

Running head: High temperatures limit fledging

1 **Title: Direct and indirect effects of high temperatures on fledging success in a cooperatively**
2 **breeding bird.**

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10 **Lay Summary**

11 Hot and dry weather limits breeding success in arid-zone birds. Southern pied babbler nestlings
12 in the Kalahari are smaller and grow less vigorously during hot and dry weather. Parents adjust
13 their feeding strategies during hot weather, but this could not compensate for the large, direct
14 effects of high temperatures on nestling size and daily growth rates. Increasingly hot conditions
15 due to climate change threaten this and other arid-zone species.

16 **Abstract**

17 High temperatures and low rainfall consistently constrain reproduction in arid-zone bird species.
18 Understanding the mechanisms underlying this pattern is critical for predicting how climate
19 change will influence population persistence and to inform conservation and management. In this
20 study, we analysed Southern Pied Babbler *Turdoides* nestling survival, daily growth rate and adult
21 investment behaviour during the nestling period over three austral summer breeding seasons. High
22 temperatures were associated with lower body mass, shorter tarsi, and reduced daily growth rates
23 of nestlings. Piecewise structural equation modelling suggests that direct impacts of temperature
24 had the strongest influence, followed by changes in provisioning rates by adults to older nestlings.

Running head: High temperatures limit fledging

25 Adjustments to adult provisioning strategies did not compensate for direct negative effects of high
26 air temperatures on nestling body mass, tarsus and wing length, or daily growth rates. Declining
27 reproductive success during hot weather poses a potentially serious threat to population
28 replacement and persistence as climate change progresses, even for currently common and
29 widespread species. Significantly lower offspring survival as a result of climate warming will
30 likely contribute to the collapse of animal communities well before temperatures regularly
31 approach or exceed lethal tolerance limits. Detailed mechanistic data like these allow us to model
32 the pathways by which high temperature causes nest failure. In turn, this could allow us to design
33 targeted conservation action to effectively mitigate climate effects.

34 **Keywords**

35 climate change, cooperative breeding, dryland ecology, environmental variability, survival of
36 young, avian reproduction, reproductive success

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Running head: High temperatures limit fledging

38 **Introduction**

39 Anthropogenic climate change is affecting wildlife populations around the world (Saino et al.
40 2011; Iknayan and Beissinger 2018; Ripple et al. 2019; Rosenberg et al. 2019; van de Ven,
41 McKechnie, et al. 2020), in part via impacts of altered temperature and rainfall patterns on
42 reproductive success (Stevenson and Bryant 2000; Cahill et al. 2013; Cunningham et al. 2013;
43 Paniw et al. 2019; van de Ven, Fuller, et al. 2020). Accurately predicting how climate change will
44 influence reproduction, and hence population persistence, requires an understanding of the
45 mechanistic links between climate and reproductive outcomes (Conradie et al. 2019; Ratnayake et
46 al. 2019). Therefore, we need to understand the mechanisms by which temperature and rainfall
47 affect reproductive outcomes via direct effects on offspring size, daily growth rates, and survival,
48 as well as indirectly via effects on parental care strategies (Buchholz et al. 2019; van de Ven,
49 McKechnie, et al. 2020).

50 Adverse weather conditions impair nestling development (Mainwaring et al. 2016; Imlay
51 et al. 2018) by causing a trade-off between devoting energy to thermoregulation or to growth
52 (Dawson et al. 2005). High temperatures constrain nestling growth (Cunningham et al. 2013;
53 Mainwaring and Hartley 2016; Andreasson et al. 2018), result in smaller nestlings overall
54 (Salaberria et al. 2014; Wada et al. 2015; Rodriguez and Barba 2016), alter corticosterone levels
55 (Newberry and Swanson 2018; Crino et al. 2020) and reduce survival probabilities (Greño et al.
56 2008; Zuckerberg et al. 2018; Bourne, Cunningham, et al. 2020a). Higher rainfall often has a
57 positive effect on nestling development (Wiley and Ridley 2016) and survival (Skagen and Yackel
58 Adams 2012; Mares et al. 2017), at least in arid and semi-arid ecosystems (Cumming and Bernard
59 1997; Hidalgo Aranzamendi et al. 2019), although see Morganti et al. (2017) and Cox et al. (2019)
60 for effects of rainy weather in temperate environments. Nestlings are substantially less likely to

Running head: High temperatures limit fledging

61 survive during droughts compared to wetter periods (Morrison and Bolger 2002; Conrey et al.
62 2016; Cruz-McDonnell and Wolf 2016; Bourne, Cunningham, et al. 2020b).

63 Effects of temperature and rainfall on nestlings may be direct, due to impacts on nestling
64 physiology, or indirect, via for example impacts on parental care behaviours and investment
65 strategies (Drent and Daan 1980; Salaberria et al. 2014; van de Ven, McKechnie, et al. 2020).
66 Several recent studies suggest that negative effects of adverse weather can be moderated by
67 adjustments in parental care strategies including brooding (Oswald et al. 2008; Mainwaring and
68 Hartley 2016) and provisioning (Auer and Martin 2017; Sofaer et al. 2018). Other studies indicate
69 that birds trade off foraging behaviour against thermoregulation when provisioning nests, reducing
70 provisioning rates as temperatures rise (Cunningham et al. 2013; Wiley and Ridley 2016; van de
71 Ven et al. 2019).

72 The Southern Pied Babbler *Turdoides bicolor* (hereafter pied babbler) is a medium sized
73 (60-90 g) cooperatively breeding passerine endemic to a semi-arid ecosystem, the Kalahari Desert,
74 characterised by hot summers and periodic droughts (Hockey et al. 2005; van Wilgen et al. 2016).
75 Rainfall is extremely variable between years (MacKellar et al. 2014) and, over the last 20 years,
76 high temperature extremes within the Kalahari have increased in both frequency and severity
77 (Kruger and Sekele 2013; Bourne, Cunningham, et al. 2020a). Previous research on this species
78 has shown that high air temperatures during early development are associated with reduced
79 provisioning rates to nestlings (Wiley and Ridley 2016), smaller nestlings (Wiley and Ridley
80 2016), reduced likelihood of fledging at least one chick per breeding attempt (Bourne,
81 Cunningham, et al. 2020a), lower recruitment of young into the adult population (Bourne,
82 Cunningham, et al. 2020c) and compromised adult foraging efficiency and body mass maintenance
83 (du Plessis et al. 2012). In short, pied babblers at our study site are likely to reproduce less

Running head: High temperatures limit fledging

84 successfully during droughts (Bourne, Cunningham, et al. 2020b) and completely fail to fledge
85 young at mean daily maximum air temperatures of $> 38^{\circ}\text{C}$ between hatching and fledging (Bourne,
86 Cunningham, et al. 2020a).

87 Pied babblers are territorial year-round residents and a habituated population at the study
88 site enables collecting detailed life history and behavioural data from known individuals (Ridley
89 2016). Here, we use detailed nestling morphometric data and adult behavioural data collected from
90 marked individuals to explore the mechanisms by which temperature, rainfall and group size
91 influence the growth and survival of young from hatching to fledging. Specifically, we used
92 piecewise structural equation modelling [piecewise SEM, (Shipley 2009; Larson et al. 2015; van
93 de Ven, McKechnie, et al. 2020)] to empirically test whether temperature, rainfall, and group size
94 influence fledging probabilities via direct effects on nestling mass and structural size (suggesting
95 a physiological mechanism) or via the indirect effects of adjustments in adult investment behaviour
96 (suggesting a behavioural mechanism). We further explored temperature, rainfall and group size
97 effects on nestling daily growth rates and the foraging and provisioning behaviour of adult group
98 members, both important for interpreting components of the piecewise SEM analyses. Detailed
99 mechanistic data like these allow us to model the pathways by which high temperatures result in
100 nest failure. In turn, this could allow us to design targeted conservation action to effectively
101 mitigate climate effects.

102 Building on previous work demonstrating the impact of temperature on nestling body mass
103 and adult provisioning rates in pied babblers (Wiley and Ridley 2016), we tested the hypothesis
104 that high temperatures and low rainfall should reduce nestling size and growth via a combination
105 of both direct effects on nestlings and indirect effects via reduced provisioning effort. Because
106 pied babblers are cooperative breeders that engage in load-lightening behaviours (Raihani and

Running head: High temperatures limit fledging

107 Ridley 2008; Ridley and Raihani 2008; Wiley and Ridley 2016), we further tested the hypothesis
108 that individuals in larger groups should allocate more time to self-maintenance activities (such as
109 foraging, resting and preening) during hot weather while maintaining the overall biomass
110 provisioned to young, sustaining nestling growth rates.

111 **Materials and Methods**

112 *Study site and system*

113 Data were collected for each austral summer breeding season between September 2016 and
114 February 2019 (three breeding seasons in total) at the Kuruman River Reserve (33 km², KRR;
115 26°58'S, 21°49'E) in the southern Kalahari. Mean summer daily maximum temperatures in the
116 region average 34.7 ± 9.7 °C and mean annual precipitation averages 186.2 ± 87.5 mm (1995–
117 2015, van de Ven, McKechnie & Cunningham 2019). The Kalahari region is characterised by
118 hot summers and periodic droughts (van Wilgen et al. 2016), with extremely variable rainfall
119 between years (MacKellar et al. 2014). Pied babblers live in groups ranging in size from 3–15
120 adults (Raihani and Ridley 2007a) and breed during the austral summer (September–March),
121 when it is hottest (Ridley 2016). Pied babbler groups consist of a single breeding pair with
122 subordinate helpers of both sexes (Nelson-Flower et al. 2011), and all adult group members
123 (individuals > 1 year old) engage in cooperative behaviours including territory defence and
124 parental care (Ridley and Raihani 2007; Ridley 2016). Pied babblers lay clutches of ~3 eggs
125 (Ridley 2016), which hatch after 14 ± 1.2 days (Bourne, Cunningham, et al. 2020a), and
126 nestlings fledge after 15.4 ± 1.7 days (Bourne, Cunningham, et al. 2020a).

127 *Nestling size and daily growth rates (nestling age day 5 and day 11)*

128 Following Ridley and van den Heuvel (2012), we monitored all nests initiated (clutches laid and
129 incubated) in the study population during each breeding season to determine hatching dates ($n =$

Running head: High temperatures limit fledging

130 103 nests in total; 2016/17 $n = 61$, 2017/18 $n = 22$, 2018/19 $n = 20$). Nestlings were measured
131 (body mass, tarsus length, and wing length) between 06h00 and 07h00 (morning) and again
132 between 18h00 and 19h00 (evening) on the 5th day after hatching (d5, representing growth during
133 a fast growth phase; $n = 93$ nestlings from 37 broods) and the 11th day after hatching (d11,
134 representing growth during an asymptote phase; $n = 77$ nestlings from 34 broods). Body mass
135 measurements (± 0.1 g) were taken by weighing nestlings on a top-pan scale. Tarsus length was
136 measured (± 0.1 mm) using clock-dial Vernier calipers and wing length (± 0.1 mm) using a stopped
137 rule. All nestling measurements were taken by the same person. Data are presented for right tarsus
138 and right wing. Natal group size (the number of adults present during the period between hatching
139 and fledging) and brood size (the number of nestlings in the brood on each measurement day) were
140 recorded for each brood on each measurement day.

141 Nestling size was recorded as evening body mass, tarsus length and wing length,
142 representing nestling mass and size at the end of a full day of provisioning by adults. Nestling
143 daily growth rates were calculated as the percentage change (Δ) in body mass, tarsus length, and
144 wing length between morning and evening measurements, standardised for differences in the time
145 between measurements using the equation presented by du Plessis et al (2012):

$$146 \quad \Delta = 100[(x_2 - x_1)/x_2]/[\Delta_t/12]$$

147 where Δ_t = number of hours between t_1 (time of morning measurement) and t_2 (time of
148 evening measurement); x_1 = mass, tarsus, or wing length measurement at t_1 and x_2 = measurement
149 at t_2 .

Running head: High temperatures limit fledging

150 *Provisioning rates to nests (nestling age day 5 and day 11)*

151 We recorded the number of provisioning visits to the nest per unit time observed during
152 the morning (08h00 to 09h30), at midday (12h00 to 13h00), and in the afternoon (15h00 to 16h30)
153 on d5 ($n = 26$ broods) and d11 ($n = 25$ broods), between morning and evening nestling
154 measurements. Data on provisioning visits were collected using a combination of video cameras
155 (Sony HDR-XR160E) placed on a tripod 4–6 m from the nest and nest watches undertaken by one
156 human observer with binoculars, seated 15–20 m from the nest. Provisioning data were captured
157 using CyberTracker software (v3.448; www.cybertracker.org) on an Android smartphone
158 (Mobicel *TRENDY*).

159 *Adult behaviour data (nestling age day 7-9)*

160 To determine effects of temperature, rainfall and group size on the proportion of time adult birds
161 allocated to parental care vs. self-maintenance, we conducted 20-minute continuous time-activity
162 focal behaviour observations (Altmann 1974) on up to four different adult birds per day within
163 each of 6 focal sessions. We focused on groups with 7- to 9-day-old nestlings, i.e. between the
164 days on which we had collected nestling morphometric measurements, at 26 different broods.
165 Focal sessions lasted two hours each, with the first starting at 07h00 and the last starting at 17h00
166 (i.e. 07h00 to 08h59, 09h00 to 10h59, 11h00 to 12h59, 13h00 to 14h59, 15h00 to 16h59, 17h00 to
167 19h00). We collected 593 focal behavioural observations (mean focal length = 19 ± 1.9 min) over
168 108 focal days (mean daily observation length over a focal day = 108 ± 17 min) during three austral
169 summer breeding seasons (2016/17 $n = 60$ days, 2017/18 $n = 32$ days, 2018/19 $n = 16$ days). We
170 observed 29 males, 29 females, and 4 individuals of unknown sex. Of these, 27 were dominant
171 individuals and 35 were subordinates. When group size was = 3 adult individuals, the pair and the
172 single adult subordinate were studied; when group size was = 4, the pair and both subordinate

Running head: High temperatures limit fledging

173 adults were studied; when group size was > 4 , the pair and two subordinate adults of opposite sex
174 (where possible) were studied. We observed each focal individual once within each of the six daily
175 focal sessions, and randomised the order in which each individual was observed within each focal
176 session (*sensu* du Plessis et al (2012)). In this way, we collected approximately six focal behaviour
177 observations per bird per day, spread evenly across the day to minimise time of day effects on
178 summarised measurements. All birds for which we had fewer than four focal observations per day
179 were removed from the analyses ($n = 6$ of 68 individuals). From these data, we could estimate
180 individual investment in young at the nest (including number of provisioning visits to the nest,
181 biomass caught vs. provisioned, and time spent attending the nest for each individual), but not the
182 total number of provisions made to the nest by all group members on that day (because we had to
183 concentrate on one focal bird at a time). Behaviour data were captured on the Mobicel smartphone
184 using Prim8 software (McDonald and Johnson 2014), in which the duration of each observed
185 behaviour can be recorded to the nearest second.

186 For analyses of time budgets, we summed time observed foraging (foraging effort,
187 including searching for and handling prey), attending the nest (all visits to the nest, including
188 provisioning, shading and brooding), resting (preening, standing, and perching) and engaging in
189 other activities (e.g. walking, flying, on sentinel duty, interacting with neighbouring groups) and
190 calculated the proportion of time allocated to each set of activities across all six focals, at the scale
191 of a 'focal day'. During each focal behaviour observation, we collected detailed information for
192 each successful foraging event, including the size class of each item caught and whether or not the
193 item was provisioned to the nest. We converted prey captures to biomass (wet g) using the
194 calculations from Raihani & Ridley (2007b). We recorded foraging success as total biomass caught
195 per bird per focal day, and provisioning rates to the nest as total biomass provisioned per bird per

Running head: High temperatures limit fledging

196 focal day. Time allocations to different behaviours were averaged over all focals per individual as
197 focal observations were spread evenly across the day to minimise time-of-day effects on
198 behavioural investment patterns between individuals ($F_{5,489} = 1.283$, $P = 0.269$; Fig S1) and ensure
199 that data analysed at the scale of the focal day were comparable between birds and days.

200 *Temperature and rainfall*

201 Daily maximum temperature (T_{\max} , in °C) and rainfall (mm) data were collected from an on-site
202 weather station at the KRR (Vantage Pro2, Davis Instruments, Hayward, CA, USA). Weather
203 variables included in statistical models were T_{\max} on the measurement day and rainfall summed
204 for the 60 days prior to initiation of the breeding attempt (Rain₆₀), to allow for known delays
205 between rainfall and invertebrate emergence in the Kalahari (Cumming & Bernard, 1997; Ridley
206 & Child, 2009).

207 **Statistical analyses**

208 Statistical analyses were conducted in the R statistical environment, v 3.6.0, using R Studio (R
209 Core Team 2017).

210 *Nestling mass, size and survival (nestling age day 5 and day 11)*

211 In other bird species, larger nestlings with longer tarsi and more developed wings are more likely
212 to survive to fledging (Kruuk et al. 2015; Mumme et al. 2015; Martin et al. 2018), and prior
213 research on pied babblers has shown that nestling mass is influenced by environmental factors
214 such as temperature and rainfall (Wiley and Ridley 2016). We therefore undertook a series of
215 piecewise SEM analyses (Shipley 2009; Larson et al. 2015; van de Ven, McKechnie, et al. 2020)
216 to specify and simultaneously quantify all hypothesised relationships regarding whether and to
217 what extent the impacts of weather conditions on survival to fledging, via d5 and d11 evening

Running head: High temperatures limit fledging

218 body mass, tarsus length, and wing length, are direct (i.e. could be inferred to result from
219 physiological limitations of nestlings) or indirect (i.e. mediated via changes in adult behaviour and
220 therefore provisioning rates to nestlings). We computed piecewise SEMs using the R package
221 *piecewiseSEM* (Lefcheck 2016), which can accommodate multiple error structures. This capacity
222 is important because the response terms of our component models have different distributions (see
223 below). Path coefficients are partial regression coefficients and can be interpreted similarly to
224 simple and multiple regression outputs. Unstandardised effect sizes are reported and statistical
225 significance taken as $P < 0.05$ (Lefcheck 2016).

226 We used piecewise SEM analyses to test the following statistical hypotheses:

227 Survival to fledging is negatively affected by low nestling body mass, short tarsi, and short
228 wings (logit);

229 Nestling body mass, tarsus length, and wing length are negatively affected by a) high T_{\max}
230 on the measurement day, b) low Rain_{60} , c) smaller group size, d) larger brood size, and e) fewer
231 provisioning events (Gaussian);

232 Number of provisioning events is negatively affected by a) high T_{\max} , b) low Rain_{60} , c)
233 smaller group size, and d) smaller brood sizes (Poisson).

234 *Nestling daily growth rates (nestling age day 5 and day 11)*

235 Because daily growth rates influence the body mass, tarsus length, and wing length attained by d5
236 and d11 nestlings at the time of the evening measurement, we considered the effect of Rain_{60} , T_{\max} ,
237 brood size, and natal group size on the percentage change (Δ) in body mass, tarsus length, and
238 wing length between morning and evening measurements on d5 and d11, including brood identity
239 as a random term. The inclusion of group identity as a random terms in addition to brood identity

Running head: High temperatures limit fledging

240 resulted in unstable models and of the two random terms, brood identity explained the greatest
241 proportion of variation while avoiding destabilising the models (Grueber et al. 2011; Harrison et
242 al. 2018a). We used maximum likelihood linear mixed-effects models (LMMs) with Gaussian
243 error structure in the R package *lme4* (Bates et al. 2015).

244 Model selection using the Akaike's information criterion corrected for small sample size
245 (AICc) was used to determine the model/s that best explained patterns of variation in the data.
246 Lower AICc values were taken to represent more parsimonious models, following Harrison et al
247 (2018b). Where there were several models within 2 AICc of the top model, top model sets were
248 averaged using the package *MuMIn* (Barton 2015). Model estimates with confidence intervals that
249 did not intersect zero were considered to explain significant patterns in the data (Grueber et al.
250 2011). Model fits were evaluated using histograms of residuals and Normal Q-Q plots.

251 *Adult behaviour (nestling age day 7-9)*

252 To determine which variables best predicted the proportion of time adults spent foraging, resting,
253 and attending the nest, we fitted binomial GLMMs with Penalised Quasi-Likelihood (glmmPQL)
254 in the R package *MASS* (Venables and Ripley 2002). The glmmPQL approach, which precludes
255 model selection (Bolker et al. 2009), was used to address overdispersion in the data not adequately
256 resolved by the inclusion of an observation level random term while still allowing inclusion of the
257 random term for brood identity. Proportion of time spent foraging was modelled as a combined
258 vector of total time spent on the selected activity (seconds) versus total time observed (seconds).
259 The models included predictor variables T_{\max} , Rain_{60} , group size, and brood size, as well as sex
260 and rank of the focal bird. Nestling age was not included in the models because all observations
261 were collected when nestlings were 7-9 days old.

Running head: High temperatures limit fledging

262 To determine which variables best predicted biomass caught and biomass provisioned, we
263 fitted GLMMs with a Poisson error distribution (log link) in the package *lme4* (Bates et al. 2015).
264 Model selection was undertaken as described for nestling daily growth rates above. Response
265 variables were rounded to the nearest digit (biomass in g). We considered the influence of T_{\max} ,
266 $Rain_{60}$, group size, brood size, sex, and rank, and included quadratic terms for T_{\max} and group size
267 when there was no significant linear effect and visualisation of the data suggested a non-linear
268 relationship. Model estimates with confidence intervals that did not intersect zero were considered
269 to explain significant patterns in the data (Grueber et al. 2011). Model fits were evaluated using
270 the dispersion parameter. Nestling age was not included in the models because all observations
271 were collected when nestlings were 7-9 days old. Biomass was modelled as the total amount per
272 observation day because fitting these data resulted in models that were more stable than those
273 generated by fitting rates (e.g. biomass per hour).

274 Results

275 Maximum temperatures on data collection days ranged from 27.2 °C to 41.6 °C (mean = 33.7 ±
276 3.5 °C), and $Rain_{60}$ ranged from 0.8 to 174.2 mm (mean = 60.2 ± 55.5 mm). Group sizes averaged
277 4 ± 1 adults (range: 2 to 6) and brood sizes averaged 3 ± 1 nestlings (range: 1 to 5). Of 99 monitored
278 nests, 65 clutches hatched, 52 broods survived to 5-days-old (first nestling measurement day), 41
279 broods survived to 7- to 9-days-old (adult behaviour observation day), and 38 broods survived to
280 11-days-old (second nestling measurement day). We did not collect all data types at every breeding
281 attempt and sample sizes achieved are stated for each analysis below.

282 *Nestling mass, size, and survival (nestling age d5 and d11)*

283 Piecewise SEM analyses for d5 and d11 nestling mass explained 11% and 22% of the observed
284 variation in fledging probability respectively (d5: Fisher's *C* for tests of directed separation =

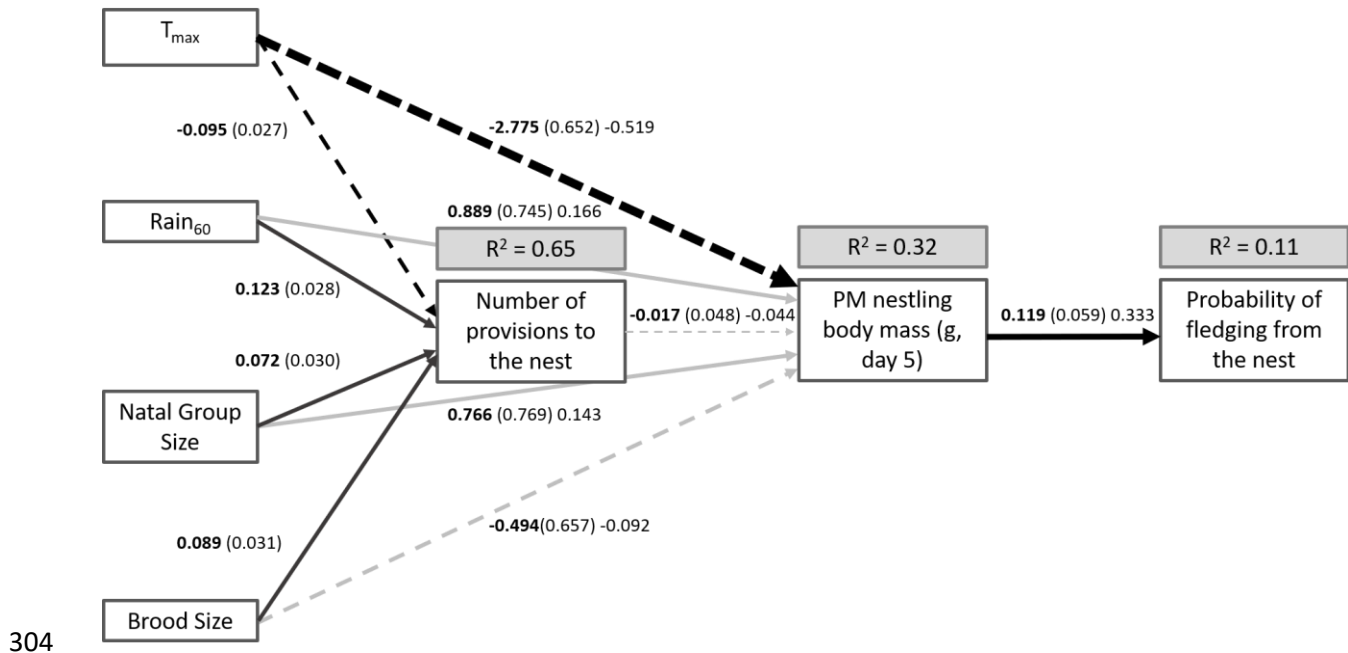
Running head: High temperatures limit fledging

285 11.95, $df = 10$, $P = 0.288$, Fig. 1; d11: Fisher's $C = 15.78$, $df = 10$, $P = 0.106$, Fig. 2). Piecewise
286 SEM analysis showed that, for d5 nestlings, direct effects of temperature on the measurement day
287 had a significant influence on nestling mass and therefore the probability of surviving until
288 fledging, whereas indirect effects mediated via provisioning rate did not (Fig 1). In contrast, both
289 of these pathways were statistically significant for d11 nestlings (Fig 2).

290 Specifically, high temperatures were directly associated with smaller nestling body mass on both
291 d5 and d11 (d5: Est = -2.775, $P < 0.001$; d11: Est = -0.482, $P = 0.018$), which in turn predicted the
292 probability of surviving to fledging in both cases (d5: Est = 0.119, $P = 0.042$; d11: Est = 0.478, P
293 = 0.043). Additionally, for both d5 and d11 nestlings, provisioning efforts by adults were
294 negatively associated with high temperatures (d5: Est = -0.095, $P < 0.001$; d11: Est = -0.154, $P =$
295 0.002). Number of provisioning visits to the nest averaged 31 on cool days ($T_{\max} < 35.5^{\circ}\text{C}$) and 22
296 on hot days ($T_{\max} \geq 35.5^{\circ}\text{C}$) for d5 nestlings, and 42 and 26 respectively for d11 nestlings. For
297 both d5 and d11 nestlings, provisioning efforts by adults were positively associated with Rain_{60}
298 (d5: Est = 0.123, $P < 0.001$; d11: Est = 0.232, $P < 0.001$), group size (d5: Est = 0.089, $P = 0.018$;
299 d11: Est = 0.155, $P < 0.001$), and brood size (d5: Est = 0.089, $P = 0.004$; d11: Est = 0.127, $P =$
300 0.004). Number of provisioning visits to the nest predicted larger nestling mass (and therefore
301 higher probability of fledging) on d11 only (d5: Est = -0.017, $P = 0.726$, d11: Est = 0.417, $P =$
302 0.033).

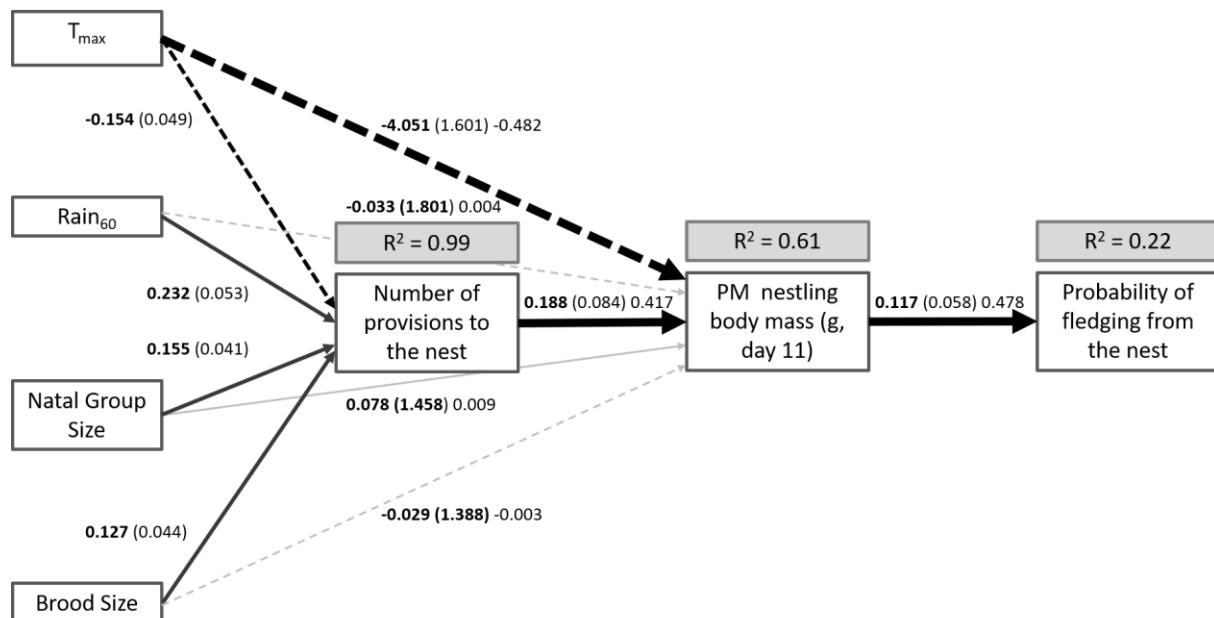
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Running head: High temperatures limit fledging



305 *Figure 1: Piecewise SEM exploring the effects of environmental factors (temperature and rainfall), group size, and brood size on*
 306 *individual probabilities of fledging via number of provisioning visits and nestling mass (evening) 5 days after hatching. Boxes*
 307 *represent measured variables. Arrows represent unidirectional relationships among variables. Solid arrows denote positive*
 308 *relationships, dashed arrows negative relationships. Path coefficients are shown in bold, followed by standard errors in*
 309 *parentheses. Standardised coefficients are shown after standard errors for all pathways except those in the Poisson-distributed*
 310 *model with number of provisions to the nest as the response variable, for which standardised estimates could not be calculated.*
 311 *Non-significant paths are grey. Path thickness has been scaled relative to the absolute magnitude of the standardised estimates,*
 312 *such that stronger effects have thicker arrows. R² for component models are given in the grey boxes above response variables.*

313



314

315 *Figure 2: Piecewise SEM exploring the effects of environmental factors (temperature and rainfall), group size, and brood size on*
 316 *individual probabilities of fledging via number of provisioning visits and nestling mass (evening) 11 days after hatching. Boxes*

Running head: High temperatures limit fledging

317 *represent measured variables. Arrows represent unidirectional relationships among variables. Solid arrows denote positive*
318 *relationships, dashed arrows negative relationships Path coefficients are shown in bold, followed by standard errors in*
319 *parentheses. Standardised coefficients are shown after standard errors for all pathways except those in the Poisson-distributed*
320 *model with number of provisions to the nest as the response variable, for which standardised estimates could not be calculated.*
321 *Non-significant paths are grey. Path thickness has been scaled relative to the absolute magnitude of the standardised estimates,*
322 *such that stronger effects have thicker arrows. R² for component models are given in the grey boxes above response variables.*

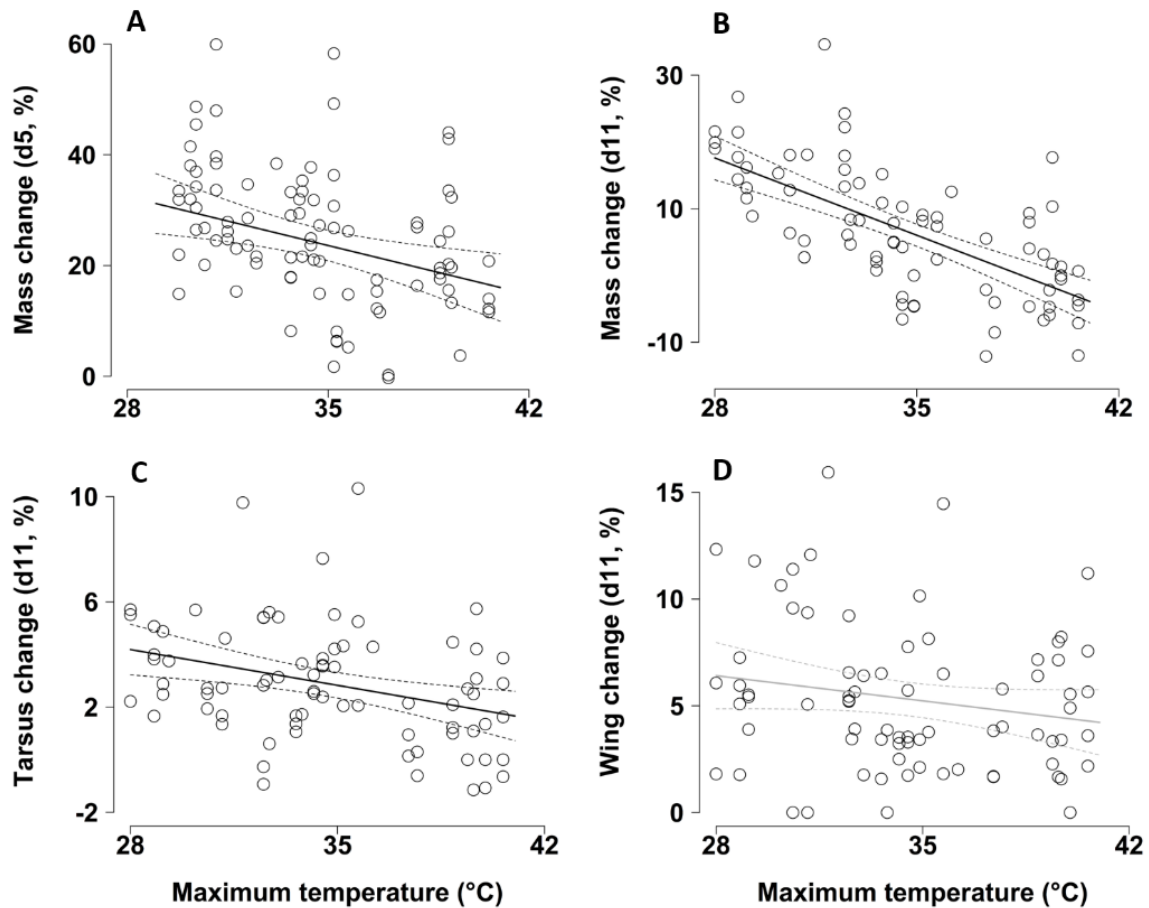
323 Piecewise SEM for tarsus length and wing length explained < 4% of the variation in
324 fledging probability in d5 nestlings and 33–36% of the variation in fledging probability in d11
325 nestlings (*Fisher's C* < 15.08, *df* = 10, *P* > 0.129 in all cases, Appendix Fig. S2–S5). Relationships
326 between T_{\max} , group size, $Rain_{60}$, brood size and provisioning rates were the same as for nestling
327 mass models above as these used identical datasets. Neither tarsus nor wing length on d5
328 influenced fledging probabilities, but nestlings with longer tarsi (Est = 0.510, *P* = 0.016) and longer
329 wings (Est = 0.213, *P* = 0.021) on d11 were more likely to fledge. We found no evidence that
330 tarsus or wing length were themselves influenced by T_{\max} , $Rain_{60}$, group size, brood size, or
331 number of provisioning visits for either nestling age class.

332 *Nestling daily growth rates (nestling age d5 and d11)*

333 T_{\max} was the most parsimonious predictor of daily mass gain both in d5 and d11 nestlings,
334 consistent with the results of the piecewise SEM (i.e. that T_{\max} was an important predictor of
335 evening body mass). Nestlings gained less mass, and sometimes even lost mass, between morning
336 and evening measurements on hotter days. For both d5 and d11 nestlings, we found single best-fit
337 models for daily mass change containing only T_{\max} (d5: model weight = 0.645; *n* = 93; Est = -
338 4.043 ± 1.986 , 95% CI: -7.922, -0.151, *t* = -2.031; Fig. 3A; d11: model weight = 1.00; *n* = 77; Est
339 = -7.028 ± 1.122 , 95% CI: -8.393, 4.034, *t* = -6.262, Fig. 3B). Percentage change in tarsus length
340 and wing length over the same 12 h period was not influenced by any of the included predictor
341 variables in d5 nestlings, but nestling tarsi grew significantly less between morning and evening
342 measurements on hotter days in d11 nestlings (top model weight = 0.772; Est = -0.804 ± 0.287 ,
343 95% CI: -1.381, -0.285, *t* = -2.797; Fig. 3C). Although the effect was not statistically significant,

Running head: High temperatures limit fledging

344 d11 nestling wings also tended to grow less on hotter days (Est = -0.651 ± 0.396 , 95% CI: -1.427,
345 0.125, $t = -1.643$; Fig. 4D). We found no evidence for effects of Rain₆₀, brood size, or natal group
346 size in any of the nestling daily growth rate analyses (see Table S1–S3 for full model selection
347 outputs).



348

349 *Figure 3: The effect of maximum daily temperature (T_{max} , °C) on nestling daily growth rates (% change over a 12 h period). Data*
350 *points show the % daily mass change of (A) 5-day-old southern pied babbler *Turdoides bicolor* nestlings and (B) 11-day-old*
351 *nestlings as well as the (C) % daily tarsus length change and (D) wing length change of 11-day-old nestlings. Solid lines represent*
352 *predictions from the models and dashed lines the 95% CIs. The regression line in (D) is greyed out as the trend shown was not*
353 *statistically significant.*

354 *Adult behaviour (nestling age day 7-9)*

355 We observed nest attendance behaviour in 54.3% of focals, and birds spent on average 11
356 $\pm 23\%$ of their time attending the nest per focal day. However, the total proportion of time

Running head: High temperatures limit fledging

357 individuals spent attending the nest did not vary significantly with any of the included predictor
358 variables (Table 1). Adults foraged at least once in 92.6% of focals and overall foraged for $53 \pm$
359 29% of the time per focal day. Proportion of time spent foraging tended to be higher for males
360 than females and was significantly lower in larger groups and after rain. Proportion of time spent
361 foraging was not influenced by rank, brood size, or T_{\max} (Table 1). Birds spent on average $28 \pm$
362 25% time resting per focal day. The proportion of time spent resting was significantly higher on
363 hot days, after rain, and in larger groups, but was not influenced by sex, brood size, or rank (Table
364 1).

365 Total biomass caught per observation day averaged 7.0 ± 4.4 g per bird per focal day ($n =$
366 108 focal days, range: 0.0–20.3 g). After averaging the two top models (combined weight = 0.784),
367 total biomass caught increased with increasing T_{\max} until $\sim 32.3^\circ\text{C}$, after which it declined with
368 increasing T_{\max} ($Z = 3.980$, $P < 0.001$; Table 2, Fig. 4A). The effect of group size was also
369 quadratic: birds in intermediate-sized groups caught less biomass per day than birds in larger and
370 smaller groups ($Z = 3.621$, $P < 0.001$; Table 2, Fig. 4B). We found no evidence that biomass caught
371 per day was influenced by sex, rank, brood size, or rainfall (see Table S4 for full model selection
372 outputs).

Running head: High temperatures limit fledging

373 *Table 1: GLMM with Penalised Quasi-Likelihood (glmmPQL) model outputs for factors influencing proportion of time spent*
 374 *foraging, resting, and attending the nest by pied babblers with nestlings aged 7 -9 days after hatching. Models fitted to data from*
 375 *593 focal observations on 62 different individuals from 13 groups collected over 88 days. Significant terms ($P < 0.05$) are*
 376 *highlighted in bold. Random term: brood identity*

Model	Parameters	estimate	SE	t-value	P-value
Proportion time spent foraging	<i>Intercept</i>	-0.047	0.109	-0.437	0.664
	Brood size	0.157	0.092	1.701	0.105
	Group size	-0.275	0.090	-3.049	0.007
	Maximum temperature	-0.114	0.094	-1.221	0.227
	Rainfall two months prior	-0.322	0.093	-3.476	0.003
	Rank	-0.013	0.102	-0.132	0.895
	Sex (Male)	0.208	0.105	1.986	0.051
Proportion time spent resting	<i>Intercept</i>	-0.965	0.134	-7.226	0.000
	Brood size	-0.176	0.104	-1.689	0.108
	Group size	0.364	0.100	3.625	0.002
	Maximum temperature	0.247	0.109	2.259	0.027
	Rainfall two months prior	0.437	0.104	4.222	0.001
	Rank	0.154	0.133	1.153	0.254
	Sex (Male)	-0.049	0.138	-0.356	0.723
Proportion time spent attending the nest	<i>Intercept</i>	-1.768	0.168	-10.507	0.000
	Brood size	-0.019	0.115	-0.164	0.872
	Maximum temperature	-0.208	0.117	-1.781	0.079
	Group size	-0.059	0.119	-0.496	0.626
	Rainfall two months prior	-0.219	0.127	-1.722	0.101
	Rank	-0.284	0.223	-1.275	0.207
	Sex (Male)	-0.403	0.226	-1.779	0.080

377

378 Total biomass provisioned to the nest per observation day averaged 1.2 ± 1.1 g per bird per
 379 focal day ($n = 108$ focal days, range: 0.0–4.5 g). Rank and group size were the most parsimonious
 380 predictors of variation in biomass provisioned to the nest (the single best-fit model had a model
 381 weight of 0.590; Table 2). Subordinate individuals provisioned significantly less (1.0 ± 0.9 g per
 382 focal day) than dominant individuals (1.4 ± 1.3 g; $Z = -2.228$, $p = 0.026$; Fig. 4C). Individuals in
 383 larger groups provisioned less than those in smaller groups ($Z = -2.133$, $p = 0.033$; Fig. 4D). We

Running head: High temperatures limit fledging

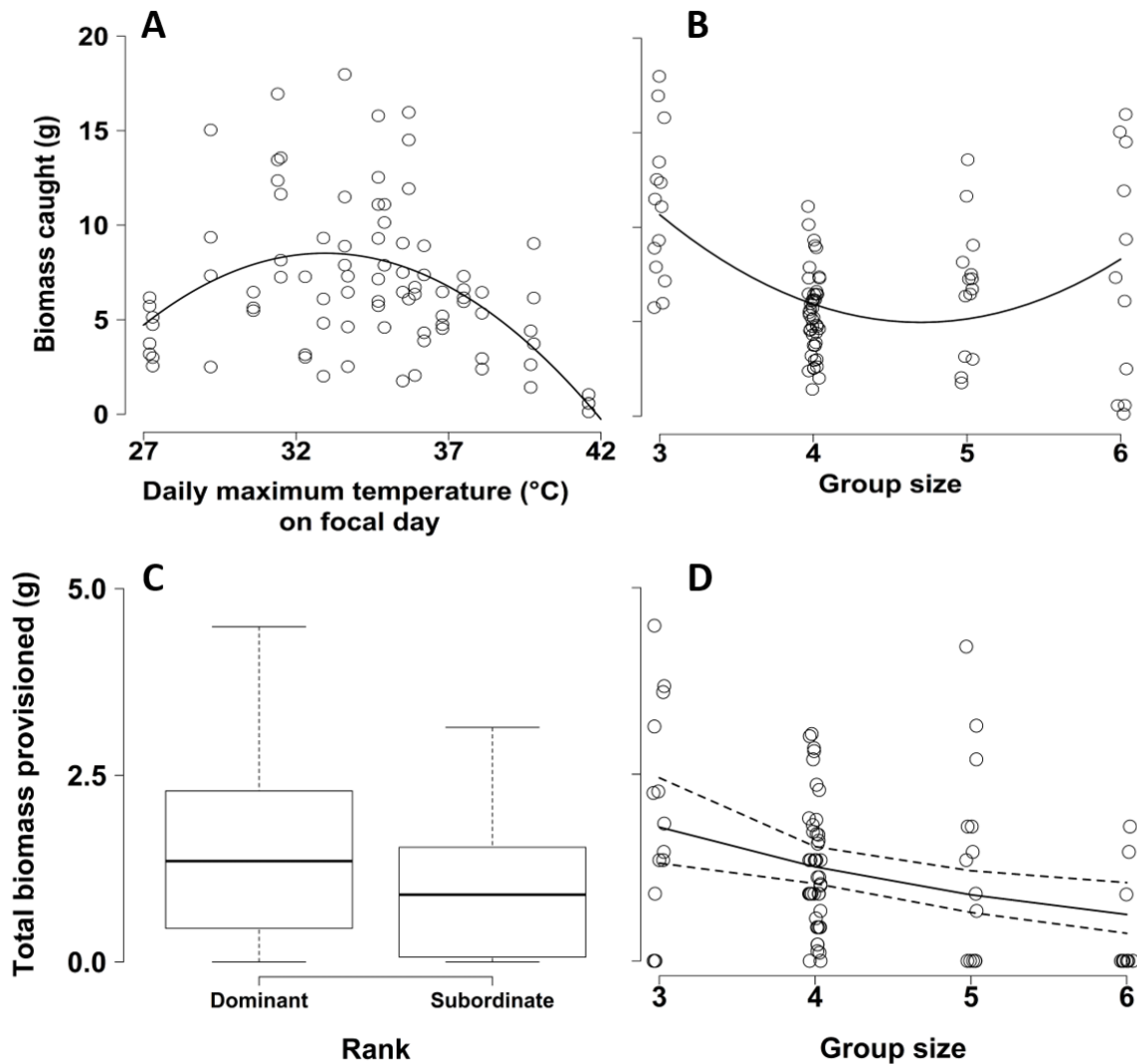
384 found no evidence that biomass provisioned per day was influenced by temperature, brood size,
 385 rainfall, or sex (see Table S5 for full model selection outputs).

386 *Table 2: Top model sets for factors influencing total biomass caught per day and total biomass provisioned per day to nestlings 7*
 387 *to 9 days after hatching. Model averaging was implemented for models with $\Delta AICc < 2$ of the 'best-fit' model. Significant terms*
 388 *after model averaging are shown in bold. Data from 56 different individuals from 23 nests by 13 groups over 84 focal days (see*
 389 *Table S4 and S5 for full model selection outputs).*

	<i>AICc</i>	<i>ΔAICc</i>	<i>ωi</i>
Response: total biomass caught per day			
Null model	438.7	17.28	0.00
<i>Top model set:</i>			
$T_{max}^2 + \text{Group size}^2$	421.42	0.00	0.55
$T_{max}^2 + \text{Group size}^2 + \text{Brood size}$	421.81	0.39	0.45
<i>Effect size of explanatory terms after model averaging</i>			
	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>
Intercept	1.903	0.092	1.719/2.085
T_{max}	-0.168	0.067	-0.301/-0.035
T_{max}^2	-0.228	0.057	-0.341/-0.116
Group size	-0.123	0.057	-0.236/-0.009
Group size²	0.169	0.046	0.077/0.259
Brood size	0.094	0.067	-0.039/.227
Response: total biomass provisioned per day			
Null model	237.1	5.6	0
<i>Top model set:</i>			
Group size + Rank	231.5	0	1
<i>Effect size of explanatory terms after model averaging</i>			
	<i>Estimate</i>	<i>SE</i>	<i>95% CI</i>
Intercept	0.223	0.177	-0.184/0.539
Rank (subordinate)	-0.468	0.210	-0.690/-0.029
Group size	-0.334	0.157	-0.890/-0.063

390

Running head: High temperatures limit fledging



391

392 *Figure 4: Biomass caught per individual per day as a function of daily maximum temperature (A, in °C) and group size (B) on*
393 *the observation day. Biomass provisioned per individual per day as a function of rank (C) and group size (D) on the observation*
394 *day.*

395 Discussion

396 We investigated the influence of temperature and rainfall on survival of young over the
397 development period from hatching to fledging, in a cooperatively breeding bird endemic to an arid
398 environment (the southern Kalahari Desert) heavily affected by climate change (Kruger and Sekele
399 2013; van Wilgen et al. 2016; Bourne, Cunningham, et al. 2020a; Bourne, Cunningham, et al.

Running head: High temperatures limit fledging

400 2020c). We found that heavier nestlings were significantly more likely to fledge, consistent with
401 previous studies showing that smaller size in nestlings correlates with reduced survival (Magrath
402 1991; Schwagmeyer and Mock 2008), and this effect was detectable in nestlings as young as five
403 days old. Piecewise SEM showed a strong negative influence of high temperatures during the day
404 on nestling body mass in the evening both directly (in both d5 and d11 nestlings) and indirectly
405 via impacts on adult provisioning rates (in d11 nestlings only). Multivariate analysis showed that
406 this result was mirrored by, and potentially explained by, compromised diurnal (12hr) mass gain
407 in both d5 and d11 nestlings on hotter days. Rainfall and group size positively influenced the
408 number of provisioning visits by adults to both d5 and d11 nestlings but did not directly influence
409 nestling structural size in the evening (tarsus and wing length) or daily growth rates. Individual
410 adult pied babblers maintained the overall proportion of time spent attending the nest as well as
411 the total biomass provisioned to nestlings at high temperatures, despite reducing the total number
412 of provisioning visits to the nest overall, and despite declines in the biomass of prey caught per
413 individual as temperatures increased.

414 That nestling growth was compromised over the course of a single hot day, and that the
415 impacts of reduced body mass on ultimate fledging probability were evident in nestlings as young
416 as five days old, suggests that isolated hot days are likely to be detrimental to nestling survival
417 regardless of whether or not they occur as part of a heat wave. This is consistent with work on
418 other Kalahari species, suggesting that single hot days, even fairly early in the nestling period, may
419 continue to affect nestlings up until fledging age (Cunningham et al. 2013). The effect of
420 temperature on tarsus and wing growth was smaller than for body mass, suggesting that pied
421 babbler nestlings prioritise limb growth over mass gain under challenging conditions. This is
422 expected because individual survival in birds depends strongly on physical traits such as wing

Running head: High temperatures limit fledging

423 length (Naef-Daenzer and Gruebler 2016; Martin et al. 2018). Longer wings allow for improved
424 mobility (Jones et al. 2017), better competitive and predator avoidance abilities (Greño et al. 2008),
425 synchronous fledging (Nilsson and Svensson 1996), and reduced mortality of juveniles (Martin et
426 al. 2018).

427 Piecewise SEM suggested that direct effects of temperature on evening mass of both d5
428 and d11 nestlings were more important than indirect effects via adult provisioning rates (also see
429 van de Ven, McKechnie, et al., 2020), despite the fact that parental care behaviours mediate effects
430 of weather conditions on nestling growth in other bird species (Weimerskirch et al. 2000; Tremblay
431 et al. 2005; Cunningham et al. 2013). In this study, the number of provisioning visits was only
432 important for predicting evening mass, and thus fledging probability, of d11 nestlings. From the
433 focal behaviour observations of adults in groups with 7- to 9-day-old nestlings, i.e. just before d11
434 nestling measurements, we learned that adult pied babblers spent a larger proportion of time resting
435 on hotter than cooler days. However, they did not significantly reduce the proportion of time spent
436 foraging or attending the nest to achieve this, suggesting that they instead reduced their time spent
437 on other behaviours (such as vigilance and defending the territory against neighbouring groups).
438 High temperatures negatively affected total biomass caught and the number of provisioning visits
439 adults made to the nest (consistent with Wiley & Ridley 2016), but not the total amount
440 provisioned per bird per day. Thus, birds flew to the nest less frequently but took larger loads each
441 time. This implies that the only concession provisioning adults make at high temperatures is to
442 shift from a rate-maximising strategy (frequent visits to the nest) to an efficiency-maximising
443 strategy (providing a consistent amount of food to nestlings, in terms of total biomass per day,
444 while limiting the number of provisioning flights by adults as temperatures rise) as temperatures
445 increase.

Running head: High temperatures limit fledging

446 Less frequent provisioning trips on hotter days are likely to help adult birds avoid raising
447 body temperature by flying (Engel et al. 2006), as previously suggested by Wiley & Ridley (2016).
448 However, shifting to an efficiency-maximising strategy appears insufficient to offset the direct
449 effects of high temperatures on nestling body mass, tarsus and wing length, and daily growth rates.
450 Wet biomass intake may therefore need to increase at high temperatures to maintain nestling mass
451 and sustain growth, due to increased nestling demand for water to aid thermoregulation under hot
452 conditions (Salaberria et al. 2014; van de Ven, McKechnie, et al. 2020; Czenze et al. 2020). If
453 chicks become dehydrated, growth could be hampered by poor physiological performance due to
454 costs associated with dehydration and subsequent high body temperatures (Angilletta et al. 2010).
455 If such elevated water demand does exist when hot, our data suggest that provisioning adults might
456 be unable to increase biomass provisioned in order meet this demand. This is because biomass
457 caught declined with increasing temperature above 32.3°C, indicating poorer foraging success (du
458 Plessis et al. 2012; Cunningham et al. 2015; van de Ven et al. 2019) and suggesting that there was
459 probably less biomass available at high temperatures with which to provision to nestlings (Conrey
460 et al. 2016; Dodson et al. 2016; Mella et al. 2018). Adults may also be constrained in their ability
461 to provision more water-rich food to nestlings at high temperatures due to the increased costs of
462 flight at high air temperatures (Klaassen 1995; Powers et al. 2017) and the need to attend to their
463 own water demands (Bourne, Ridley, et al. 2020; Czenze et al. 2020).

464 Nestling body mass, tarsus and wing length, and daily growth rates were not affected by
465 group size (also see Wiley & Ridley 2016), suggesting that the benefits of cooperation accrue to
466 adult group members rather than young in this species in terms of nestling growth (Mumme et al.
467 2015; Savage et al. 2015; Langmore et al. 2016). In keeping with this, adult behaviour was affected
468 by group size. Nestlings received the same level of care across group sizes, but adults in larger

Running head: High temperatures limit fledging

469 groups invested less per individual in raising young than adults in smaller groups: they spent less
470 time foraging and more time resting than individuals in smaller groups, and provisioned less
471 biomass to young per individual on average than those in smaller groups. This adds further support
472 to previous evidence that ‘load-lightening’ occurs in pied babblers (Raihani and Ridley 2008;
473 Ridley and Raihani 2008; Wiley and Ridley 2016).

474 *Conclusion*

475 High temperatures during the nestling period affected the mass, tarsus length, and survival to
476 fledging of pied babbler nestlings, consistent with prior research on passerines (Greño et al. 2008;
477 Salaberria et al. 2014), including this species (Wiley and Ridley 2016; Bourne, Cunningham, et al.
478 2020a). Piecewise SEM analysis suggests that the majority of this effect is driven by direct effects
479 of temperature on nestlings, and to a lesser extent by temperature-mediated changes in
480 provisioning rate to older nestlings. Although parental care strategies are flexible in response to
481 both climate and social conditions, these strategies have limits (Cunningham et al. 2013; van de
482 Ven, McKechnie, et al. 2020). Our results suggest that mitigatory actions by provisioning adults
483 (e.g. the behavioural shifts from rate-maximising to efficiency-maximising provisioning strategies
484 documented here) failed to compensate fully for direct effects of high temperatures on nestling
485 growth and development. Repeated exposure to high temperatures during breeding attempts could
486 therefore undermine population replacement via low recruitment of young into the adult breeding
487 population, leading to an increasingly detrimental impact of high temperatures on population
488 persistence over time (Bourne, Cunningham, et al. 2020a; Bourne, Cunningham, et al. 2020b;
489 Bourne, Cunningham, et al. 2020c). This suggests a mechanism by which predicted temperature

Running head: High temperatures limit fledging

490 increases in the Kalahari (MacKellar et al. 2014) could negatively affect population growth and
491 persistence (Cunningham *et al.* 2013, Conradie *et al.* 2019).

492 We highlight the need to quantify multiple simultaneous factors with direct as well as
493 indirect pathways that influence fledging probabilities, including adult behaviour, investment in
494 parental care, and offspring growth and development, to identify mechanisms by which birds are
495 at risk under global change. Sublethal costs of high temperatures such as those documented here
496 should not be overlooked as they are likely to prove powerful drivers of population decline under
497 climate change (Conradie et al. 2019; Román-Palacios and Wiens 2020; Trisos et al. 2020).
498 Impacts on breeding success appear to operate similarly across multiple species (Cunningham et
499 al. 2013; Salaberria et al. 2014; Cooper et al. 2019; Sharpe et al. 2019; Exposito-Granados et al.
500 2019 Sep 24; Bourne, Cunningham, et al. 2020a; van de Ven, McKechnie, et al. 2020) and could
501 cause collapses of animal communities (Iknayan and Beissinger 2018; Riddell et al. 2019; Ripple
502 et al. 2019; Rosenberg et al. 2019) long before temperatures reach and begin to regularly exceed
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