Understanding the potential impact of climate change on the behavior and demography of social species: The pied babbler (*Turdoides bicolor*) as a case study

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1. Introduction

The evidence that the climate is changing, and indeed changing rapidly, is overwhelming (Cook et al., 2016; Oreskes, 2018). Tens of thousands of research papers agree that we have entered a period of anthropogenically induced rapid climate change (Cook et al., 2016; Petersen, Vincent, & Westerling, 2019). While these effects are expected to vary across the planet, with arctic areas predicted to increase in temperature more rapidly for example (Cohen et al., 2014; Overland et al., 2019; Sanderson, Hemming, & Betts, 2011), it is expected that there is no habitat that will be unaffected by climate change (IPCC, 2014). This rapid change in climatic conditions represents a challenge to wildlife populations (Pecl et al., 2017; Thomas et al., 2004; Urban, 2015). First, conditions may surpass critical physiological tolerance limits for some species, which could have lethal or sublethal effects on individuals (Böhm et al., 2016; Mitchell, Rodriguez, Kuchling, Arnall, & Kearney, 2016; Sinervo et al., 2010). This could lead to population declines, or render some previously inhabited areas no longer habitable (Hoffmann, Williams, Hipsey, & Mitchell, 2020). Second, the change in conditions may require some species to move to an area with more suitable habitat or environmental conditions. However, the ability of animals to move to more suitable areas is severely threatened by habitat fragmentation in some places, or the resources they rely on to be available (for example, frugivores can only move to areas with sufficient mature fruiting trees to feed on), as well as their own mobility (Bouma, Kuchling, Zhai, & Mitchell, 2020; Monzón, Moyer-Horner, & Palamar, 2011; Razgour et al., 2018).

Considerable recent research on climate change impacts on plant and animal populations enables us to extrapolate the potential future climate impacts on a wide range of wild populations. For example, Conradie, Woodborne, Cunningham, and McKechnie (2019) and Conradie et al. (2020) used existing long-term data on thermal thresholds associated with lethal and sublethal fitness impacts in several avian species inhabiting southern Africa and Australia to extrapolate future impacts on populations of these species under different climate scenarios. Studies such as these are an extremely useful way to attempt to quantify the potential impact of climate change on species’ population viability over time. It is of course not possible to generate these trends for all species, for a number of reasons: (a) we do not have as much detailed information on all species, (b) we do not have sufficient funding and personnel to be able to gather such detailed
information on every species and (c) it is not efficient to do so. Instead, we can collect detailed information on a number of representative species, and use the patterns to extrapolate the likely impacts of climate change on species with similar habitat and resource needs (Mathewson et al., 2017; Wingfield & Ramenofsky, 2011). Using “indicator species” has been an effective tool in conservation biology for several decades (Caro & O’Doherty, 1999).

Long-term studies have made a major (and disproportionate) contribution to our understanding of the causes of variation in individual survival and reproductive success, and at a broader level, our understanding of ecological and evolutionary processes in wild populations (Clutton-Brock & Sheldon, 2010; Culina et al., 2020). It has recently been acknowledged that this exceptional value of long-term research projects has an important role to play in understanding how natural populations currently (and forecasting into the future) respond to a changing climate (Paniw, Maag, Cozzi, Clutton-Brock, & Ozgul, 2019), and can therefore facilitate conservation and wildlife management strategies. The increasing recognition of long-term studies for combining ecological and evolutionary information to benefit conservation and climate-related management has led to the development of an international database for long-term avian studies (SPI-birds https://www.spibirds.org), to encourage data comparison and collaboration between sites, populations and species.

Long-term studies have the benefit of being able to track individuals over their lifetime, thus measuring the impact of environmental conditions during early development compared to conditions experienced at later life history stages (Culina et al., 2020). In addition, long-term studies can allow multiple events to be compared over time (such as breeding investment patterns relative to weather events), allowing higher predictive power regarding the impact of variable conditions on survival and fitness (Culina et al., 2020). Fitness is a term often used but rarely able to be directly measured in the wild, particularly for long-lived species. This is because lifetime fitness is defined as the cumulative reproductive success over an individual’s lifetime, and it is relatively rare that individuals in the wild can be followed over the course of their whole lives (though note that there are many different definitions of fitness in evolutionary biology (Orr, 2009)). The exception to this is those animals repeatedly observed over time in long-term studies, which provide actual lifetime fitness measures. Such studies, and particularly those providing fitness measures relative to average longevity under different environmental conditions, are likely to be highly instructive in determining the potential impacts of climate on future demographic changes in wildlife
populations worldwide. We believe this is where long-term studies have exceptional value in allowing us to empirically test potential climate impacts on wildlife populations. Recent publications investigating the impact of climate change on wild populations include long-term studies of red deer (*Cervus elaphus*, Bonnet et al., 2019), meerkats (*Suricata suricatta*, Paniw et al., 2019), yellow-bellied marmots (*Marmota flaviventris*, Cordes et al., 2020), great tits (*Parus major*, Charmantier et al., 2008) superb starlings (*Lamprotornis superbus*, Guindre-Parker & Rubenstein, 2020), superb fairy wrens (*Malurus cyaneus*, Lv, Liu, Osmond, Cockburn, & Kruuk, 2020), Sonoran desert lizards (Flesch, Rosen, & Holm, 2017) and pied babblers (detailed in full below), and have proven the value of long-term datasets for understanding the potential impact of climate change.

Recent meta-analyses have revealed that while many species have displayed a phenological response to the changing climate, such as advances in breeding and migration times, for example, morphological changes have been limited (although some body size changes have been detected, see Gardner et al., 2019; Yom-Tov, Yom-Tov, Wright, Thorne, & Du Feu, 2006). These limited morphological changes suggest some species may not be able to adapt rapidly enough to the changing climate (Radchuk et al., 2019). Declines in reproduction or survival can be at least partially offset by physiological or behavioral changes that reduce the extent of the mismatch between the phenotype and environment (Radchuk et al., 2019; Socolar, Epanchin, Beissinger, & Tingley, 2017), and this is therefore where more empirical evidence is needed. Behavioral plasticity is well known (Snell-Rood, 2013), and indeed there are many examples of species that can rapidly adapt to changed conditions, such as heavily modified urban and natural environments (Ducatez, Sol, Sayol, & Lefebvre, 2020; Noakes & McKechnie, 2020). Invasive species in particular are a good example of species that display rapid behavioral adaptations to novel environments (Sol, González-Lagos, Moreira, Maspons, & Lapiedra, 2014).

1.1 Environmental variability and the benefits of cooperation

Cooperative breeding is a strategy whereby three or more individuals help to raise the young produced from a breeding attempt (Cockburn, 1998; Koenig & Dickinson, 2016). Cooperation can take many forms, from facultative to obligate cooperation, and from occasional helping to frequent
helping behavior (Koenig & Dickinson, 2016). A key question that sits at the core of cooperative breeding research is why individuals help one another. If help is costly (as originally formulated by Hamilton (1964) reviewed in Heinsohn and Legge (1999)), then individuals should only invest in helping behavior if they gain a benefit from doing so. One potential benefit of helping behavior is through kin selection, where individuals gain benefit from helping kin due to shared genes (Hamilton, 1964). This hypothesis has helped to explain patterns of helping behavior in some cooperative species (Green, Freckleton, & Hatchwell, 2016; Griffin & West, 2003; Kay, Keller, & Lehmann, 2020), but not others (Dunn, Cockburn, & Mulder, 1995; Kingma, 2017; Riehl, 2013). In species where helpers are not related to those that they help, alternative explanations for group-living and helping behavior are required. Such explanations include the ecological constraints hypothesis (Emlen, 1982), the benefits of philopatry hypothesis (Koenig, Pitelka, Carmen, Mumme, & Stanback, 1992), the bet-hedging/variable conditions hypothesis (Rubenstein, 2011), and the dual benefits hypothesis (Shen, Emlen, Koenig, & Rubenstein, 2017). These hypotheses do not exclude kin selection as an explanation for helping behavior, but incorporate other factors influencing helping behavior. Several of these hypotheses suggest that, where ecological conditions for independent breeding are harsh or highly variable (such that successful dispersal and/or reproduction may not be possible each year), delaying reproduction and instead cooperating to raise young produced by other group members may be a more beneficial breeding strategy, generating more stable survival and reproduction rates each year. While these hypotheses have been investigated as a way to understand the evolution of cooperation, under a rapidly warming climate the hypotheses also generate some testable predictions about cooperative breeding strategies under changing environmental conditions. For example, if cooperation does buffer individuals against the survival and reproductive costs of environmental variation, would a cooperative breeding strategy become more common in species inhabiting areas where a greater frequency of extreme weather events are forecast? Would a minimum group size be needed to ensure population viability of social species that are being reintroduced into wildlife areas (as is the case for Wild Dogs Lycaon pictus (Courchamp, Rasmussen, & Macdonald, 2002))? These are important questions to ask in a rapidly changing climate, and we believe that they require the collaboration of researchers in conservation, ecological, evolutionary and physiological disciplines.
2. Pied babblers as a model system

The pied babbler is a medium sized (adult body mass range 61–89 g) passerine endemic to the semi-arid acacia savanna of southern Africa (Ridley, 2016; Ridley & Raihani, 2007a) (Fig. 1). It is a cooperatively breeding bird species, where each group has a dominant breeding pair that monopolizes access to reproduction (>90% of young hatched are offspring of the dominant pair (Nelson-Flower et al., 2011)), with adult helpers of both sexes that help to raise the young of the dominant pair (Ridley & Raihani, 2007b). Group sizes typically range between 3 and 12 adult birds, and 1–5 juveniles (individuals <12 months post-hatching), with all adult group members observed to participate in helping behavior (juveniles also help, but considerably less often than adults (Ridley & Raihani, 2007b)). Breeding pairs without helpers do occur in the population but are ephemeral, occupying marginal territories and rarely staying as a pair for more than one breeding season (Ridley & Van Den Heuvel, 2012). Pied babblers occupy and defend a territory year-round, and typically breed from October–March (Humphries, Finch, Bell, & Ridley, 2015). The peak of breeding coincides with the start of the rainy season and typically extends over the hottest months of the year, except in cases of drought and high temperatures, where babblers will typically breed at reduced rates (Bourne et al.,

![Image](https://example.com/fig1.jpg)

**Fig. 1** Pied babblers are a highly social species that live in groups year-round, and move together throughout their territory each day. All adult group members contribute to territorial defence, offspring care, and sentinel activity. Copyright Nicholas Pattinson.
—or in extreme weather conditions, not attempt to breed at all. Each group will build one nest per breeding attempt, with a typical clutch size of three eggs (range 2–5). Breeding activity is highly dependent on both environmental and social conditions (breeding occurs during the hot summer months, but is more common during periods of higher rainfall and lower temperatures within those summer months (Bourne et al., 2020a, 2020b, 2020c)), while larger groups are able to produce more clutches per season (Ridley & Raihani, 2008). Helping behavior in this species takes the form of sentinel activity, predator mobbing, territory defense, provisioning of young, incubation and brooding of young, and teaching behavior (Raihani & Ridley, 2008; Ridley, Nelson-Flower, & Thompson, 2013; Ridley & Raihani, 2007b). Helping behavior can be prolonged: young typically take over 100 days from hatching to reach independence—the point at which they are able to forage for themselves without requiring supplementation from adult group members (Ridley & Raihani, 2007b). In addition, multiple broods may be raised per breeding season (Ridley & Raihani, 2008), resulting in a period of up to 6 months of continuous helping behavior toward dependent young.

We established a habituated population of pied babblers in 2003 and have been closely monitoring their behavior ever since. We initially established a population of six habituated groups, which grew to up to 18 groups being monitored per year by 2009. The number of groups monitored per year varies, due to natural extinction events (particularly during drought years). Each bird in the population is ringed with a unique combination of colored and metal rings for ease of in-field identification. We also weigh each group member each time we visit a group (groups visited approximately once per week, range 1–6 times per week), to determine changes in body mass over time relative to weather, social and breeding events. This is achieved by enticing individuals to jump onto a top-pan scale for a small food reward at first light (before foraging begins), and again at the end of the observation a few hours later, as well as at the end of the day. This accumulated detailed dataset of over 40,000 body mass measures provides the opportunity to investigate changes in body mass per individual over the course of a day, overnight, and over the duration of a breeding season.

Habituation allows us to reliably locate groups at each visit, and to observe their behavior at close quarters (approximately 5–10 m), without causing any disturbance or modification of their natural behavior. By getting the birds used to our quiet presence, they tend to ignore the presence of observers most of the time. It also allows us to closely monitor all breeding
events. To standardize comparisons of offspring development relative to social, parental and environmental factors, we take morphometrics of each nestling at 11 days post-hatching (young typically fledge between 14 and 17 days post-hatching). To date, we have monitored the breeding events per season for an average of 11 groups per year, for 17 years. We have taken the measurements of 412 11-day old nestlings and observed the breeding outcomes (failure or fledged) for over 489 breeding attempts at 50 groups. However, the period between fledging and independence is a time of high mortality (Ridley & Van Den Heuvel, 2012), and therefore we believe that survival to independence (when individuals are able to catch all their food for themselves) and adulthood (1 year post-hatching) are more informative measures of reproductive success. We have therefore monitored the survival to these two life history stages for 160 fledglings. In addition, we have monitored the lifetime reproductive success for over 90 individuals in the population. We have thus established a long-term study population where we are able to monitor almost all reproductive events, conduct short-term non-invasive experiments and collect samples non-invasively (e.g., collection of feces) in a highly variable environment, allowing us to monitor behavioral and demographic changes in this highly cooperative bird species relative to both social and environmental factors.

2.1 Study site

The Kalahari desert is a highly variable environment, with considerable annual and seasonal fluctuations in rainfall and temperature (Bourne et al., 2020b). Currently, daily maximum temperatures at our study site during the breeding season range between 27.6°C and 41.6°C (mean 33.7°C, Bourne et al., 2020c). Droughts, defined as ≤75% of regional average precipitation during the rainy season, happen once every 4 years on average, and droughts combined with high temperatures often lead to significantly lower breeding rates in pied babblers (Bourne et al., 2020c). Over the duration of the Pied Babbler Research Project, from 2003 to 2020, seasonal rainfall has varied widely, from >350 mm, to less than 70 mm—with an overall trend of increasing daily maximum temperature and declining rainfall (Bourne et al., 2020b; Fig. 2). This highly variable environment inhabited by the cooperatively breeding pied babbler presents an excellent opportunity to investigate different hypotheses for the evolution of delayed dispersal and cooperation, and to determine the potential future impact of a changing climate on the demography and population stability of a strongly group-structured population.

Long-term studies of individually recognizable animals are by their very nature rare, since they require years of continuous, standardized monitoring. This requires a constant source of funding, site access and researchers, with a
steady stream of research questions that one can ask of the population, to make it a continuous viable research source. Indeed, continuous monitoring of individuals and populations year-round can be very costly, but can help to avoid the systematic biases that can arise when individuals are censused only a few times per year (Clutton-Brock & Sheldon, 2010; Kidd, Sheldon, Simmonds, & Cole, 2015). Below, we use our detailed data from 18 years of monitoring marked individuals within the same population to look at causes of variation in survival, reproduction, offspring development and dispersal.

3.1 Survival

Some of the most important parameters to understand in populations are the causes of variation in survival among individuals. This is particularly important for breeding adults, since they are the source of new recruitment into the population. In pied babblers only some adults breed (primarily only the dominant pair in each group, with rare exceptions (Nelson-Flower et al., 2011)), and the rest of the non-breeding adults in the population are known as subordinates. We measured changes in annual survival per year (from the end of the previous breeding season to the start of the next breeding season) between breeding adults (dominant individuals), subordinates and juveniles (Fig. 3). We found that breeding adults were more likely to survive than other categories of individuals in the population (Wiley, 2017). While this may seem like an initially surprising result, given that there is much empirical evidence to show that breeding is costly (Clutton-Brock, 1991), survival rates between or within life history stages may be different in cooperative species compared to non-cooperators species for several reasons. First, it is not only the breeding adults that provide care to the young they produce in cooperatively breeding species. Indeed, in some species (including pied babblers), parents may terminate care in young before helpers do (Pike, Ashton, Morgan, & Ridley, 2019; Ridley & Raihani, 2008). Second, with multiple adults present to invest in young, load-lightening behavior (where there is no net decrease in the amount of care provided to young, but less contributed per adult in larger groups (Crick, 1992; Heinsohn, 2004; Meade, Nam, Beckerman, & Hatchwell, 2010; van Boheemen et al., 2019)) may occur. This results in less effort per breeding attempt for individuals living in groups compared to pairs and may reduce the costs of breeding. Because there was a difference in survival rates between life history stages, we looked at the rate of transition of individuals between each
stage, to determine the rate of movement in or out of the dominant breeding position. Dominant (breeding) individuals never transitioned to subordinate status, but did occasionally transition to becoming floaters (Wiley, 2017). Floaters are individuals that have no fixed territory or group and instead float between territories in the population; floater status primarily occurs via failed dispersal attempts, or eviction from the group (Raihani, Nelson-Flower, Golabek, & Ridley, 2010; Ridley, Raihani, & Nelson-Flower, 2008). Juveniles almost exclusively became subordinates (transition from juvenile to dominant status was extremely rare), while subordinates had approximately 30% chance of attaining dominance annually. This chance was higher when ecological conditions were favorable (no drought or heatwave events, Wiley, 2017). Floaters generally had a low chance (<20%) of attaining dominance except under exceptionally favorable ecological conditions (Wiley, 2017). The low annual rate of transition from being a subordinate (or floater) to attaining a dominant breeding position reflects the high survival rate of

Fig. 3 Annual variation in life history stage-specific survival estimates (± 95% confidence intervals) from 2004 to 2015. The variations in survival are associated with ecological conditions: low survival rates during 2006 and 2012 were during drought conditions, while low survival rates in 2008 were during a breeding season with multiple heatwave events.
breeding individuals, suggesting group-living benefits may be higher for this life history stage than other stages in terms of annual survival benefits.

Elasticity provides a measure of the proportional change in population growth rate as a result of the proportional change in a vital rate, such as survival or reproduction. It can therefore identify those stages of an individual’s life history that contribute the most to lifetime fitness (Benton & Grant, 1999). We conducted elasticity analyses and found that the elasticity of population growth rate to changes in the survival of dominant individuals was highest, indicating that proportional changes in this vital rate have the greatest effect on population growth rate (Wiley, 2017). The elasticity for fecundity was lower, suggesting population growth rate is less sensitive to changes in fecundity rate than to changes in the annual survival rates of dominant individuals (Wiley, 2017). Elasticity for transitions between life history stages were all very low, suggesting these are having a lesser influence on population growth rate in pied babblers. Our elasticity analyses therefore confirm that the survival of dominant (breeding) individuals is the main factor affecting population growth rate in this species, and therefore causes of mortality during this life history stage should be a focus for future management of this species if populations decline (as is predicted by our population viability analysis, see Fig. 4).

Density-dependent effects at the population level are well known in ecology, with population growth declining as a population approaches carrying capacity (Rockwood, 2015). This decline is often the result of lower reproductive success and survival as competition for resources increases in dense populations. Understanding the factors affecting population growth, whether they are internally or externally regulated, are a fundamental aspect of population ecology, conservation and wildlife management (Fryxell, Sinclair, & Caughly, 2014). However, for cooperatively breeding species, which tend to form group-structured populations, density dependent effects at the group level may be more important than density-dependent effects at the population level (Angulo et al., 2018; Bateman & Ozgul, 2012; Courchamp, Clutton-Brock, & Grenfell, 1999; Courchamp, Grenfell, & Clutton-Brock, 1999). Indeed, some cooperatively breeding species have a minimum group size, below which groups are too small to be able to successfully raise young and persist as a stable group (Angulo, Rasmussen, Macdonald, & Courchamp, 2013; Courchamp et al., 2002; Gregory & Courchamp, 2010). This effect is known as the Allee effect, and can make populations prone to extinction, particularly following consecutive social or climatic perturbations that lead to reductions in group size (Angulo et al.,
In our analysis of density dependent effects on pied babblers, we found no evidence of population-level density dependence. However, we did find a group-level density dependence effect: individual longevity was greater at higher group densities over an individual’s lifespan (Wiley, 2017). A higher group density could lead to benefits such as load-lightening and greater mating and dispersal opportunities. We have seen these patterns in our study population, where (a) male dispersal was most likely to occur at high group densities (Nelson-Flower, Wiley, Flower, & Ridley, 2018), and (b) there was evidence for a load-lightening effect at higher densities, with adults in larger groups contributing less to chick provisioning behavior per individual, and losing less body mass over the duration of a breeding season (Wiley & Ridley, 2016).

**Fig. 4** Population viability of pied babblers based on different climate scenarios. The top graphs represent 100 stochastic simulations of 30-year projections of total population numbers - where the red line represents the population at the start of each simulation, and the green line represents the point at which the population goes extinct. The bottom graphs represent 1000 simulations of 30-year projections of the frequency of simulated population growth rates. The red line represents a stable population (population growth begins at a replacement value of 1).
3.2 Reproduction

Age is expected to affect all aspects of an individual’s behavior, and age-related differences in survival and reproduction are considered a fundamental aspect of understanding population ecology (Clutton-Brock & Sheldon, 2010). However, we suggest that it is not just age, but the tenure of the pair bond (in species where this is present) that may be an important aspect of reproduction. The fact that pair bond tenure often correlates with age may be masking the importance of pair bond tenure in some wild populations. While pair bond tenure has been known to generate survival and reproductive benefits in monogamous species (Forslund & Larsson, 1991; Sánchez-Macouzet, Rodríguez, & Drummond, 2014), less attention has been paid to this breeding aspect in cooperative species, where more attention has focused on group size and kin-selected benefits of cooperation (Kingma, 2017), rather than the benefits a stable pair bond may provide. We found that pair bond tenure (which averages 609 days, but can last as long as 1940 days, or six breeding seasons) was a strong predictor of reproductive success in pied babblers, with significantly higher annual chick recruitment from pairs with longer tenure (Wiley & Ridley, 2018), suggesting pair bonds are more important than age AND group size at predicting reproductive success. Additionally, pair bond tenure was an important predictor of group stability: immigration of unrelated subordinates was less likely at groups where the breeding pair had been bonded for longer (Wiley & Ridley, 2018). This is an important result, since immigration events can generate competition between individuals, leading to group instability and lower reproductive success (Nelson-Flower, Flower, & Ridley, 2018; Nelson-Flower et al., 2013). This observed effect of pair bond tenure on group stability was remarkably strong: less than 2% of immigration events occurred at groups where the breeding pair had been bonded for more than 2 years, despite such pairs comprising more than 30% of our pair bond dataset (Wiley & Ridley, 2018).

Higher reproductive success—whether directly or indirectly via kin selection—is an oft-cited benefit of the occurrence of group-living and cooperative breeding behavior (e.g., Canestrari, Marcos, & Baglione, 2008; Cockburn, 1998; Kingma, Hall, Arriero, & Peters, 2010; Tanaka, Frommen, & Kohda, 2018; Woxvold & Magrath, 2005). However, we did not find a benefit of larger group size on reproduction in pied babblers (Bourne et al., 2020b)—although we did find a benefit of living in a group of any size vs living in a pair (Ridley & Van Den Heuvel, 2012). Instead, we
found a critical group size effect, where a group size of 5–6 adult babblers tended to have the highest reproductive success (Ridley, 2016). Groups larger than this critical group size experienced an increase in intragroup competition that caused a reduction in reproductive success, via overt aggression among reproductive competitors, as well as infanticide (in pied babblers infanticide takes the form of oocide—the destruction of eggs by competitors (Nelson-Flower et al., 2013; Ridley & Nelson-Flower, 2021)). Dispersal rates in large groups increased with increasing rates of aggression, often leading to reductions in group size (Ridley & Nelson-Flower, 2021).

Our long-term dataset revealed the importance of considering the multiple potential factors across early life-history stages that may be influencing reproductive success: we found that ecological factors (rainfall, drought and temperature) were more important than social factors at influencing reproductive success during the earliest stages of offspring development (Bourne et al., 2020b). In latter stages, group size influenced juvenile survival indirectly through its effect on nestling body mass: juveniles that were heavier nestlings were more likely to survive to 1 year of age, and heavier nestlings tended to be from larger groups (Bourne et al., 2020b). This result highlights the importance of considering the crucial post-fledging period of development (a developmental stage with a high mortality rate, Bourne et al., 2020b; Ridley & Van Den Heuvel, 2012), and considering survival to reproductive maturity, rather than the traditional measure of nestling survival. In a similar study in Florida Scrub-jays (Aphelocoma coerulescens), the beneficial effect of helpers was not detected in the first two life history stages (the incubation and nestling period), but was detected in later life history stages (the post-fledging period (Mumme, 1992)). Our research therefore reveals that group size is related to reproductive benefits in some stages of offspring development, but not others, and that both social and ecological factors should be considered together when determining the main causes of variation in reproductive success.

Beyond the traditional focus on group size, there are other ways that parents can influence the reproductive success of their offspring, such as through nepotistic tolerance. Delayed dispersal, where offspring stay on their natal territory beyond the period of independence, is common among cooperatively breeding species (Koenig et al., 1992; Koenig, Dickinson, & Emlen, 2016). Delayed dispersal may be an adaptive strategy when there are ecological constraints on independent breeding opportunities, leading to benefits being available on the natal territory that are unavailable elsewhere, and/or when the benefits of group living are high (Emlen, 1982). Delayed
dispersal may also occur when breeding at an older age is adaptive (e.g., due to the acquisition of breeding experience, fighting skills, or good body condition (Covas & Griesser, 2007)). However, the presence of subordinate adults on the territory can represent a cost to the breeding pair—via both reproductive and resource competition (Curry, 1988). There is therefore a trade-off between the costs of retaining adult young on the natal territory, and the costs of expelling them. We found that nepotistic tolerance was important in pied babblers, particularly for males, who retained subordinate tenure for longer when the dominant male on the natal territory was their father (Nelson-Flower & Ridley, 2016). However, when the dominant male was unrelated, subordinate males were more likely to leave the group (via forced eviction or voluntary dispersal) to become subordinate in a non-natal group: leading to lower dominance acquisition rates and lower survival (hence directly affecting future reproductive success (Nelson-Flower, Flower, & Ridley, 2018; Nelson-Flower & Ridley, 2016)). These results therefore support the theoretical prediction that nepotism influences the evolution of delayed dispersal and helping behavior (Kokko & Ekman, 2002), and highlight the importance of nepotism as a determinant of reproductive success in cooperatively breeding species.

3.3 Offspring development

Conditions experienced early in life are considered to have important impacts in later life, including size, dispersal success, thermal tolerance, age at first reproduction and lifetime reproductive success (English, Huchard, Nielsen, & Clutton-Brock, 2013; Lindström, 1999; Monaghan, 2008; Nord & Giroud, 2020; Vasilieva & Tchabovsky, 2020). In the pied babblers, we have followed over 700 individuals from hatching to death throughout the history of the project. We have been fortunate enough to be able to follow individuals as they attempt to disperse, and investigate both success and failure rates of dispersal. Dispersal is often a very difficult behavior to follow, and at times it is difficult to distinguish dispersal from death when an individual disappears (Koenig et al., 1992). However, in pied babblers dispersal (and dispersal attempts) are a highly overt and vocal process, which we are able to follow relatively easily. Dispersal attempts typically involve the potential disperser flying between territory boundaries and initiating a vocal exchange with the group inhabiting the territory. These displays can be prolonged vocal interactions of over 10 min that can sometimes turn into both a vocal display and physical fight (Ridley, 2016). The primary
vocal used during these interactions is the territorial “long call” that can be heard over several hundred meters. Dispersal attempts can last for several days and can involve aggression between the disperser and the group into which they are attempting to disperse (Ridley, 2016). Dispersal can also be highly predictable based on pre-dispersal behaviors, such as a marked decline in helping behavior (Ridley, 2016), and an increase in responsiveness and calling behavior to neighboring groups (Humphries et al., 2015). We are particularly interested in dispersal, since it often marks the beginning of the reproductive period for adults. Pied babblers can begin reproduction in two ways: inheritance of the breeding position on the natal territory, or dispersal to a territory with unrelated individuals (since pied babblers do not breed with close relatives (Nelson-Flower, Flower, et al., 2018; Nelson-Flower, Hockey, O’Ryan, & Ridley, 2012; Raihani et al., 2010)). Dispersal most commonly occurs among individuals that are 2 years or older, however we found that dispersal success was strongly related to the amount of care received during the post-fledging period: individuals that received care for a longer time during the post-fledging period were more likely to have higher body mass at independence, were better foragers, were more likely to successfully disperse and survive to adulthood (Ridley & Raihani, 2007b). Therefore conditions experienced in early life post-fledging had a direct effect on adult life history.

The post-fledgling period of care is considerably longer than the nestling period in pied babblers (31–90 day post-fledging dependent period, compared to a 14–17 day nestling period), and its significant influence on development and dispersal success highlights it as a crucial life history period in this, and potentially other species with extended periods of post-fledging/post-emergence care (English et al., 2013). Considering the number of species that display extended periods of post-fledgling care (a common trait in cooperatively breeding species (Langen, 2000)), we encourage greater investigation of this life history period. Given the importance of care received during early life on later life history, it is important to understand why there is such variation in levels of care received by developing young. In terms of “care,” there are a number of helping behaviors that young receive from group members, but here we focus on the most common and arguably important: the direct provisioning of food to dependent young. By observing the provisioning behaviors of all adult group members to young during both the nestling and dependent post-fledging stage, we have identified several causes of variation in the amount of food young receive, including the group adult: fledgling ratio (Ridley & Raihani, 2007b), group size (Bourne,
Ridley, McKechnie, Spottiswoode, & Cunningham, 2021; Bourne, Ridley, Spottiswoode, & Cunningham, 2021), brood overlap (Ridley & Raihani, 2008), and climatic factors (Wiley & Ridley, 2016). Of all the factors affecting provisioning rates to young, climatic factors are by far the most important, strongly affecting the survival and development of young, particularly during periods of very high temperatures or low rainfall (Bourne et al., 2020a, 2020b, 2020c). These results suggest that climate-related factors may be more important than social factors such as group size.

4. Behavioral and demographic responses to climate

The way that wild animals respond to environmental change is a fast-expanding area of biology due to overwhelming evidence of a rapidly changing climate. Predictive models to estimate the impact of a changing climate on animal populations are becoming more common and sophisticated (Conradie et al., 2019; Mathewson et al., 2017; Monzón et al., 2011; Razgour et al., 2018), and yet empirical data on the behavioral responses of wild animals to temperature variations are urgently needed to improve the predictive power of these models. Behavioral changes can occur when animals experience temperatures outside of their thermal optimum (Mitchell et al., 2018; Stillman, 2019). These changes can include shifts in movement or habitat use to seek microsites closer to the animal’s thermal optimum, or cessation of activities such as foraging in order to offset heat (Cunningham, Martin, & Hockey, 2015; du Plessis, Martin, Hockey, Cunningham, & Ridley, 2012; Sinervo et al., 2010; van de Ven, McKechnie, & Cunningham, 2019). Parents may even trade off their own survival against the survival of their young when conditions become sub-optimal (Edwards, Mitchell, & Ridley, 2015; Ghalambor & Martin, 2001; Oswald, Bearhop, Furness, Huntley, & Hamer, 2008; Sharpe, Cale, & Gardner, 2019), with potential long-term consequences for reproductive success and population growth. Therefore, it is vital to prioritize empirical work that investigates the behavioral changes of wild animals in both the short- and long-term in relation to prevailing environmental conditions, and how these affect social dynamics and population growth.

4.1 Short-term behavioral changes in response to climate

At the most basic level, climate-related interruptions to feeding and resting activity will affect individual time budgets. In pied babblers, individuals invest in bill-gaping (“panting”) and wing-spreading behavior to offset heat, beginning at air temperatures from the early to mid-30s °C (du Plessis et al., 2012).
Because pied babblers are terrestrial foragers, using their bill to dig in the soil for invertebrates (Ridley & Raihani, 2007a), they cannot efficiently offset heat and forage simultaneously. This means that the time spent investing in heat dissipation behavior represents foraging opportunity time lost. We found that the foraging efficiency of pied babblers decreased as temperatures increased, with foraging efficiency at temperatures above 40°C less than half of that when temperatures were 33°C or less (du Plessis et al., 2012). Concurrent with the loss of foraging time at high temperatures, individuals gained less body mass on hot days, and even lost body mass on days with maximum daily temperatures above 38°C (du Plessis et al., 2012). Body mass maintenance is an important issue, since continued body mass loss can led to lethal or sub-lethal effects and reduced investment in young (Clutton-Brock, 1991). Therefore consecutive days of high temperatures (which are increasingly likely to occur due to the evidence of local warming trends in the Kalahari over the last 20 years (Paniw et al., 2019)), may lead to considerable body mass loss in species exposed to these conditions. Indeed, similar effects have recently been found in other species inhabiting the Kalahari desert (Kemp et al., 2020; van de Ven et al., 2019).

Short-term changes in activity budgets associated with behavioral thermoregulation can strongly impact the development of young if high temperature events occur during the breeding season. In pied babblers, we investigated provisioning rates to nestlings in relation to temperature. Since adults capture less food when it is hot (du Plessis et al., 2012), they may be limited in their ability to provision young on these hot days. We confirmed this effect: adults gave away significantly less food to young as temperatures increased (Wiley & Ridley, 2016). Consequently, nestlings raised during periods of high temperature had significantly lower body mass, which has long-term negative implications for their survival to adulthood (Bourne et al., 2020c). We found that the additional cost of raising young led to greater body mass loss of adults during high temperatures (Wiley & Ridley, 2016). This suggests that reproduction carries an additional cost under high temperature conditions, in addition to the cost of trading off behavioral thermoregulation with other behaviors. Importantly, this provides behavioral evidence that short-term changes in behavior can have longer-term consequences on reproduction and offspring survival.

4.2 Longer term reproductive and demographic impacts of climate

Given the potential of short-term behavioral responses to climate to impact longer term processes (Stillman, 2019), we conducted a longer-term
investigation into the impact of climate conditions on offspring survival and development (Bourne et al., 2020a, 2020b, 2020c), as well as adult survival (Bourne et al., 2020a, 2020c; Wiley, 2017). Our results pointed to an overwhelmingly significant and detrimental effect of high temperatures on survival and development at almost every life history stage.

4.2.1 Adult survival

The factors impacting the survival of dominant individuals are of particular importance, since they are the source of new recruits to the population via breeding success. Using a multistate capture-mark-recapture model, we found that the annual survival probability of dominant individuals was negatively impacted by both above average temperatures and drought events (Wiley, 2017). Looking more closely at the impact of drought on survival, we documented a decline of over 50% in the survival probability of dominant individuals following hot droughts compared to when droughts associated with mild temperatures (Bourne et al., 2020c), highlighting the significant impact of hot temperatures combined with low rainfall conditions. In addition, fecundity was lower during hotter and drier years, leading to an overall population decline in these years (Wiley, 2017). Given the frequency in which these weather events are experienced in the Kalahari, population declines were observed in over 40% of our observation years. Using the combined information on adult survival rates and fecundity rates according to environmental conditions, we were able to generate population viability models for the pied babblers for the next 30 years. We modeled three different scenarios: population viability if (a) current conditions remain unchanged into the future, (b) there is a doubling of the frequency of drought conditions and (c) there is a doubling of the frequency of high temperature events (these latter two are considered highly likely to occur due to climate change (IPCC, 2014). The population viability analyses reveal an increased probability of extinction under scenarios (b) and (c), but particularly under scenario (c) (Fig. 4). Given that temperatures are already increasing at the study site (Bourne et al., 2020b), we consider scenario (c) to be quite likely, suggesting considerable population decline and future local extinctions for this species. Given that pied babblers are a relatively common bird species (IUCN red list, https://iucnredlist.org) with a wide distribution, this decline in the face of increasing temperatures and declining rainfall should be taken as a red flag for the future population viability of other species (particularly those species whose current population status renders them more vulnerable to population decline) inhabiting semi-arid environments.
where temperature increases beyond thermal tolerance limits are being observed. Interestingly, population decline was also considered more likely than population increase if conditions remain unchanged. We suggest this is because higher temperatures and drought have already been increasing over the last 20 years, causing population viability to already be in decline. It is important to note that our predictive analyses were restricted to a doubling in the frequency of drought and high temperature events. An increase in the frequency of extreme climate events (such as extreme heatwaves), such as is predicted to happen in some parts of the world under climate change, may have stronger effects on population growth.

4.2.2 Offspring survival and development

We investigated factors affecting the outcome of 489 breeding attempts by 50 groups over 14 breeding seasons to determine the potential importance of climatic conditions on offspring survival and development. We found that temperature was a greater determinant of hatching success than social factors such as group size: hatching probability declined as average maximum daily temperatures during the incubation period increased (Bourne et al., 2020b). Importantly, this effect was not linear: we identified a breakpoint in the data at 35.4 °C. Below this point, there was no relationship between temperature and hatching probability. Above this point, hatching probability decreased significantly with increasing temperature (Bourne et al., 2020b). High temperatures also had a strong impact on nestling survival to fledgling: probability of survival declined at temperatures above 33.1 °C, and a breakpoint was detected above 37 °C, where probability of survival declined dramatically (Bourne et al., 2020b), and when mean maximum daily temperatures during the nestling period were above 38 °C, no nestlings survived to fledgling age (Bourne et al., 2020b). This is therefore a critical thermal tolerance limit for young nestlings and should be included in population viability analysis models. A complete lack of recruitment of young when average maximum temperatures during early development are above a critical thermal threshold could lead to sharp population declines. This was observed in our demographic analyses above, where population declines were observed following breeding seasons with high temperatures and drought conditions (Fig. 3). Higher temperatures during the nestling period also led to lower nestling body mass, which in turn led to lower probability of survival to independence (Bourne et al., 2020b). On some of the hottest days observed during the nestling period, nestlings lost body mass, rather than the traditional rapid weight gain typical during this development period (Bourne, Ridley,
McKechnie, et al., 2021; Bourne, Ridley, Spottiswoode, et al., 2021). We also found that temperature negatively impacted juvenile survival to adulthood, and high temperatures in combination with drought were associated with a seven-fold decrease in juvenile survival probability (Bourne et al., 2020c). Our findings of a consistent negative effect of higher temperatures on offspring survival and development are consistent with recent findings in other species, including the Burrowing owl (Athena cunicularia, Cruz-McDonnell & Wolf, 2016), meerkats (Paniw et al., 2019), common fiscals (Lanius collaris, Cunningham, Martin, Hojem, & Hockey, 2013), and southern yellow-billed hornbills (Tockus leucomelas, van de Ven, McKechnie, Er, & Cunningham, 2020).

Given that cooperative breeding is considered (in some cases) a breeding strategy that is selected for under highly variable climatic conditions (Jetz & Rubenstein, 2011; Rubenstein & Lovette, 2007), we hypothesized that group size would buffer individuals from the impacts of a variable climate. We considered that larger group size might act as a buffer by (a) more adults being available to feed young, and hence at higher temperatures young in larger groups would receive more food than young in smaller groups simply because there are more adults available to feed them (depending on brood size) (b) larger groups may be able to acquire and defend higher quality territories, allowing a greater range of thermal microsites to forage in, offsetting the effect of higher temperature on foraging behavior (Cunningham, Gardner, & Martin, 2021) or (c) individuals in larger groups can invest less in helping behaviors (the load-lightening effect), and have more time to invest in behaviors such as foraging and self-maintenance. However, we did not find evidence of a group size buffering effect—larger groups did not have higher survival rates of adults, nor better survival and development rates of young than smaller groups during high temperature or drought events (Bourne et al., 2020a, 2020b). Although we did find evidence of load-lightening (Bourne, Ridley, McKechnie, et al., 2021; Bourne, Ridley, Spottiswoode, et al., 2021; Wiley & Ridley, 2016), this did not translate to survival benefits of adults or young. This does not mean there is no benefit of being in a larger group, or that there is no benefit of breeding cooperatively. Instead, it does not support the hypothesis that larger group size buffers individuals against the effects of climatic events better than small group size.

5. Uniting behavior and physiology

Collaborations between the fields of physiology and behavioral ecology have the potential to provide significant advances in our understanding of the potential future impacts of climate change on animal populations
(Andreasson, Nilsson, & Nord, 2020; Conradie et al., 2020; Cooper, Withers, Hurley, & Griffith, 2019; Stillman, 2019; Wingfield et al., 2017). The impact of climate on behavior, development and survival of wildlife populations can be best understood with the help of concurrent physiological measures (Stillman, 2019).

Maintaining body temperature within safe thermal tolerance bounds is fundamental to survival, and can be achieved both by behavioral and physiological adjustments (Stillman, 2019; Wingfield et al., 2017). At environmental temperatures above an endotherm’s thermoneutral zone, the physiological costs of thermoregulation (in terms of energy and/or water) increase (Mitchell et al., 2018). The temperature thresholds above which physiological costs increase are species-specific, as are species’ efficiencies in managing thermal loads physiologically, and their maximal thermal tolerances (i.e., heat tolerance limits, the maximum environmental temperature which species can tolerate before losing control of their body temperature (McKechnie et al., 2017; Smit et al., 2018)). To mitigate the increased physiological costs of thermoregulation at high air temperatures, animals can use a range of thermoregulatory behaviors to reduce the heat loads to which they are exposed and facilitate the dissipation of excess heat. These adjustments can take the form of shade-seeking behavior, panting or gular flapping to facilitate evaporative water loss, adjustment of use of thermal microsites to particular times of the day, or adjustment of foraging times (from diurnal to crepuscular for example), and reductions in overall activity. However, these behavioral adjustments are traded off against other essential activities (such as foraging, vigilance and offspring care), and may also lead to significant costs, many of which we have identified in pied babblers, including body mass loss, reduced foraging efficiency, lower provisioning rates to young, and reduced offspring growth and survival.

Recent research, in both pied babblers and other species, has identified thermal thresholds above which behavioral adjustments to manage heat loads are associated with declines in body mass of adults (du Plessis et al., 2012; Kemp et al., 2020; van de Ven et al., 2019). These behavioral thermal thresholds are likely to be shaped by underlying species-specific physiological responses to temperature, which, along with state-dependent factors, likely dictate the behavioral adjustments animals make to mitigate physiological thermal costs. This need to combine physiological and behavioral approaches is made ever more important by the fact that animals are limited in their thermal tolerance plasticity (Noakes & McKechnie, 2019) and the current rapid rate of warming suggests that this limited plasticity will not be able to keep pace with increases in both the frequency and intensity of
heatwaves (Gunderson, Dillon, & Stillman, 2017; Gunderson & Stillman, 2015). For species restricted to low latitudes this issue is of particular concern, given that those species adapted to the warmest habitats tend to have the lowest adaptive plasticity to heat tolerance (Iknayan & Beissinger, 2018; Stillman, 2003). Therefore, to understand the potential impact of temperature increase on wildlife, we need to understand both behavioral and physiological responses to high temperature events, and the costs and consequences of these.

5.1 Physiological studies—Invasive vs non-invasive sampling

Thermal physiology is a well-established field of research, with research outputs of high significance both ethically and economically. The impact of the thermal environment on the welfare, growth and meat production of animals in the livestock industry, for example, is of global importance (Caulfield, Cambridge, Foster, & McGreevy, 2014; Johnson, 2018; Morrison, 1983). Similarly, the impact of the thermal environment on the safety, work productivity and cognition of humans has received considerable attention (Hancock, 2020; Mazloumi et al., 2014; Razmjou, 1996). Among wildlife, considerable thermal physiology research has also been conducted, but the majority of this research has been conducted on animals in captivity (Stillman, 2019). While such research does provide extremely valuable data, there are some potential issues with captive research. First, the invasive sampling regime may increase stress and generate values that are not representative of typical responses observed in wild, free-living individuals of the same species (Dickens, Earle, & Romero, 2009). Second, captive sampling does not allow researchers to explore physiological correlates of behavioral strategies observed in-field. Individuals in captivity typically do not invest in the same behaviors that they do in the wild, such as searching for food or water, seeking thermal microsites (not possible in temperature-controlled labs), finding mates, defending territories and remaining vigilant for predators or competitors. This means the values in captive animals may not be directly applicable to wild animals, and studies of physiological responses to high temperatures under natural conditions to be able to determine habitat and species-typical responses to these events are needed. While capturing animals in the field, sampling and then releasing them may overcome some of these issues (Pavlova et al., 2018; Romero & Reed, 2005), they do not overcome the issue of capture stress.
The potential issues of invasive sampling can be overcome with non-invasive techniques. For example, measuring daily energy expenditure typically requires that a sample from each individual is collected 24 h, or a multiple thereof, after the first sample (Fig. 5A). While daily energy expenditure and water turnover values are typically extracted from blood samples, feces as an alternative suitable matrix have received attention (Anava, Kam, Shkolnik, & Degen, 2000; Gotaas, Milne, Haggarty, &

Fig. 5 A comparison of the methodology used for (A) standard sampling of wildlife for the doubly labelled water protocol and (B) the non-invasive sampling strategy we used for our research on wild free-living pied babblers (Bourne et al., 2019).
Tyler, 1997; Speakman & Hambly, 2016), and using feces to quantify metabolized glucocorticoid levels (fecal glucocorticoid metabolites—fGCM), for example, is a common practice in wildlife studies (reviewed by Palme, 2019). The benefit of fecal sampling is it can be done non-invasively—droppings can be collected immediately after deposition without the need for animal capture (Fig. 5B). To confirm that fecal sampling is as reliable as blood sampling, species-specific validation studies are required. We conducted these studies in pied babblers: individuals were captured from the wild and taken into captivity. Blood and fecal samples were collected concurrently over time, and the levels of fGCM and the ratio of oxygen–18 (measured as δ¹⁸O) and deuterium (measured as δ²H) after dosing with doubly labeled water (DLW) in these different sample types were compared. We were able to confirm that there was no significant difference in either the fGCM levels or the δ¹⁸O/δ²H detected in the blood vs fecal samples taken from the same individuals at the same time (Bourne et al., 2019; Jepsen et al., 2019). This confirms feces as a suitable alternative matrix to collect as samples for testing of free-living wildlife.

5.2 Non-invasive sampling reveals reliable physiological measures in free-ranging animals

Our non-invasive sampling techniques employed in our wild population of pied babblers, following the validation techniques described in Section 5.1, provided extremely valuable data. While repeated sampling in the wild can be notoriously difficult, particularly for shy, rare or cryptic species (Palme, 2019; Speakman & Hambly, 2016; Stillman, 2019), our study population of pied babblers can act as a model species for the value of non-invasive sampling for physiological studies in wildlife due to their habituation and terrestrial foraging habits: making it relatively easy to follow them throughout the day and collect samples immediately (described in Bourne et al., 2019). Our comparison of adrenocortical response, an indicator of stress (Palme, 2005; Touma & Palme, 2005), between captive and wild pied babblers confirmed the impact that captivity can have on individuals: fGCM levels in captive pied babblers ranged between 32 and 43 times higher than those of wild pied babblers (Jepsen et al., 2019). This is a huge difference in stress levels and should be taken as an indicator that studies of adrenocortical responses in captivity should be considered with caution when applied to wild animal populations. Physiological adjustments to the endocrine system are an important component of an animal’s response to environmental stressors (Jensen, Moseby, Paton, & Fanson, 2019; Palme, 2019). High levels of
stress, both short-term and long-term, can negatively impact reproductive and social behaviors, as well as body condition and survival (Bókony et al., 2009; Kitaysky, Piatt, & Wingfield, 2007; Rubenstein, 2007), and therefore reliable measures of stress are extremely important. Although our research revealed low levels of stress in wild pied babblers overall, we did find some variation in levels of stress between individuals (Jepsen et al., 2019). Of particular interest was an increase in fGCM levels with increasing daily maximum temperatures (L. Moagi, unpublished data). We identified a breakpoint at 38 °C, beyond which fGCM levels increased sharply, becoming twice as high as fGCM levels measured at cooler temperatures (L. Moagi, unpublished data). This indicates a physiological stress response in pied babblers at high temperatures. In addition, the breakpoint at 38 °C for fGCM levels is the same breakpoint as that observed for a sharp increase in nestling mortality in this species (Bourne et al., 2020b), identifying 38 °C as a critical thermal threshold in this species.

As well as measuring fGCM levels, we also measured daily energy expenditure (Bourne et al., 2019) and water turnover (Bourne, Ridley, McKechnie, Spottiswoode, & Cunningham, 2020) in wild pied babblers via isotopic enrichment in fecal samples. This was achieved by injecting doubly labeled water doses into beetle larvae carcasses that were then consumed by the focal individual, a technique similar to that adopted by (Anava et al., 2000) on the congeneric Arabian babbler (Turdoides squamiceps). Fecal samples were collected before ingestion of the dosed beetle carcass by the focal babbler, and then for the next 24 h after dosing. Our data revealed daily energy expenditure values slightly higher than captive pied babblers (as expected, given captive pied babblers have restricted movement), and very similar to those measured for free-living congeneric Arabian babblers (Anava et al., 2000; Bourne et al., 2019). Importantly, we found a significant relationship with maximum daily air temperature: daily energy expenditure declined as air temperature increased (Bourne et al., 2019). This is as expected given that we know (a) babblers spend more time heat dissipating and less time foraging and provisioning young on hot days (du Plessis et al., 2012; Wiley & Ridley, 2016) and (b) there is typically a decrease in resting metabolic rate with increasing temperature (up to an upper temperature limit (Scholander, Hock, Walters, Johnson, & Irving, 1950; Tomlinson, 2016)). We also observed incubating pied babblers, recording nest-attendance behavior and DLW samples concurrently, and found that the ability to stay hydrated declined as individuals spent more time incubating on hot days (above 35 °C), but not cool days (Bourne et al., 2020d). This
suggests that the physiological costs of incubation are substantially higher during hot weather. Our results therefore confirm that these non-invasive sampling techniques are sensitive enough to predict relationships between physiological factors (such as fGCM levels, daily energy expenditure and water turnover) and predictor variables of interest, such as temperature, behavioral indicators of heat stress (panting, wing splaying) and other environmental and behavioral variables. By sampling behavior and physiology concurrently in the same individuals under natural conditions, we were able to identify specific temperature thresholds in physiological response that can help to explain observed impacts of high temperatures on, for example, breeding outcomes. The physiological correlates of behavior, and the associated temperature thresholds, can be used to inform predictive biophysical (Conradie et al., 2019) and population viability models, improving our understanding of the likely impacts of current and future global climate change on wildlife.

6. A research approach for quantifying the impact of climate change on wildlife

In this paper, we have provided an overview of the benefits of merging demographic, behavioral and physiological data to get a detailed and quantifiable insight into the potential effects of climate change on a wildlife population. These detailed insights are important because (a) population viability models, which are currently one of the most powerful tools available to project the probability of population growth into the future, require detailed information to run reliable projections (Chaudhary & Oli, 2020), (b) there is considerable evidence the climate is rapidly changing, meaning wildlife management actions to mitigate against local extinctions urgently need predictive models regarding the consequences of different management attempts. For example, in some cases climate change may mean that animals will no longer be able to persist in their current habitat (Gunderson & Stillman, 2015; Radchuk et al., 2019; Stillman, 2019). However, the ability to move may be constrained by habitat fragmentation, resource limitation, disease, competition or predation (Mathewson et al., 2017; Mitchell et al., 2018; Pecl et al., 2017). In such cases, extreme interventions such as assisted colonization (Mitchell et al., 2016) may be required. Identifying new habitats for species that can no longer persist in their current habitat due to climate change requires a sound knowledge of the species ability to adapt physiologically and behaviorally to a new habitat (Gunderson &
Stillman, 2015). Knowledge of the behavioral and physiological thermal thresholds of these species will thus help determine the suitability of new habitats (Cunningham et al., 2021; Mathewson et al., 2017; Mitchell et al., 2016).

We recommend the following research approach to enable better predictions of the impact of climate change on wildlife populations:

1. A stronger collaboration between the fields of physiology, population ecology and behavioral ecology to identify physiological correlates of behavioral strategies, and the short and long-term consequences of these at the individual and population level. As Stillman (2019), points out, physiological research can provide the evidence-based “smoking gun” to prove that climate change has direct impacts on organisms.

2. Non-invasive sampling in wild animals (where possible) to get reliable measures of physiological variables in wild populations. We recommend repeated sampling within individuals, as well as sampling of as wide a range of individuals as possible. This is because different categories of individuals (such as breeding and non-breeding adults, males and females, subordinate and dominant individuals) may show significantly different levels of stress (Jepsen et al., 2019) and thermoregulatory response (Cunningham, Thompson, & McKechnie, 2017). We encourage concurrent measures, so that non-invasive physiological and behavioral samples are taken at the same point in time, allowing a better understanding of the behavioral outcome of physiological state.

3. A consideration of social, environmental and demographic conditions concurrently. There are likely to be multiple factors that influence an individual’s survival, growth and reproduction. These factors are likely to be numerous, and in some cases even compound one another. For example, factors influencing reproductive success in cooperatively breeding species showed a biased focus on social factors until fairly recently. A number of recent papers (Bonnet et al., 2019; Bourne et al., 2020c; Lv et al., 2020; Paniw et al., 2019; van de Ven, Fuller, et al., 2020; van de Ven, McKechnie, et al., 2020) have recognized the highly significant effect that environmental factors have on reproduction, with these factors often superseding the importance of social factors (Bourne et al., 2020c).

4. Continued monitoring of marked individuals over time, to track the short vs long-term effect of stressors on lifetime reproductive success. Long-term studies have disproportionately contributed to our understanding of factors affecting life history variation and population change.
over time (Clutton-Brock & Sheldon, 2010; Culina et al., 2020). While the importance of short-term studies should not be under-estimated, the value of long-term studies for elucidating the effects of climate change on wildlife populations are perhaps of exceptional importance.

(5) Consideration of the importance of habitat heterogeneity and the importance of thermal refugia within territories (for territorial species) and habitats in general. Animals must adopt behavioral strategies to mitigate physiological thermoregulatory costs at high temperatures, especially as these costs increase non-linearly as temperatures exceed the thermoneutral zone (Mitchell et al., 2018). This includes shade-seeking and heat dissipation behavior, for which thermal refugia are crucial.

(6) International data-sharing between researchers with data on animal responses to environmental perturbations in different environments. These datasets can hold considerable value for identifying large-scale similarities in responses, allowing a broader and powerful overview of the likely impact of climate change on wildlife. Data-sharing initiatives such as SPI birds (https://www.spibirds.org), Movebank (https://www.movebank.org) and the Covid-19 Biologging database (https://www.bio-logging.net) show great potential for identifying broad-scale patterns, and for the promotion of data-sharing and collaboration between researchers of diverse expertise.

7. Conclusion

Our long-term research on the pied babbler provides an overview of the factors affecting growth, reproduction and survival at the individual level, and the impact that this has on population growth and viability. We have been able to determine that both social and environmental factors strongly influence variation in individual life histories, but importantly, we have been able to identify thermal thresholds and correlates of physiology and behavior that lead to both lethal and sub-lethal effects in this species. By applying our basic knowledge of social and environmental factors affecting reproduction, we have been able to generate population viability models. These models reveal that under increasing heat and drought events (which are a likely future scenario), there is a high probability of local extinction for the pied babbler. These findings allow the pied babbler to be used as a model system for other species living in group-structured populations, or species that inhabit warm environments and are already close to their
thermal limit. However, we acknowledge that species vary widely in their physiological responses to heat, and therefore physiological results cannot always be directly compared between species (McKechnie et al., 2017; Smit et al., 2018). Despite this phylogenetic variation, we hope that our non-invasive techniques have the potential to be broadly applied to physiological studies of wild, free-living animals. Overall, this review of our extensive research into pied babbler ecology provides an integrated yet cautionary insight into the potential effect of climate change on wild populations that we hope can prove useful for studies of other species worldwide.

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