

REPORT FROM A BOU-FUNDED PROJECT

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

Amanda Bourne^{1*}, Susan Cunningham¹, Lisa Nupen², Andrew McKechnie^{3,4} & Amanda Ridley^{1,5}

¹ DST-NRF Centre of Excellence at the FitzPatrick Institute, University of Cape Town, Rondebosch 7001, South Africa

² Organisation for Tropical Studies, Kruger National Park, South Africa

³ DST-NRF Centre of Excellence at the FitzPatrick Institute, University of Pretoria, Hatfield 0028, South Africa

⁴ National Zoological Gardens of South Africa, Pretoria 0001, South Africa

⁵ Centre for Evolutionary Biology, School of Biological Sciences, University of Western Australia, Crawley 6009, Australia

* abourne.uct@gmail.com

Background

Previous research has shown that, at daily maximum temperatures exceeding 35.5 °C, Southern Pied Babblers *Turdoides bicolor* are unable to gain enough mass from foraging during the day to counter typical overnight mass loss (du Plessis et al. 2012). In addition, breeding babblers substantially reduce their provisioning effort to young when this threshold is crossed (Wiley & Ridley 2016). High temperatures during the nestling period subsequently result in low nestling body mass at 11-days of age (Wiley & Ridley 2016). Whether there are sex-specific differences in the impacts of extreme heat has not been investigated in pied babblers.

In many vertebrates, including birds, male-biased mortality during ontogeny is commonplace (Clutton-Brock, Albon & Guinness 1985; Sandman, Glynn & Davis 2013). Several theories exist to explain this, including that 1) the heterogametic sex suffers from environmental dependence in the expression of deleterious recessive alleles, 2) where sexual dimorphism is present in adults, larger males require greater nutritional input to achieve the same viability, and 3) male phenotypes associated with, for example, higher levels of testosterone result in reduced general immunocompetence in vertebrates (Clutton-Brock, Albon & Guinness 1985; Sheldon et al. 1998; Kruuk, Osmond & Cockburn 2015).

As females are the heterogametic sex in birds, environmental dependence in the expression of deleterious recessive alleles can be ruled out as an explanatory factor in this case. Sheldon et al. (1998) found that sexual size dimorphism likely explains sex-specific responses to adversity best in their size-monomorphic study species Collared Flycatchers *Ficedula albicollis*. However, there remains evidence in other size-monomorphic species of higher juvenile mortality in males (Clutton-Brock, Albon & Guinness 1985), and no evidence for a reversal of this trend in species where females tend to be larger. *T. bicolor* is a monomorphic species and we have used a long-term nest life history database to test for any sex-specific differences in size, mass, and survival of nestlings exposed to high temperatures during early development. Studying sex-specific

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differences in a monomorphic avian species is interesting because any evidence of male-biased mortality would lend support to a physiological basis of sex-specific responses to adversity.

Implementation and findings

Southern Pied Babblers (60-90g) are size monomorphic cooperative breeders found in the semi-arid savannas of southern Africa's Kalahari (Ridley 2016). Detailed nest life history data has been collected from a study population on and around the 33 km² Kuruman River Reserve (26°58'S, 21°49'E) since 2003 (Ridley & Raihani 2007; Ridley 2016). Individuals are marked as nestlings with a unique combination of metal and colour rings for individual identification.

On the 11th day after hatching, nestlings were weighed to one decimal place on a top-pan balance scale (2005 to 2017, n = 368) and tarsus length measured to the nearest mm (2009 to 2017, n = 217). Survival of nestlings to independence was calculated from 237 nest life histories (2005 to 2017, n = 551 nestlings). All nestlings were blood sampled on the measurement day. Molecular sexing was undertaken using the CHD-Z and -W PCR-gel-band technique described in Fridolfsson & Ellegren (1999), and all nestlings included in this analysis were of known sex.

Nestling body mass and tarsus measurements were analysed using linear regression models with sex, proportion of days exceeding 35.5 C, and the interaction between the two as explanatory variables. Probability of reaching independence was analysed using logistic regression models with a logit link function with sex, proportion of days exceeding 35.5 C between measurement and 90 days after fledging, rainfall during the same period, and the interactions between these as explanatory variables. Group, season, and nest were included as random factors in all models. All analyses were conducted in R v3.4.1 (R Development Core Team 2011) using the package lme4 v1.1-13 (Bates et al. 2017).

As Wiley & Ridley (2016) have shown previously, *T. bicolor* nestlings weigh less at 11 days of age as the proportion of days during the nestling period above the critical temperature threshold of 35.5 °C increases. Additionally, tarsus length of 11-day-old nestlings decreases by approximately 2mm (95% CI 0.2mm – 3.6mm, t = 2.145, p = 0.033) for every 1% increase in the proportion of hot days experienced while in the nest. However, there is no significant difference between male and female nestlings in terms of either body mass or tarsus length at day 11, or the response of body mass and tarsus length to maximum air temperature on day 11 (Fig. 1).

Although the root cause of this is not known, the sex-ratio of nestlings at day 11 is slightly female skewed, with approximately 54% females to 46% males. This slight female bias is maintained in babblers that survive to independence, where approximately 55% are female. Approximately 60% of all nestlings in our study population survive to independence. There is, however, no significant difference between male and female nestlings in terms of survival from 11 days of age to independence 90 days after fledging (95% CI -0.399% – 0.46%, t = 0.14, p = 0.888).

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High temperatures after leaving the nest do not affect survival to 90 days (95% CI -1.96% - 0.96%, $t = -0.667$, $p = 0.505$). There is an effect of rainfall, with individuals more likely to survive to independence during higher rainfall periods (Fig. 2). The odds of survival to independence increase by approximately 6 % per gram increase in nestling mass at day 11 (GLM: 95% CI 2.6% - 10.2%, $z = 3.313$, $p = 0.0009$). As demonstrated above, mass at day 11 is strongly affected by temperatures endured in the nest. There is no interaction with sex.

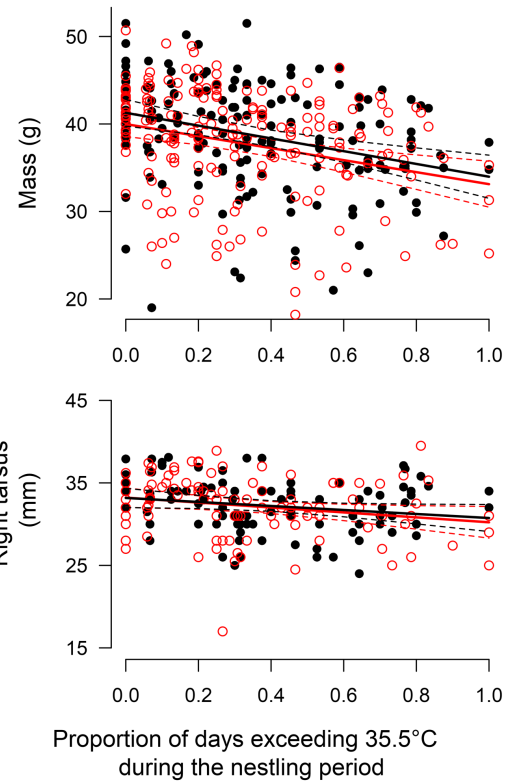


Figure 1. Southern Pied Babbler *Turdoides bicolor* nestlings are affected by high temperatures in the nest – with nestlings both weighing less and having shorter tarsi at 11 days old at high proportions of hot days during the nestling period. This effect of temperature does not differ between male (black filled circles and black lines) and female (red open circles and red lines) nestlings. Solid lines represent the regression output and dashed lines the 95% confidence interval.

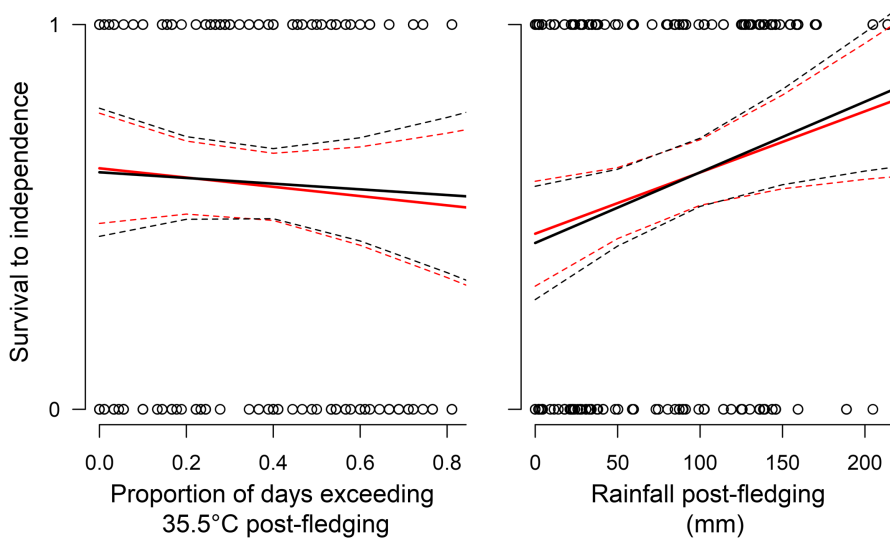


Figure 2. Juvenile survival to independence (90 days after fledging) in Southern Pied Babbler *Turdoides bicolor* is affected by rainfall but not by temperature after leaving the nest. Effects do not differ between male (black lines) and female (red lines) nestlings. Solid lines represent the regression line and dashed lines the 95% confidence interval.

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Discussion and conclusions

As may be expected for a highly monomorphic species, there is no evidence for sex-specific responses to high temperatures in terms of nestling growth and survival. While there are no sex-specific differences, there is evidence for significant climate-related impacts on nestling development which warrants further investigation. There is also evidence for a small but consistent female-skew in sex ratios at various stages during ontogeny that may be worth further research.

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