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The effects of temperature on offspring provisioning in a cooperative breeder



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While most current predictive models agree that the climate is changing, it is not yet clear what impact these changes will have on animal populations. It is vital to determine the potential consequences in order to develop future management and conservation strategies. Climate change may impact population stability by prompting changes in breeding behaviour. For example, if above-average temperatures negatively affect adult body condition, this will increase the cost of parental care. Theory suggests that under this scenario, individuals may trade off their own body condition and survival against that of their young. Despite convincing evidence that this parental care trade-off exists in nature, the potential impact of climate change on parental investment strategies has rarely been investigated. In cooperatively breeding species, group-living adults can gain group size benefits, such as assistance with raising young. These benefits may mediate the effects of climate change on adult condition and subsequent investment in young. Here, we investigated the extent to which high temperatures and rainfall variation affect (1) adult provisioning rates to dependent nestlings, (2) offspring development and (3) the cost of offspring care in the cooperatively breeding pied babbler, Turdoides bicolor. We found that overall, adults provisioned young significantly less on hot days. However, this pattern was affected by rank: dominant individuals provisioned significantly less while subordinates did not. Offspring development was negatively affected by heatwave events, suggesting that young suffer from reduced investment on hot days. However, there was no evidence that the cost of provisioning young increased during heatwave periods, perhaps owing to the reduction in investment by adults. This study provides some of the first evidence that higher temperatures affect investment decisions in cooperative breeders and that dominant and subordinate individuals respond differently to this stressor.

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The way in which organisms respond to environmental change is fast becoming one of the most pertinent issues in biology due to the threat of rapid climate change. Climate change is globally recognized as one of the biggest threats to biodiversity (Foden et al., 2013; Parmesan & Yohe, 2003; Selwood, McGeoch, & Mac Nally, 2015). The Intergovernmental Panel on Climate Change's (IPCC, 2012) special report on global warming predicted substantial warming and higher temperature extremes by the end of the 21st century. The report concluded it is very likely that the length, frequency and intensity of extreme weather events such as heatwaves

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will increase over most land areas, with a 1-in-20 year hottest day likely to become a 1-in-2 year event by the end of the 21st century. This was corroborated in the 2014 synthesis report, where it was stated to be 'virtually certain that there will be more frequent hot, and fewer cold temperature extremes over most land areas on daily and seasonal timescales, due to an increase in global mean surface temperature' (IPCC 2014, p. 60). Determining the implications of these predicted climatic changes for animal populations is now a priority for ecological research if we are to implement appropriate future management strategies.

Physiological research has recognized that extreme environmental fluctuations may have detrimental effects on body size, breeding success and population density (Walther et al., 2002; Williams & Tieleman, 2005). However, the direct impacts of rising temperatures on the ability of species to effectively forage, breed and interact are poorly understood. In hot and arid







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environments, some (particularly smaller) bird species rapidly exceed their physiological tolerance limits (McKechnie & Wolf, 2010). Following a 2009 mass die-off of budgerigars, *Melopsittacus undulatus*, during a heatwave in Western Australia, McKechnie & Wolf (2010) suggested that the frequency and intensity of extreme weather events over short time periods can be more important than long-term temperature rise. It has therefore become critical to document the direct effects extreme weather events are having on species, and to consider the ramifications of such impacts for future population management.

The impact of environmental variation on life history, physiology and population growth rate has been addressed in several influential papers on noncooperative species (Bickford, Howard, Ng, & Sheridan, 2010; Ozgul et al., 2010; Saether et al., 2000), but comparative data are not available for cooperative breeders. Cooperatively breeding species normally have group-structured populations (Nelson-Flower, Hockey, O'Ryan, & Ridley, 2012; Rollins et al., 2012), and therefore their population dynamics differ from those of conventional breeders (Courchamp, Grenfell, & Clutton-Brock, 1999). Cooperative species may respond differently to external stressors than nonsocial species, because reproductive success and survival can be affected by group size and the behaviour of other group members, rather than a pair or single individual. In defined and generally stable groups (Brown, 1978; Emlen, 1997), task-partitioning behaviours (such as antipredator defence, hunting, territory defence and raising young) often occur, which provide individual fitness benefits (Clutton-Brock, 2009; Raihani & Ridley, 2007b).

In some cases, breeders may reduce their investment in young, facilitated by the presence of helpers, a behaviour known as load lightening (Crick, 1992; Johnstone, 2011; Meade, Nam, Beckerman, & Hatchwell, 2010). Load-lightening behaviour can have a positive effect on parental survival and condition by reducing the cost of parental care without young receiving less care overall (Allainé, Brondex, Graziani, & Coulon, 2000; Cockburn et al., 2008; Woxvold & Magrath, 2005). The presence of helpers could to some extent buffer the effects of variation in environmental conditions on reproductive success, through task-partitioning and load-lightening behaviours (Heinsohn, 2004; Ridley & Raihani, 2008). Therefore, we may expect that individuals in large groups are less likely to be affected by environmental stressors when making reproductive investment decisions, than individuals in smaller groups.

Parental care is a costly form of investment (Clutton-Brock, 1991; Ridley & Raihani, 2007; Smith & Fretwell, 1974; Smith & Wootton, 1995; Walker, Gurven, Burger, & Hamilton, 2008). Life history theory predicts that in species that produce many offspring but have low adult survival rates, parents should value current offspring survival over their own survival, whereas those that produce fewer offspring but have a greater likelihood of surviving to breed again should value their own survival over that of their current young (Ghalambor & Martin, 2001; Sofaer, Sillett, Peluc, Morrison, & Ghalambor, 2013; Trivers, 1972; Zanette, White, Allen, & Clinchy, 2011). Previous research has investigated switches in reproductive strategy in response to environmental change (Fontaine & Martin, 2006; Schwagmeyer & Mock, 2008), revealing that in several long-lived species (e.g. puffins, Fratercula arctica; albatross, Diomedea exulans), large annual variation in environmental conditions is reflected in highly variable reproductive effort (Erikstad, Fauchald, Tveraa, & Steen, 1998; Weimerskirch, Cherel, Cuenot-Chaillet, & Ridoux, 1997). Our study addresses offspring care strategies in cooperative breeders by assessing how the care of dependent young is affected as a direct short-term behavioural response to environmental stressors. We investigated (1) individual short-term behavioural responses to an environmental variable (the effect of heat on brood provisioning rate), and (2) the relationship between two environmental variables (rainfall and temperature) and one offspring trait (nestling body mass).

One of the first detailed studies to directly measure the potential impact of increasing temperatures on behavioural patterns and the ability to maintain body mass in arid zone bird species confirmed that pied babblers, Turdoides bicolor, exhibit heat stress above a daytime temperature of 35.5 °C (du Plessis et al., 2012). Here, we further explored the ramifications of this observed critical temperature effect by (1) determining the ability of individuals to maintain provisioning rates to young (a costly activity, Ridley & Raihani, 2007b) during temperatures above 35.5 °C, and (2) determining the cost of provisioning young at different temperatures, in terms of body mass loss. We would expect higher temperatures to affect the cost of offspring care for adults, with consequent impacts on the growth and development of young. We also expect that a change in investment in response to environmental stressors could be affected by group size, with young from larger groups (where there are more adults providing offspring care) less affected by reduced provisioning rates at high temperatures.

METHODS

Study Site and Species

We investigated cooperative brood care in pied babbler groups at the Pied Babbler Research Project, based in the 33 km² Kuruman River Reserve (KRR) in the southern Kalahari region of South Africa (26°58′S, 21°49′E). The study site has a subtropical climate and is primarily semiarid grassland and acacia savanna (see Ridley & Thompson, 2011 for description of habitat types). The area has a mean annual rainfall of 197 mm, with most rain falling during mid–late summer in January and April (Kong, Marsh, van Rooyen, Kellner, & Orr, 2015). In mid-summer (January) mean daily maximum and minimum temperatures are 34.7 °C and 22.2 °C, respectively, but can reach highs of 45.4 °C (Steenkamp, Vogel, Fuls, van Rooyen, & van Rooyen, 2008).

Temperature and rainfall

Temperature (°C) and rainfall (mm) data were collected daily from the weather station at the Kuruman River Reserve. High temperature extremes (>45.4 °C) have been recorded at the study site once in the decade 1996-2005 (1 day only) and six times in 4 different years, from 2006 to the current day (three 1-day events and three 3-day events). The average duration of the (six) more recent events was 1.92 days (see Appendix Table A1, weather station data, KRR). Rainfall was summed for each relevant provisioning period (i.e. total rainfall in the month prior to behavioural observations). One month was chosen due to the typical delay between rainfall and insect emergence in the Kalahari (Cumming & Bernard, 1997; Ridley & Child, 2009). Maximum temperature (T_{max}) was recorded daily at the study site. A hot day was defined as greater than 35.5 °C (hereafter referred to as $T_{\rm crit}$), because this was the temperature du Plessis et al. (2012) recognized as critical for the pied babbler, beyond which foraging efficiency declined, heat dissipation increased exponentially and individuals were unable to maintain body weight. Furthermore, the number of days per year where the temperature was over 35.5 °C has Download English Version:

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