72%), when temperatures are high (Fig.1a). Most pied

230 babbler breeding activity occurs between Oct and Dec (68%), when conditions are generally

231 drier and cooler than later in the season (Fig.1a). The total number of days (Oct–Mar) exceeding

232 35.5°C, identified as a critical temperature threshold in pied babblers [56,57], has increased

233 significantly at the study site since 2005 ($F_{1,12} = 7.448$, $p = 0.018$; Fig.1b). Total summer rainfall

234 (Oct–Mar) over the same time period was highly variable but showed a declining, non-

235 statistically significant trend ($F_{1,12} = 1.616$, $p = 0.228$; Fig.1c). Both the number of nests fledged

236 (a non-significant trend; $F_{1,12} = 3.747$, $p = 0.077$; Fig.1d) and the number of surviving young

237 produced ($F_{1,12} = 5,285$, $p = 0.040$; Fig.1e) have declined at the study site since 2005, despite the

238 number of groups monitored remaining relatively constant between years (coefficient of

239 variation = 0.17).

240 *Survival probabilities during each development stage*

241 Overall, 31.4 ± 10.9% of breeding attempts produced at least one fledgling that survived to

242 nutritional independence. Mean (± se) survival probabilities of young differed between life

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243   stages (incubation, nestling, dependent fledgling), with lower survival probabilities during early

244   development in the nest, on average, than post-fledging (Fig. S1c).

245   Of 489 breeding attempts by 50 groups over 14 breeding seasons, 339 hatched (69.3%).

246   The probability of at least one egg per clutch hatching decreased as mean daily maximum

247   temperatures (mean T_{maxInc}) increased (Table 1a). We found no evidence that mean T_{minInc}, mean

248   T_{varInc}, rainfall or group size, or interactions between environmental conditions, influenced the

249   probability of hatching (see Table S2 for full model output). For the period between initiation of

250   incubation and hatching, a breakpoint was detected at 35.4°C (95% CI: 33.9, 36.9): there was no

251   effect of mean T_{maxInc} on age at hatch/fail below 35.4°C ($F_{1,399} = 0.008$, $p = 0.926$), whereas

252   above 35.4°C, age at hatch/fail significantly declined with increasing temperature ($F_{1,85} = 9.490$,

253     $p = 0.003$, Fig. 2a).

254   Of 339 hatched nests by 46 groups over 14 breeding seasons, 210 fledged at least one

255   chick (61.9%). The probability of at least one nestling per brood surviving to fledge increased

256   with increasing mean daily maximum temperatures during the nestling period (mean $T_{maxBrood}$)

257   until ~33.1°C, above which survival probability decreased (Table 1b). We found no evidence

258   that mean $T_{minBrood}$, mean $T_{varBrood}$, rainfall or group size, or interactions between group size and

259   environmental conditions, influenced the probability of fledging (see Table S3 for full model

260   output). For the period between hatching and fledging a breakpoint was detected at 37.3°C (95%

261   CI: 36.5, 38.0). Age at fledge/fail tended to increase with increasing mean $T_{maxBrood}$ until 37.3°C

262   ($F_{1,317} = 3.239$, $p = 0.073$), above which age at fledge/fail declined significantly with increasing

263   temperature ($F_{1,20} = 13.370$, $p = 0.002$, Fig. 2b). At mean $T_{maxBrood} > 38$°C (n=12), no nests

264   fledged young.

12

265   Of 198 fledged broods with complete weather data by 36 groups over 14 breeding

266   seasons, 160 produced at least one fledgling that survived to nutritional independence (80.8%).

267   The probability of surviving to nutritional independence increased as rainfall during the post-

268   fledging period increased ($Rain_{90}$; Table 1c). We found no evidence that mean T_{min90c}, mean

269   T_{max90}, mean T_{var90}, group size or interactions between group size and environmental conditions

270   influenced the probability of fledgling survival to independence (see Table S4 for full model

271   output). We also found no evidence for a breakpoint in the data related to variation in mean

272   T_{max90} for the period between fledging and independence (Davies' test $p = 0.288$). While

273   temperature was not a significant predictor of survival to nutritional independence in either of the

274   model sets, no breeding attempts produced surviving young at mean $T_{max90} > 38°C$ (n=8).

275   *Influence of nestling mass on fledgling survival*

276   The confirmatory path analysis model explained 47% of the variation in survival from fledging

277   to independence (Fig. 3; $X^2 = 0.689$, $p = 0.708$). Higher $Rain_{90}$ was directly associated with an

278   increased probability of surviving to independence, and larger group sizes were indirectly

279   associated with increased survival via the positive effect of larger group size on nestling $Mass_{11}$.

280   High mean $T_{maxBrood}$ was associated with reduced survival both directly and indirectly (high

281   mean $T_{maxBrood}$ was associated with reduced nestling mass, which in turn predicted reduced

282   survival). There was no evidence for a direct effect of either mean T_{max90} or natal group size on

283   survival to independence, or an effect of rainfall prior to the breeding attempt ($Rain_{60}$) on

284   nestling $Mass_{11}$.

285   Specifically, larger nestlings were more likely to survive to independence (Est = 0.116, p

286   = 0.019), as were fledglings that experienced higher $Rain_{90}$ (Est = 0.750, $p < 0.001$). However,

287   fledglings were less likely to survive (Est = -0.169, $p = 0.003$) when they had experienced higher

13

288   mean $T_{maxBrood}$. Nestlings were heavier when raised by larger groups (Est = 0.118, p = 0.021) and

289   lighter when they experienced higher mean $T_{maxBrood}$ (Est = -0.224, p < 0.001). There was an

290   indirect negative effect of mean $T_{maxBrood}$ on survival via nestling mass [Est = -0.026 (calculated

291   by multiplying standarised estimates for each component of the indirect path: -0.244 × 0.116; see

292   Fig. 3)]. The combined direct and indirect effect of mean $T_{maxBrood}$ (via nestling mass) on survival

293   was negative [-0.195, calculated by summing standardised estimates for direct and indirect paths:

294   -0.169 + (-0.026); see Fig. 3]. The direct effect of mean $T_{maxBrood}$ was more prominent (~87% of

295   the combined effect) than the indirect effect via nestling mass (~13% of the combined effect).

296   Natal group size had an indirect positive effect on survival via nestling mass [Est = 0.014 (=

297   0.118 x 0.116)], with an overall effect of natal group size = 0.132 (0.059+0.014).

298   **Discussion**

299   We investigated the impacts of environmental conditions and the potential for larger group sizes

300   to buffer against these impacts in a cooperatively breeding bird, focusing on egg, nestling, and

301   fledgling survival. We present three main findings. First, exposure to high mean daily maximum

302   temperatures during early development was associated with significant reductions in survival

303   probabilities, in keeping with other recent studies [24,26,82]. Second, both environmental

304   (largely direct) and social (indirect) factors were important for predicting survival during

305   different development stages. Third, contrary to our expectations, we found no evidence that

306   effects of T_{max} and rainfall on reproduction were moderated by group size, despite considerable

307   statistical power to detect such interactions. Taken together with evidence that temperatures are

308   increasing and rainfall decreasing at the study site, and that the number of surviving young

309   produced in the study population showed similar declines, the impacts of high temperatures on

310   mortality during early development are concerning.

14

Impacts of high temperatures during early development

In pied babblers, high mean daily maximum temperatures during early development were associated with a significantly increased risk of mortality. Adverse weather is known to impair egg [83] and nestling development [84]. For example, survival to fledging can be compromised both by sub-optimally cool [85] and sub-optimally hot conditions [26,28]. For the early development stages before fledging, we identified temperature thresholds in the mid- to high-30s (35.4°C during incubation, and 37.3°C for nestlings) above which survival of eggs and young became significantly less likely. These temperatures are within ~2°C of an apparent upper limit (38°C) above which we recorded no successful breeding in this species over 15 years of research. While we did not detect a direct effect of high temperatures on post-fledging mortality (i.e. between fledging and independence) at the brood scale, path analysis revealed that the probability of individual fledglings surviving to independence was influenced by high temperatures experienced as a nestling (Mean $T_{maxBrood}$), both directly and indirectly via the effect of high temperatures on nestling $Mass_{11}$. This suggests that dependent pied babbler fledglings, similar to the young of other species [86,87], are influenced by carryover effects of high temperatures they experienced while still in the nest . With temperatures increasing rapidly in the Kalahari (van Wilgen *et al.* 2016), the 38°C limit for successful breeding in this species suggests that pied babblers may increasingly experience conditions that do not allow successful breeding. This could undermine population growth and ultimately lead to local extinctions for this species, although the effect may be mitigated by behavioural adjustments such as breeding earlier in the season or engaging in compensatory breeding during good years [63].

Different drivers of survival for each early development stage

15

The primary climatic (temperature and rainfall) and social (group size) drivers of survival probability were different across the three development stages. Mean daily maximum temperature was the strongest predictor of survival probability during both the incubation and nestling development stages. At high temperatures over prolonged periods, incubating birds may not be able to sustain nest attendance to regulate egg temperature [88], leaving eggs vulnerable to overheating and becoming unviable [15,83]. Likewise, several studies have reported that high temperatures constrain nestling growth [26,84,89], result in smaller nestlings overall [27,90,91], alter corticosterone levels [92,93], and reduce nestling survival probabilities [94,95].

Rainfall was the strongest predictor of survival probability during the dependent fledgling stage. Higher rainfall periods are associated with greater food availability [21,96], which likely enhanced both provisioning rates to fledglings [97] and their ability to find food for themselves [98,99]. In cooperative breeders, survival of young during this stage often improves with increasing group size [36,53]: larger groups may provision more regularly (Meade *et al.* 2010; but see Wiley & Ridley 2016), better detect and repel predators [52], or access higher quality territories or nest sites [16]. We did not find a direct effect of group size on survival to independence at the brood scale. However, path analysis indicated that group size influenced individual fledgling survival probabilities indirectly, via a positive effect on nestling mass. Nestling mass is a well-established positive predictor of post-fledging survival in cooperative breeders [16,77]. Larger nestlings are more mobile and better developed at fledging, enabling them to forage more effectively and avoid predators [100]. The presence of both direct and indirect (via negative effects on nestling $Mass_{11}$) effects of mean T_{max} during the nestling period on survival to independence suggests that carryover effects of high temperatures during early development continue to impact individual survival probabilities post-fledging [101,102].

16

Buffering effect of group size

357 We found a lack of a buffering effect of group size on the effects of high mean T_{max} on offspring

358 survival. While, as discussed above, we found an indirect positive effect of larger group size on

359 survival from fledging to independence, group size did not interact with the large and persistent

360 negative effects of high mean T_{max} on survival observed across all development stages to buffer

361 the detrimental effects of high temperatures on survival from one early development stage to the

362 next. This suggests that physiological tolerance limits [103] and resource constraints [104] at

363 high temperatures may exceed any potential buffering effect of group size on offspring survival

364 in cooperative breeders in arid and semi-arid environments [10].

365 *Conclusion*

366 In this study, negative effects of adverse climate conditions on breeding success in a cooperative

367 breeder were not moderated by group size, suggesting that reproduction in pied babblers is

368 constrained by available resources and physiology at high temperatures and low rainfall,

369 regardless of group size. Climate change is one of the defining challenges of our time, posing a

370 serious threat to biodiversity [3] and society [1]. The Intergovernmental Panel on Climate

371 Change predicts that the incidence of hot extremes will continue to become more frequent and

372 the length, frequency, and intensity of heatwaves will continue to increase over most land

373 masses [105]. At higher average and extreme temperatures, arid zone bird species may

374 increasingly experience temperatures that preclude successful breeding. We have observed both

375 increasing temperatures and declining rainfall, along with declining offspring survival, at the

376 study site over the last 15 years. Over time, the negative effects of these high temperatures on

377 offspring survival could limit population recruitment and lead to local extinctions. Despite the

378 intuitive appeal of the hypothesis that cooperative breeding may buffer against some of these

379　effects, we found no evidence this will be the case in pied babblers. Taken together, our findings

380　raise concerns for the long-term persistence of arid zone species in the face of rapidly changing

381　environmental conditions, and suggest that the presence of more helpers in a group is unlikely to

382　provide a buffer against reproductive failure as average and maximum temperatures increase

383　with advancing anthropogenic climate change.

18

Ethics statement

All data were collected under animal ethics permit numbers R2012/2006/V15/AR and 2016/V6/SC from the University of Cape Town and 1216/2016 from the Department of Environment and Nature Conservation, and blood samples were collected and bird banded by licenced professionals [blood sampling was authorised by the South African Veterinary Council (AL17/15885) and bird banding licences were issued by SAFRING (11663)].

Data accessibility statement

The datasets underlying all analyses presented in this study have been archived at the University of Cape Town's open access institutional data repository, ZivaHub (a figshare platform), where they are publicly available at doi: 10.25375/uct.12441899.v1.

Data accessibility statement

The authors declare that they have no competing interests.

Author contributions statement

ARR, SJC, ARB, and CNS conceived the study and secured funding. ARR started habituation of the study animals and collection of life history data in 2003 and has maintained it ever since; this was central to making the study possible. ARB undertook all fieldwork from 2016 onwards. ARB and ARR analysed the data. ARB drafted the manuscript. All authors contributed substantially to revisions, and gave final approval for publication.

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669   *assessment report*. Cambridge: Cambridge University Press.

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672 **Tables**

673 *Table 1: Top GLMM model set for factors influencing survival during early development. Model*

674 *averaging was implemented for models with ΔAICc < 5 of the 'best-fit' model. Significant terms*

675 *after model averaging are shown in bold. Null models shown for comparison with top model*

676 *sets.*

Table 1a: Factors influencing survival from initiation of incubation to hatching Data from 489 clutches by 50 different groups over 14 breeding seasons			
	AICc	ΔAICc	ωί
Null model	600.60	5.36	0.00
Top model set:			
Mean T_{maxInc}	595.24	0.00	0.47
Mean T_{maxInc} + $Rain_{60}$ + Mean T_{maxInc} * $Rain_{60}$	595.76	0.52	0.36
Mean T_{maxInc} + Natal group size + Mean T_{maxInc} * Natal group size	597.31	2.06	0.17
Effect size of explanatory terms after model averaging	*Estimate*	*SE*	*95% CI*
Intercept	0.870	0.114	0.645/1.094
Mean T_{maxInc}	**-0.281**	**0.102**	**-0.481/-0.081**
$Rain_{60}$	0.025	0.070	-0.113/0.163
Natal group size	0.024	0.069	-0.112/0.161
Mean T_{maxInc} * $Rain_{60}$	0.071	0.114	-0.153/0.295
Mean T_{maxInc} * Natal group size	0.005	0.043	-0.080/0.089

*Residual deviance: 577.369 on 486 degrees of freedom (ratio: 1.188)

Table 1b: Factors influencing survival from hatching to fledging Data from 339 broods by 46 different groups over 14 breeding seasons			
	AICc	ΔAICc	ωί
Null model	452.20	20.47	0.00
Top model set:			
Mean $T_{maxBrood}$ + Mean $T_{maxBrood}$ ^2 + Mean $T_{varBrood}$ + Natal group size	431.73	0.00	0.50
Mean $T_{maxBrood}$ + Mean $T_{maxBrood}$ ^2 + Natal group size	433.02	1.29	0.26
Mean $T_{maxBrood}$ + Mean $T_{maxBrood}$ ^2 + Mean $T_{varBrood}$	434.20	2.47	0.15
Mean $T_{maxBrood}$ + Mean $T_{maxBrood}$ ^2	435.17	3.43	0.09
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*
Intercept	0.862	0.163	0.540/1.182
Mean $T_{maxBrood}$	-0.074	0.121	-0.312/0.165
Mean $T_{maxBrood}$ ^2	**-0.373**	**0.097**	**-0.564/-0.183**
Mean $T_{varBrood}$	-0.146	0.149	-0.439/0.147

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Natal group size	0.200	0.157	-0.108/0.508

*Residual deviance: 411.141 on 334 degrees of freedom (ratio: 1.231)

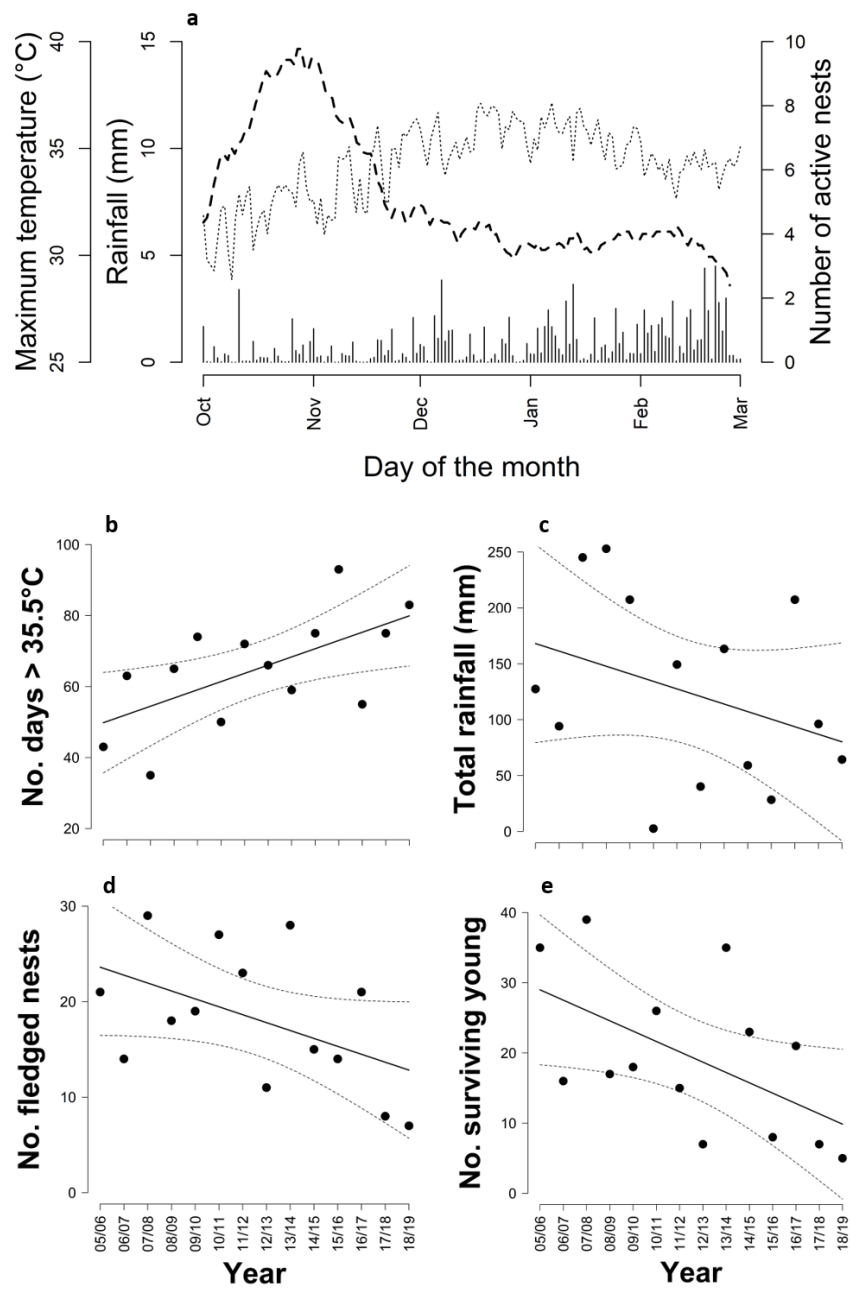| Table 1c: Factors influencing survival from fledging to nutritional independence Data from 198 broods by 35 different groups over 14 breeding seasons			
	AICc	*ΔAICc*	*ωí*
Null model	195.90	87.52	0.00
Top model set:			
Mean T_{max90} + $Rain_{90}$ + Mean T_{max90} * $Rain_{90}$	108.38	0.00	0.44
Natal group size + $Rain_{90}$ + Natal group size * $Rain_{90}$	108.40	0.03	0.44
$Rain_{90}$	111.01	2.64	0.12
Effect size of explanatory terms after model averaging	*Effect*	*SE*	*95% CI*
Intercept	4.936	1.091	2.787/7.086
Mean T_{max90}	0.249	0.566	-0.865/1.364
Natal group size	-0.761	0.998	-2.720/1.198
$Rain_{90}$	**4.748**	**1.028**	**2.721/6.775**
Mean T_{max90} * $Rain_{90}$	0.482	0.725	-0.943/1.907
Natal group size * $Rain_{90}$	-0.544	0.772	-2.061/0.974

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Figure legends

680 *Figure 1: (a) breeding activity between Oct and Mar (average number of active nests per day:*

681 *dashed line), relative to temperature (average daily maximum temperature (°C) per day: dotted*

682 *line) and rainfall (average rainfall (mm) per day: vertical bars). (b) the number of days >*

683 *35.5°C at the study site (c) total summer rainfall, (d) number of southern pied babbler* Turdoides

684 bicolor *nests fledged in the study population, and (e) number of surviving young produced in the*

685 *study population per breeding season per year (austral summer: 1 Oct to 1 Mar) since 2005 .*

686 *Black lines represent predictions from the models, and dashed lines the 95% CIs.*

687 *Figure 2: Survival from (a) initiation of incubation to hatch and (b) hatch to fledge as a function*

688 *of mean daily maximum air temperature during the corresponding time period. Lines represent*

689 *segmented linear regressions for the relationship between survival age and air temperature*

690 *above and below the detected temperature thresholds. Open circles indicate that the clutch (a) or*

691 *brood (b) transitioned to the next development stage; crosses indicate failure of the clutch (a) or*

692 *brood (b).*

693 *Figure 3: Confirmatory path analysis exploring the effects of environmental factors (temperature*

694 *and rainfall) and group size on nestling body mass and survival to nutritional independence (90*

695 *days). Boxes represent measured variables. Arrows represent hypothesised unidirectional*

696 *relationships among variables. Solid arrows denote positive relationships, dashed arrows*

697 *negative relationships. Unstandardised path coefficients are shown in bold, followed by standard*

698 *errors in parentheses, standardised estimates, and an indicator of statistical significance of the*

699 *effect (*). Non-significant paths are grey. The thickness of significant paths has been scaled*

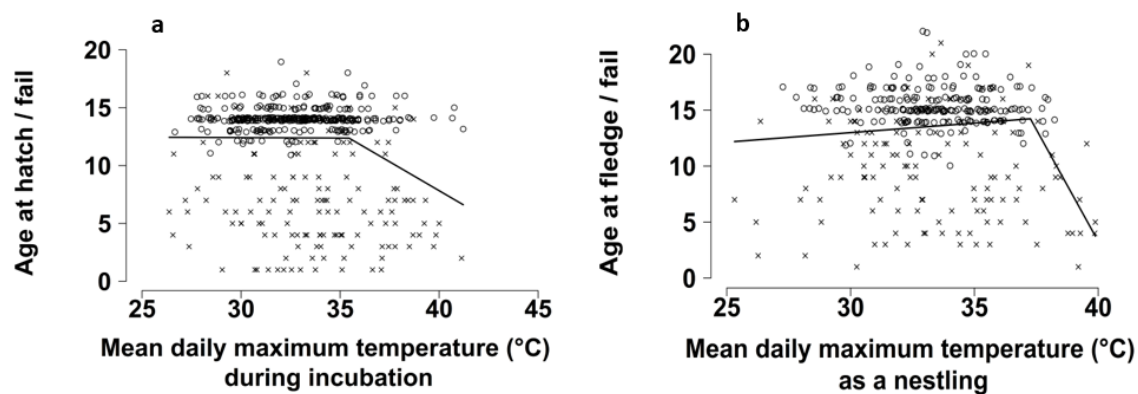700 *relative to the absolute magnitude of the standardised estimates, such that stronger effects have*

701 *thicker arrows. R^2 for component models are given (grey shaded boxes) above response*
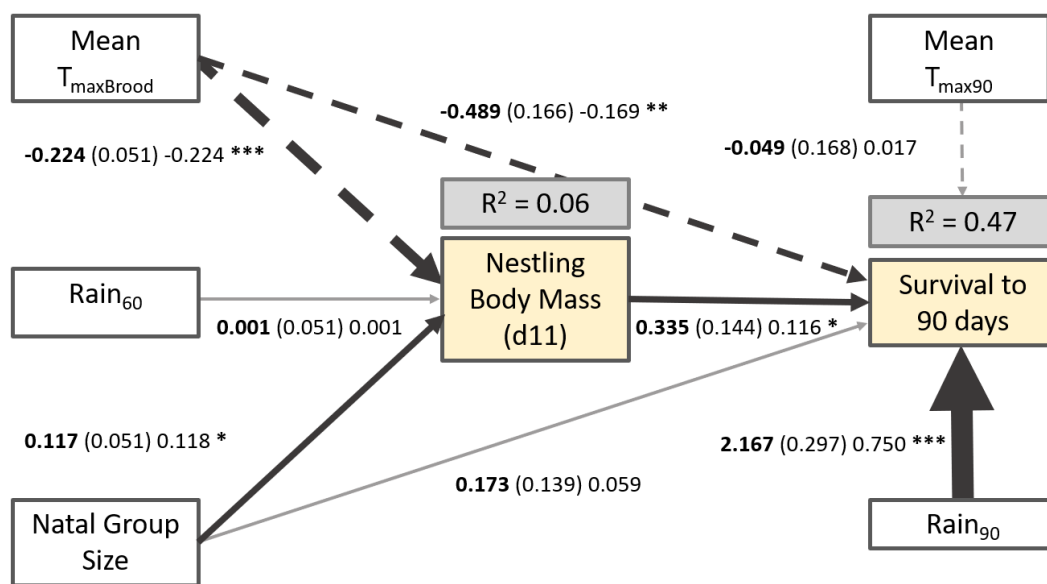
702 *variables (orange shaded boxes).*

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Figure 1

707 **<u>Figure 2</u>**

Mean daily maximum temperature (°C) during incubation

Mean daily maximum temperature (°C) as a nestling

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711 **Figure 3**

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