Acute and chronic heat stress risk in Kalahari Desert birds under past, present and future climates

by

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Submitted in partial fulfilment of the requirements for the degree of

Master of Science in Zoology

In the Department of Zoology and Entomology

Faculty of Natural and Agricultural Sciences

University of Pretoria

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September 2018

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Acknowledgments

Foremost, I would like to thank both my supervisors Prof. Andrew McKechnie and Prof. Stephan Woodborne for their dedication, support and guidance throughout this project. I have learnt an immense amount during my time under their supervision and they made this project all the more enjoyable. The discussion we had about science at lab meetings, on field trips and at conferences has impacted my process of thinking and will have a lasting influence on my future career. I am incredibly grateful for the numerous opportunities you have provided me with.

I would also like to thank Dr. Susie Cunningham and the rest of the Hot Birds Research Group for their invaluable input into my project and all the further support along the way. A special thanks to the members of the UP bird lab: Matthew Noakes, Ryno Kemp, Sekgwari Malematja, Celiwe Ngcamphalala, Samantha Naidoo, Barry van Jaarsveld, Michelle Thompson and Gabriel Foley for all the laughs, puns and support.

This project would not have been possible without several participating members who previously collected and analyzed the data which was made available to me. Thanks to BirdLife International and NatureServe for the species distribution information for southern African bird species.

Lastly, I would like to thank my parents and amazing boyfriend for the support and confidence in me which I could not have done without. You have provided me with so much encouragement, laughter and unconditional motivation. I am extremely grateful to have such wonderful and supportive parents and such a kind, patient and adventurous boyfriend. Thank you.

Plagiarism declaration

I, Shannon Conradie declare that the dissertation, which I hereby submit for the degree Master of Science in Zoology at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature:

Name: Shannon Conradie

Summary

Earth's climate is warming at an unprecedented rate, with climate change affecting virtually every habitat on the planet. Organisms can potentially adjust their physiology, behaviour, morphology and/or geographic distribution in response to changes in climate, although their capacity for such adjustments may be constrained by biotic and/or abiotic factors. Organisms' niches are part of a dynamic system that responds to changing climates and has resulted in species distributional shifts in the past, and will surely continue to do so in the future. Past climate data combined with species responses to climate change provide a tool for predicting extinction risk and reducing uncertainty for species responses to future climate change. Trajectories of species distributions and extinction risk in response to changing environmental conditions have not considered climate histories and the physiological responses that organisms might have expressed. I developed a dynamic tool interrogating spatial-temporal climate models, allowing identification of areas of acute and chronic heat stress risk in arid-zone birds. Birds are particularly vulnerable to increased air temperatures (T_a) due to their predominantly diurnal lifestyle, small size, and their high energy and water requirements. When exposed to short-term (typically hours) increases in T_a, birds experience acute heat stress where their only avenue of heat dissipation to maintain body temperature below environmental temperatures is evaporative heat loss. The rate of evaporative water loss in response to air temperatures reveals critical thresholds (T_{thresh}) of lethal dehydration risk. All passerines modelled here experience occasional risk of lethal dehydration under current conditions, with the threat increasing in frequency, severity and geographic area under a high risk climate change scenario (RCP 8.5) by the end of the century. This is most obvious for Burchell's Starling which will experience approximately 6 – 10 $d \cdot y^{-1}$ of risk over a large proportion of their range. Similarly Scaly-feathered Finches and White-browed Sparrow-weavers will be exposed to an increase in the number of heat stress days within and around their ranges. When hot weather persists over periods of days to weeks, birds experience trade-offs between foraging and thermoregulation which have chronic, sublethal negative impacts on individual survival and fitness. Currently species in southern Africa are experiencing < 10 consecutive days where $T_a > T_{thresh}$, however these conditions are likely to increase by approximately 830% for Southern Pied Babblers and Common Fiscals ($T_{thresh2}$), and 283% for Common Fiscals ($T_{thresh1}$) in the southern Kalahari Desert region, under unmitigated climate change (RCP 8.5, 2080 – 2090). The number of consecutive days per year where $T_a \geq 35.5$ °C (conditions where diurnal mass gain is insufficient to counteract overnight mass loss) in the southern Kalahari Desert was 3.5 days (austral summer, 2000 and 2010) and are likely to increase to approximately 29 $d \cdot y^{-1}$ by 2080 – 2090 under a high risk climate change scenario, resulting in poor body condition for a large proportion of the breeding season. Given the expected increases in frequency and extent of

high temperatures and the inability to maintain body condition at these temperatures, successful breeding attempts are likely to decrease by the end of the century in desert birds. I suggest that these chronic, sublethal effects will be more important in terms of species persistence than the risk of acute mortality events under future climate change.

Chapter I: Literature review

Control of climate on biology

Over the past 100 years the global climate has warmed by > 1 °C (IPCC, 2014; Pacifici et al., 2015; Walther et al., 2002). During the first two decades of the 21st Century the rate of warming was approximately double the rate of the 1910 to 1945 warming period, making it the fastest warming event within the past 1000 years (Folland et al., 2001; Papalexiou et al., 2018). Global average temperatures are predicted to increase by > 1.5 – 2 °C by the end of this century, even if the terms of the 2015 Paris agreement (UNFCCC, 2015) are met (Millar et al., 2017; Landman, Malherbe, & Engelbrecht, 2017). The 2015 Paris agreement targets aim to limit global average temperature increases to 2 °C above pre-industrial conditions (Millar et al., 2017). A scenario which is becoming increasingly unlikely with approximately 5 % chance of being met by the end of the century (Raftery et al., 2017). Brown & Caldiera (2017) found that observationally informed projections indicate that future warming under unmitigated climate change is likely to be 15% warmer than climate simulations are currently predicting.

The socio-economic effects of the projected warming are likely to be extreme with cascading effects on human well-being, biodiversity and economic advancement in developing countries in Africa. A recent study on the risk of lethal temperatures to humans predicts that almost three-quarters of the human population could be exposed to these climatic conditions by 2100 under a low mitigation scenario (Thornton et al., 2009; Zinyengere, Crespo, & Hachigonta, 2013). These authors also reported that combined with the risk of lethal temperatures to humans, agricultural productivity is expected to decline under future climate change scenarios. Agricultural productivity in sub-Saharan Africa has been declining over the past 50 years but demand and population growth have been increasing alongside a more variable climate regime (Kotir, 2011; Hall et al., 2017).

Climate variability influences biological processes at various levels ranging from species to ecosystems, and the integrity and survival of some of the world's most biologically important ecosystems are suggested to be threatened by climate change (Beaumont et al., 2011). Species are unlikely to respond to changes in global average temperatures *per se*. Instead, species respond to environmental changes within their ecoregion, where an ecoregion is defined as a large geographic area with distinct geology, species composition and environmental conditions (WWF, 2012). In these ecoregions the composition of biological communities will change, but the overall functioning of ecosystems will generally be more resilient to the effects of warming (Scholes et al., 2015). Changes in climate across ecoregions tend to be spatially variable, where large heterogeneity in warming allows species to respond with cascading effects within the community, population and eventually ecosystem (Walther et al., 2002). Species responses to changes in the climate system may still be inadequate given the projected increase in climate variability and average temperatures, producing a likely threat to future biodiversity (Beaumont et al., 2011).

Changes in air temperature (T_a) affect organisms through compromising or altering physiological performances and vulnerability to heat stress in ectotherms (Deutsch et al., 2008; Frishkoff, Hadly, & Daily, 2015; Huey, 1991; Seebacher & Franklin, 2012) or heat loads in endotherms (Huey et al., 2012; Kearney, Wintle, & Porter, 2010; Mathewson et al., 2016; Porter, 2000; Porter & Kearney, 2009). Numerous studies have examined the effects of changing temperatures on species (Hughes, 2000; Janzen, 1994; Lovegrove, 2003; McKechnie & Wolf, 2010; Parmesan, 2006). One notable study reported that over the past 20 to 140 years approximately 59% of 1598 species shifted either their distribution and/or phenology in the direction expected from regional climate change (Parmesan & Yohe, 2003). Present environmental attributes alone cannot account fully for current patterns of biodiversity (Huntley et al., 2016), and both current and historical factors need to be considered for a more complete understanding of global and regional patterns of biodiversity (Huntley et al., 2016; Huntley et al., 2014).

The consequences to biodiversity of past and present changes in climate are of fundamental importance given that not all species will respond in the same way (Erasmus et al.,2002). Characteristic differences in physiological tolerances (Oswald et al., 2011), life-history strategies (Hillaert et al., 2015; Jenouvrier, 2013), probabilities of extinction and dispersal abilities (Huntley et al., 2012) provide the basis for highly variable responses to change. Species responses are therefore variable and often reflect species-specific factors determining vulnerability to change.

Vulnerability

Vulnerability as defined by the Intergovernmental Panel on Climate Change (IPCC) is the tendency of a system to be negatively affected. Williams et al. (2008) developed an integrative framework to evaluate the characteristics promoting the vulnerability of a species to changing climates. This framework outlined which species, habitats and ecosystems are most vulnerable, which aspects of their biology determine their vulnerability and how to best manage and minimize the realized effects thereof. The vulnerability of a species is determined by its *sensitivity* to changes in the environment as well as the *exposure* to that change. A species' sensitivity is determined by ecological and evolutionary aspects (e.g. genetic diversity, phenotypic plasticity) as well as the resilience or recovery from disturbances (e.g. life history traits, dispersal ability). The interaction between climate change, extreme climatic events and the vulnerability of an exposed species determines the *impact*

(Foden et al., 2018). The magnitude of climate-induced impacts depend on intrinsic and extrinsic factors. For instance, ecological and evolutionary responses that do not keep pace with temperature changes may result in extinction. An example of a species vulnerable to extinction is the great tit (*Parus major*) whose lifetime reproductive success is declining due to the inability to keep pace with the rapid rate of warming over its geographic range for the last 30 years (Nussey et al., 2005). Understanding species responses to environmental change and the relevant thresholds at which these responses are no longer sufficient becomes critically important to predict and manage the resulting ecological consequences (Smith 2011).

Sensitivity in hot deserts: acute and chronic heat stress

Conditions associated with desert biomes include high environmental temperatures, low primary productivity, scarce and unpredictable water resources and high potential evapotranspiration further constraining free water sources (White et al., 2007). These hot, arid environments regularly present animals with extreme climatic conditions capable of increasing body temperature (T_b) above tolerable thresholds (Williams & Tieleman, 2005). Exceeding these tolerance thresholds affects species both directly (e.g. mass mortality events) and through more subtle influences on components of a species' fitness (e.g. breeding success, mass loss and offspring provisioning and growth rates). Most endotherms are homoeothermic and maintain a relatively constant normothermic body temperature (T_b, approximately 35 – 40 °C) by adjusting physiology, morphology or behaviour (Huey et al., 2012). In desert environments the frequency of extreme weather events and their intensity are as important, if not more important, than long-term average conditions (McKechnie, Hockey, & Wolf, 2012).

Physiological thermoregulation

The ability of species to survive and reproduce is affected by physiological responses [e.g. evaporative cooling (Albright et al., 2017); insulation and posture (Porter & Kearney, 2009)] which are critically affected by extreme or even subtle changes in average daily maximum temperatures (T_{max}). When exposed to short-term (typically over hours) increases in air temperature (T_a) to values above T_b, birds experience acute heat stress (Albright et al., 2017; Whitfield et al., 2015), where their only avenue of heat dissipation to maintain T_b below environmental temperatures is through evaporative heat loss (EHL), (Dawson & Whittow, 2000). During very hot weather, evaporative water loss (EWL) in small birds can exceed 5 % of their body mass per hour, even when inactive and/or in fully sheltered microsites (McKechnie & Wolf, 2010; Wolf & Walsberg, 1996). Our understanding of avian upper thermoregulatory limits and capacities for evaporative cooling during exposure to acute heat stress (where T_a exceeds T_b), has increased in the last decade with empirical data on species specific limits and the relationship between body mass and EWL becoming increasingly available (Whitfield et al., 2015; McKechnie, Smit, et al., 2016; McKechnie, Whitfield, et al., 2016; O'Connor et al., 2017). For endotherms living in hot environments where T_a routinely approaches or exceeds T_b, sensitivity to acute heat stress can be readily determined through modelling physiological responses to heat stress [e.g. lethal dehydration, hyperthermia, loss of body mass (Albright et al., 2017)]. Exposure can be derived from climate model simulations to determine the regional and local factors a species experiences within its geographic range (e.g. microclimate) (Williams et al., 2008).

Behavioural thermoregulation

A potential mechanism to minimize the physiological costs of keeping cool is through behavioural thermoregulation (Angilletta et al., 2010). Individuals making use of thermally buffered microsites (e.g. burrows and patches of shade) should be able to significantly decrease heat stress during the hottest times of the day (Cunningham, Martin, & Hockey, 2015; Sears, Raskin, & Angilletta, 2011). Despite the apparent benefits, behavioural thermoregulation does have consequences, such as lost opportunity costs which could translate into fitness costs (Cunningham et al., 2015).

When increased T_a persists over periods of days to weeks, birds experience chronic heat stress (Mathewson et al., 2016). Conditions of chronic heat stress result in trade-offs between thermoregulation and foraging resulting in sublethal fitness costs (e.g. inability to maintain body condition, compromised foraging efficiency and nestling provisioning rates) (Cunningham et al., 2013; du Plessis et al., 2012). A study by du Plessis et al. (2012) on a habituated population of Southern Pied Babblers (*Turdoides bicolor*), for example, revealed that prolonged periods of high T_a resulted in compromised foraging efficiency and the inability to maintain body condition. Both acute and chronic heat stress may result in distributional, physiological, phenotypic, or genetic changes or extinction in extreme cases (Albright et al., 2017; Walther et al., 2002).

Traditional bioclimatic modelling approaches

The assumption that the subset of climatic conditions currently experienced by a species is an accurate predictor of its future distribution under climate change underlies the climate-envelope approach to modelling species’ responses (e.g. Erasmus et al., 2002). However, factors other than climate affect distribution, survival and reproduction, which for some species violates the main assumption inherent in the use of climate-envelope models (Pearson & Dawson, 2003). The correlative, pattern-based approach of climate-envelope models decreases predictive capacity for future distributions as variables relating to habitat availability, physiology and behaviour are not incorporated (McKechnie et al., 2012; Urban et al., 2016). For instance, recent shifts in the ranges of birds have been inconsistent with the predictions of climate-envelope models (Hockey & Midgley, 2009; Okes, Hockey, & Cumming, 2008).

Mechanistic models, in contrast, use behavioural, physiological and microclimate data to predict future species distributions. Forecasting abilities for species distributions and population ecology under predicted climate change scenarios have been greatly advanced through mechanistic models (Kearney & Porter, 2009; Kearney et al., 2009). A major disadvantage of mechanistic models is that they require detailed species-specific (and sometimes population-specific) physiological information that may not always be available (Smit et al., 2013), and which moreover are time consuming and require a large amount of effort to construct and validate (Kearney & Porter, 2009).

Both climate-envelope models and mechanistic niche models use current climatic conditions and forecast future species responses accordingly. Past climatic conditions can provide critical insight into historic species distributions and reduce uncertainty for species responses to future climate change. The paleoclimatic record has become an insightful resource into species distribution modelling (Hilbert, Graham, & Hopkins, 2007; Mcguire & Davis, 2013). Past distributions have been modelled through:

1. Applying current data to a paleoclimate layer to hindcast species distributions, habitats, biodiversity or ecosystems, using a climate-envelope approach (Hilbert et al., 2007; Mcguire & Davis, 2013; Rodríguez-Sánchez & Arroyo, 2008).

or

2. Predicting complete species distributions from an under-sampled or data-sparse period using known fossils or paleoclimate data as proxies (Mcguire & Davis, 2013; Rodríguez-Sánchez & Arroyo, 2008).

Climate change

Southern Africa's climate

With the exception of the equatorial zone, the African continent is characterised by arid and semi-arid conditions (Nicholson et al., 2013). Southern Africa's annual average temperatures are generally higher than 18 °C, with the exception of the Namibian coast and South Africa's southern and eastern escarpment areas (Engelbrecht et al., 2015). The southern part of the continent is bounded by the cold upwelling Benguela current to the west and warm Agulhas current (AC) to the east (Blamey &

Reason, 2009). The AC is a key driver of weather and climate patterns in this region (Zinke et al., 2014) and is regarded as one of the strongest western boundary currents in the Southern Hemisphere. An additional key driver of climate variability in the Southern Hemisphere is the Southern Annular Mode (SAM), influencing the position of latitudinal rainfall and temperature (Abram et al., 2014). These drivers produce high degrees of variability in the rainfall regime at the annual and decadal level. Summer rainfall variability over this area is linked to the El Niño Southern-Oscillation (ENSO) phenomenon. Another contributing factor to the southern African rainfall regime is sea surface temperature (SST) (Reason, 1998; Richard et al., 2001; Woodborne et al., 2015, 2018). The instrumental and observational evidence for climatic and environmental change over southern Africa over recent decades is overwhelming (Hulme et al., 2001; Kruger & Sekele, 2013; Kruger & Shongwe, 2004; New et al., 2006; Nicholson, 2001; van Wilgen et al., 2016). Climate change in this region is likely due to a combination of factors including aforementioned natural variations in the climate system and anthropogenic factors (Engelbrecht et al., 2015; MacKellar, New, & Jack, 2014).

Climate evolution over the last millennium

Our understanding of past climates has increased in recent years through the use of proxy data reconstructions (Crowley, 2010; Nicholson et al., 2013) and dynamic climate model simulations based on physical laws acting on earth system processes (Jones et al., 2009). In recent decades the study of the last millennium's climate has increased through the use of both reconstructions and model simulations (Crowley, 2010; Jones et al., 2009; Jones, Osborn, & Briffa, 2001; Schmidt et al., 2012; Tyson et al., 2000). The last millennium is particularly interesting as it has seen two prominent events illustrating the dynamisms of climate systems, namely the Medieval Warm Period (before 1000 – 1300 CE) and the subsequent Little Ice Age (from 1300 – 1800 CE) (Tyson et al., 2000). The Little Ice Age was the coldest recorded period during the past 12 000 years (Mann et al., 2009) with the southern African interior experiencing temperatures approximately 0.9 – 1.4 °C colder than the 1960 – 1990 period (Sundqvist et al., 2013). Although some areas would have displayed temperatures equal or higher than those experienced in the last decade, several authors have argued that temperatures during the Medieval Warm Period were relatively warm, but still well below global average temperatures in the 21st century (Bradley, Hughes, & Diaz, 2003; Mann et al., 2009; Nicholson et al., 2013). Examining the climate of the last millennium provides insight into the dynamism of climate systems and if any regions have experienced conditions similar to the 21st century warming. This will improve our understanding of how ecological systems have responded to conditions of warming in the past and how they will likely respond In the future.

In recent years anthropogenic climate change contributed to warming by approximately 0.93 °C above mid-19th Century temperatures (Millar et al., 2017). In 2015 and 2016 the total warming due to both natural variability (e.g. the El Niño Southern Oscillation) and anthropogenic factors exceeded 1 °C for the first time since the mid-19th Century period (Morice et al., 2012). Subtropical southern and North Africa are currently experiencing rates of warming exceeding those predicted by general circulation models (e.g. CMIP3 and CMIP5) (Engelbrecht et al., 2015). For example, the Kgalagadi Transfrontier Park and Richtersveld Transfrontier Park in South Africa have experienced temperature increases of approximately 2 °C and 1.2 °C respectively since 1990 exceeding temperature changes predicted for the next 20 – 40 years (van Wilgen et al. , 2016).

Global trends and predictions

The Fifth Assessment Report (ARP5) of the Intergovernmental Panel on Climate Change (IPCC) predicts that average temperatures will increase by 0.3 – 2.5 °C globally by 2050 relative to climatological averages of the 1985 – 2005 period (IPCC, 2014). Future climate change projections depend on the concentration of atmospheric greenhouse gases, where human behaviour at various levels, including policymakers, industrial organizations, government sectors and general society, will determine the pathways of greenhouse gas (GHG) emission scenarios (van Vuuren et al., 2011). Future climate change scenarios therefore operate under a variety of possible conditions. The IPCC describes a number of possible GHG emission scenarios termed the Representative Concentration Pathways (RCPs) in the ARP5 (IPCC, 2014). The aim of these RCPs is to standardize future climate change predictions in a manner comparable across research groups. The various RCP scenarios consist of information on greenhouse gas concentrations and emissions characterised into four pathways namely: RCP 8.5, RCP 6, RCP 4.5 and RCP 2.6. These scenarios are representative of the literature and include a low mitigation (RCP 2.6), two medium stabilization (RCP 4.5 and 6) and one very high emission scenario (RCP 8.5) (van Vuuren et al., 2011). The use of RCP scenarios becomes critically important in the assessment of biodiversity responses and tolerances to environmental conditions under a range of possible futures, which may inform policy making and environmental protection acts in response to climate change (Lewis & King, 2017; Mora et al., 2017; van Vuuren et al., 2011).

Climate reconstructions and models

Use and limitations of climate reconstructions and models

Past atmospheric conditions are typically reconstructed using general circulation models (GCM or AOGCM for atmospheric-ocean coupled climate models) (Svenning et al., 2011) or from natural resources such as ice cores, tree rings, corals or ocean and lake sediments (Braconnot et al., 2012). The most common method used for large-scale climate reconstructions uses a selection of climate proxy records which are standardized, averaged, centred and scaled over the region of interest (Jones et al., 2009). A second method adapts proxy records into reconstructions highlighting spatial patterns of historical climates. The latter method can be used to compare climate models and their underlying patterns of climate forcing. Thus proxy reconstructions can be used to validate climate models and models in turn can test the robustness of proxy reconstructions (Jones et al., 2009). Proxy reconstructions have been used to study the variability in atmospheric and earth system processes through time (Ahmed et al., 2013; Cook et al., 2010; Cook, Esper, & D'Arrigo, 2004; Wang et al., 2007). Climate reconstructions reveal that the earth experiences natural spatial variations in climate producing warm periods (e.g. Medieval Warm Period before 1000 – 1300 AD) and cool periods (e.g. Little Ice Age from 1300 – 1800 AD) through time (Cook et al., 2004). Paleoclimatology is greatly advanced through improved climate reconstructions providing insight into climate dynamism and climate forcings in the last millennium.

One of the limitations of proxy reconstructions is that their interpretation can be complex (Nicholson et al., 2013). For example, environmental or physical factors other than temperature may have influenced the proxy records considerably and can remain undetected (Barker et al., 2001). Second, the spatial distribution of proxy data is biased and limited to certain parts of the globe leaving several areas under-represented. Assessing spatial – temporal patterns of climatic variation are therefore constrained to either highly specific trends at a regional scale or general trends at a broader scale (Nicholson et al., 2013).

Projections of future climate change are primarily constructed using dynamic climate models. These models operate using the physical laws acting on earth system processes (Landman et al., 2017). In this regard models use internal forcings, which include natural and anthropogenic warming and is distinct from external Malankovitch forcing [e.g. orbital variations (Jansen et al., 2007)], to construct future climate change scenarios. The use of climate models has become increasingly common and has several advantages, however limitations of climate models still exist (Jiang et al., 2015). A major source of uncertainties in climate modelling is the representation of processes (parameterization) and the complexity in mathematically representing them. For example, atmospheric interactions at the boundary layer in large-scale circulations remain uncertain, which in turn influences uncertainties in radiation and spreads through the coupled climate system (Flato et al., 2013). Observational uncertainty in evaluation data and parametrization, resolution, model complexity and model domain are additional sources of uncertainty in climate model simulations. Despite these uncertainties the accuracy and predictive power of climate models are improving due to our increased knowledge and understanding of climate system processes and their inclusion in climate models (Flato et al., 2013). Using multi-model ensemble approaches further reduce uncertainties in climate model projections but requires high and often limited computational power (Jiang et al., 2015). Due to these multi-model ensemble approaches and quantitative performance metrics based on historical observations our confidence in model performance is improving and suggests that these models are accurate and reliable for climate change studies (Flato et al., 2013; Sundqvist et al., 2013; Jiang et al., 2015).

The use of general circulation models is widely accepted as a tool for climate simulations despite their limitations and uncertainties surrounding climate forcings (Kotir, 2011). The development and application of climate models are often constrained or compromised by the required computational power (Flato et al., 2013). For example, high-resolution climate models increase model accuracy but lead to increased computational requirements. The inclusion of various climate system processes (e.g. the carbon cycle, ENSO) further increases computational costs while increasing the accuracy of the climate simulation (Hurrell et al., 2009). Observations of past climates are used to validate climate models but are constrained to variables, processes, regions and specific events for which observations exist. Using multiple independent observational data sources reduces these limitations although uncertainties in climate models are not completely eliminated (Braconnot et al., 2012; Flato et al., 2013).

Predictions for southern Africa's climate

Global climate models all predict significant warming by the end of the 21st Century relative to the pre-industrial era. The African continent has been identified as the most vulnerable to climate change, with average temperatures over subtropical Africa projected to increase at about 1.5 X the global rate (Davis-Reddy & Vincent, 2017; Engelbrecht et al., 2015; IPCC, 2007; Kotir, 2011). The rates of warming for subtropical southern Africa, subtropical North Africa and parts of central tropical Africa over the last five decades are twice that of the global rate of temperature increase (Engelbrecht et al., 2015). Strengthening or even persistence of these trends under future climate change scenarios will have dramatic consequences for agriculture (Thornton et al., 2011), biodiversity (Engelbrecht & Engelbrecht, 2016; Engelbrecht et al., 2015), and water security (Sperna et al., 2012). Moreover, Africa has relatively low adaptive capacity (Engelbrecht et al., 2015). Engelbrecht et al. (2015) predict the majority of the southern Africa region to face a 4 – 6 °C increase in average temperatures by 2071 – 2100 relative to 1961 – 1990 (under a low mitigation scenario). The modelled patterns for rainfall are more variable, with drier conditions generally predicted in the west and wetter conditions predicted for the east.

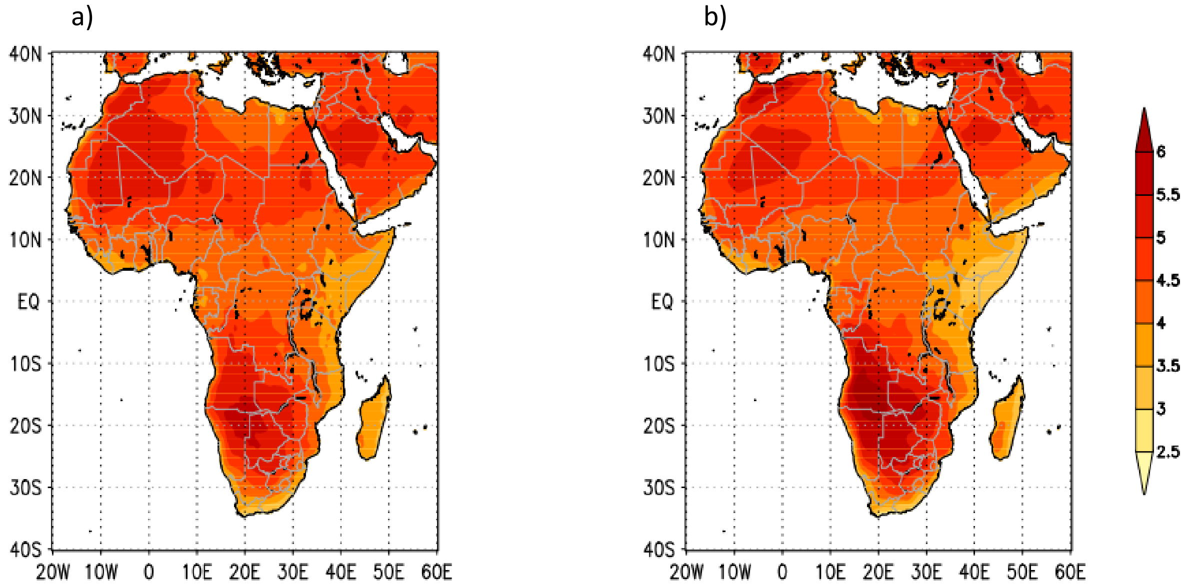

Figure 1. Projected changes in annual-average (a) and maximum (b) temperatures (°C) over Africa for 2070 - 2100 relative to the 1960 – 1990 time period (Adapted from Engelbrecht et al., 2015).

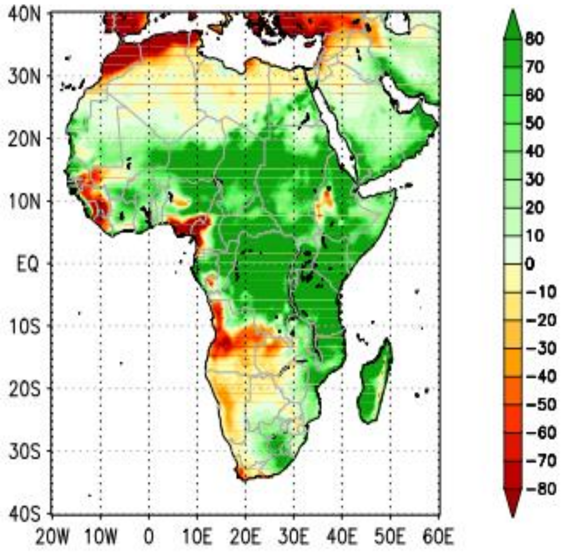

Figure 2. Projected changes in annual-average rainfall (mm) over Africa for 2070 - 2100 relative to the 1960 – 1990 time period (Adapted from Engelbrecht et al., 2015).

Combined with the unprecedented rates of warming, the number of heat wave days (IPCC, 2007; Meehl & Tebaldi, 2004) and frequency of fire events are projected to increase significantly by the end of the century (Engelbrecht et al., 2015). An evaluation of how climate varies through time, combined with current knowledge of species responses to climate, are therefore critically important for biodiversity assessments under anticipated climate change scenarios.

Desert ecoregions, in particular, are characterised by extreme climates and have experienced warming more rapidly than any other ecoregion over the past 50 years (Zhou et al., 2015). These hostile conditions and rates of warming are predicted to continue through the end of the century (IPCC, 2014). Beaumont et al. (2011) suggest that species' responses may become inadequate given the projected increase in climate variability and average temperatures. Responses of certain arid-zone bird species in desert ecoregions are already insufficient to keep pace with the current rates of climate change. For example, Iknayan & Beissinger (2018) evaluated the responses of arid-zone birds to these extreme changes in the Mojave Desert, United States. These authors found that historic avian survey sites lost on average 43% of their species from 1908 – 1968 to 2013 - 2016. Similarly, hot arid regions of Australia have experienced mass mortalities and large population declines of desert bird species (McKechnie & Wolf, 2010, 2012). In southern African studies on behavioural (Cunningham et al., 2013; du Plessis et al., 2012) and physiological (Whitfield et al., 2015; McKechnie, Smit, et al., 2016; McKechnie, Whitfield, et al., 2016) responses of arid-zone birds to climate change suggest that these species may already be responding inefficiently to current rates of climate change with potentially dramatic consequences for future arid-zone bird communities.

Aims and objectives

The objectives of this study are to determine if past climatic trends constrained the current distribution and vulnerability of desert bird species and how these constraints will change in their distribution and vulnerability in the future. I aim to model exposure to acute and chronic heat stress risk in desert birds under past, present and future climatic conditions across southern Africa. I predict that desert birds are experiencing conditions of heat stress risk more frequently in modern times than they have within the last 1000 years and conditions are likely to increase in severity and frequency under climate change scenarios.

The specific objectives of the study are to:

1. Develop a generic spatial-temporal dynamic interrogation tool for analysing temporal trends in the temperature dataset spanning the past 1000 years in southern Africa.

2. Assess acute and chronic vulnerability to climate change in desert birds under past, present and future climates.

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Chapter II: Climate variability across southern Africa in the past, present and future.

Introduction

The terms "climate" and "weather" are often loosely, and incorrectly, used interchangeably. Climate refers to long term trends and patterns of variation in atmospheric condition, whereas weather describes short-term atmospheric conditions (Gutro, 2005). A variety of weather conditions are associated with different habitat types across southern Africa. Weather conditions can be organised into unique spatial-temporal clusters producing vastly different climatological regions (Landman, Malherbe, & Engelbrecht, 2017; Nicholson, 2001; Nicholson et al., 2013). Southern Africa is one such climatological region characterised by extreme weather and climate events including floods and droughts (Landman, Malherbe, & Engelbrecht, 2017). The most well-known natural driver of these extreme weather events is the short-term climate variability in Earth system processing resulting from the El Niño Southern Oscillation system (ENSO) (Gutro, 2005).

Temperature variability in southern Africa

Evidence of how large-scale average surface temperatures have changed over southern Africa over the past few thousand years is limited (Jansen et al., 2007). Paleoclimate relates to these trends in atmospheric condition at some point in geological time spanning from hundreds to millions of years. Paleoclimate data combined with information about ecological responses to climate change are a way of reducing uncertainty for species responses to future climate change (Araújo et al., 2005; Jansen et al., 2007; Pacifici et al., 2015). In southern Africa the climate of the Medieval Warm Period was highly variable but sites such as Makapansgat Valley, South Africa were on average 3 – 4 °C hotter around 1250 CE than present conditions (Tyson et al., 2000). These conditions were approximately equivalent in magnitude and duration to those predicted by the IPCC and Engelbrecht et al. (2015) for the future, providing critical insight into temperature tolerance thresholds, species resilience to extreme conditions, possible local extinctions and areas of refuge for organisms currently and in the future (Willis et al., 2010).

Africa's tropical and subtropical ecoregions have been classified as highly vulnerable under climate change projections (Engelbrecht & Engelbrecht, 2016). Average monthly temperatures across Africa are projected to increase by two standard deviations (σ) of the mean 1961 – 1990 baseline period by 2070 (Beaumont et al., 2011). These temperature increases will result in extreme monthly temperatures being routinely experienced in Africa (Beaumont et al., 2011). Warming to this extent in southern Africa will have major consequences on economic development, primarily through agriculture, wildlife and tourism (Jury, 2013). Consistent with global predictions, southern Africa's vulnerability to increased greenhouse gas emissions and its associated effects could lead to regional desertification with cascading effects on biodiversity and economic processes (Hulme et al., 2001; Jury, 2013).

Climate models

Observational data are limited in both spatial and temporal dimensions from which climate data can be derived. Climate models however can extend further back in time and over larger spatial extents than instrumental data. Climate models use internal forcings which operate using physical laws acting on earth system processes to reconstruct past climates and to predict future climate change scenarios (Landman et al., 2017). Modelling efforts for global and regional climate change scenarios have increased in the last two decades with growing establishments of international collaborative programmes for the understanding of current and projected future high-resolution climate data (Engelbrecht et al., 2011). A feature of these collaborative programmes [e.g. the Climate Model Intercomparison Project (CMIP)], is the convergence between models, meaning that the absolute values for changes in the future may vary slightly between simulations but the tendency is likely to be the same.

Climate models of past, present and likely future climates can be combined with temperature-dependent species responses. For example, species-specific thermal tolerance limits can be combined with climate models to predict the risk of exposure to lethal temperatures (Albright et al., 2017; Mora et al., 2017). Albright et al. (2017) demonstrated how the risk of lethal dehydration in desert passerines is predicted to increase to levels previously not experienced across the species range. I aim to combine the use of climate models and species tolerance limits in a generic, versatile modelling approach. This will allow the model output to be a flexible product which is continuously improved as advancements in climate models and species tolerance limits are made.

Research questions

I aimed to develop a generic spatial-temporal dynamic interrogation tool for the past 1000 years in southern Africa. The interrogation tool was designed to answer the following questions:

a. Which areas experience subtle changes in temperature trends respectively in the past, present and likely future?

b. Which areas experience extreme changes in temperature trends respectively in the past, present and likely future?
c. How does our understanding of past climatic trends contribute to predictions of future species responses under climate change scenarios?

Methods

Study area

The study area encompasses most of southern Africa, with the exception of the eastern parts of Mozambique. Africa is divided into seven climatic zones: Mediterranean, mountain, middle latitude dry, tropical rainforest, tropical wet and dry, tropical dry, and humid sub-tropical (Kotir, 2011). These climatic zones are subdivided into 16 subtypes according to the Köppen-Geiger climate classifications, with 11 of these subtypes present within the southern Africa study region (Fig. 3) (Engelbrecht & Engelbrecht, 2016). Along with the array of climatic zones, sub-Saharan Africa hosts several different vegetation and habitat types inhabited by distinct communities of organisms, often with a long biogeographic association with a particular climatic zone (Hempson, Archibald, & Bond, 2015; White, 1983).

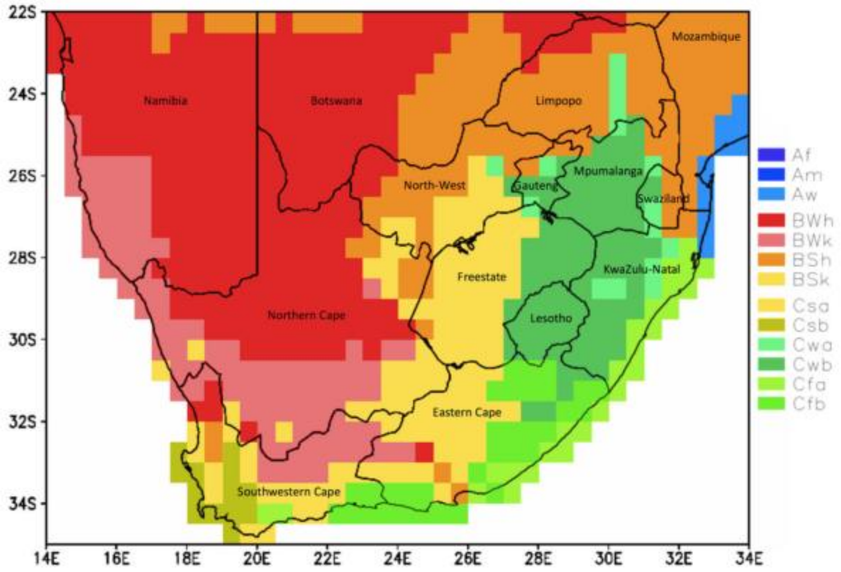


Figure 3. The Köppen-Geiger climate classification observed within the southern Africa study region between 1961 – 1990 (CRU TS3.1 rainfall and temperature) (Adapted from Engelbrecht & Engelbrecht, 2016). Af: tropical rainforest, Am: tropical monsoon, AW: tropical savanna zone; BWh: hot desert zone; BWk: cold desert zone, BSh: hot steppe zone; BSk: cold steppe zone; Csa: hot temperate zone, dry summer; Csb: warm temperate zone, dry summer; Cwa: hot temperate zone, dry winter; Cwb: warm temperate zone, dry winter; Cfa: hot temperate zone, no dry season; Cfb: warm temperate zone, no dry season.

Geospatial temperature time series

The selected millennium climate simulation was IPSL-CM5A-LR, experiment r1i1p1, obtained from the PMIP (Paleoclimate Modelling Intercomparison Project III, model: CSIRO-Mk3L-1-2, https://pmip3.lsce.ipsl.fr/). This global dataset characterised daily average maximum air temperature for 1050 – 1850 CE, where the forcing fields were interpolated to 3.15° latitude by 5.63° longitude. Data for modern climate conditions (1850 – 2014 CE) were obtained from NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, available at https://www.esrl.noaa.gov/pds/. The model selected was the reanalysed data from NOAA-CIRES 20th Century Reanalyses (v2c), where the forcing fields were interpolated to 1.88° latitude by 1.88° longitude. The temporal coverage was subsetted from six three-hour daily averages to day time values only (from 06:00 – 18:00). Future climate change projections (2076 – 2100 CE) were obtained from NCAR (National Center for Atmospheric Research) Boulder, CO, USA, available from at https://esgf-node.ipsl.upmc.fr/search/cmip5-ipsl/. Two future climate projections selected from this website were CCSM4, experiment r6i1p1, RCP 4.5 and CCSM4, experiment r6i1p1, RCP 8.5, where the forcing fields were interpolated to 0.95° latitude by 1.25° longitude. The temporal coverage was further subsetted to austral summer months (October – March) only for the historical, modern and future climate scenarios.

Climate models were selected based on their ability to characterise daily average maximum air temperature with sufficient spatial (paleoclimate < 6.0 x 6.0 °; current and future < 2.0 x 2.0 °) and temporal (monthly for paleoclimate and daily for current and future projections) resolution. An additional selection criterion was the size of the model (< 2 GB per data file) due to computational constraints and limitations during the model building phase. The models were further selected to best approximate the climate during past, present and future scenarios. Historical and future climate models were part of intercomparison projects which evaluate models against both observational data and other climate models (Braconnot et al., 2012). Climate models from intercomparison projects are generally in agreement and correctly assimilate large-scale climate features in both space and time (Braconnot et al., 2012; Flato et al., 2013; Schmidt et al., 2012). The specific future climate simulation (CCSM4) was selected as it has a flexible design that can be used across various hardware and software platforms, it has a higher resolution than previous CCSM models and it encompasses various ecological and earth system processes into the simulations. The following section describes the methodological basis for the development of a spatial – temporal dynamic interrogation tool using robust models that have been evaluated through various intercomparison projects. The principle contribution of this study is the interrogation tool which can be utilized using any climate model or ensemble in the expert analyses of climate variability and species responses.

Data analyses and model building

All data analyses were run in the R programming environment (R Core Team 2015) using the R Studio (version 3.2.3) interface. Average daily maximum temperatures (T_{max}) were averaged over 10-year periods for the austral summer seasons (ONDJFM) only for the historical data set (last millennium, 1050 – 1850 CE). For both modern (1850 – 2013 CE) and future (2076 – 2100 CE) climate simulations the T_{max} were averaged at a yearly resolution and decadal resolution for the austral summer seasons only (e.g. online resource 1: https://drive.google.com/file/d/1ZU3rHusJj9KKUyw9UsnXR4J6U3ghBuf_/view?usp=sharing). Absolute maximum temperatures during each summer period were mapped over the same area as the average maximum temperatures for historic, modern and future data sets. These average and absolute maximum temperatures were mapped respectively across southern Africa's arid to semi-arid areas (South Africa, Botswana, Namibia, Zimbabwe, southern parts of Angola and Zambia) and maps were sequenced into chronological time frames. In order to visualize the changes in average and absolute maximum summer temperatures over the last millennium (decadal), modern years and likely future conditions, a climate movie was constructed using Windows Movie Maker (Version 2012, Build 16.4.3528.0331) (Appendix A). Using the constructed climate movies time series analyses were run for coordinates within areas characterised by either extreme or moderately variable temperatures.

The interrogation tool was designed to be versatile and applied to any climate model and over any geographical area (provided the spatial resolution is defined in the R script) (Fig. 4). The R script codes for various temperature thresholds at which biological information on critical temperature threshold where animals experience various degrees of heat stress can be incorporated into the visual interrogation tool. The exposure to different temperature thresholds can be interrogated by defining the temperature threshold and respective timescale (acute or chronic) in the R script. For example, the number of consecutive days exceeding a threshold temperature can be modelled across any location specified in the R script. Climate movies of the exposure to both acute and chronic heat stress risk by specific species can therefore be constructed to visualize the biological consequences of changing climates in the past, present and likely future.

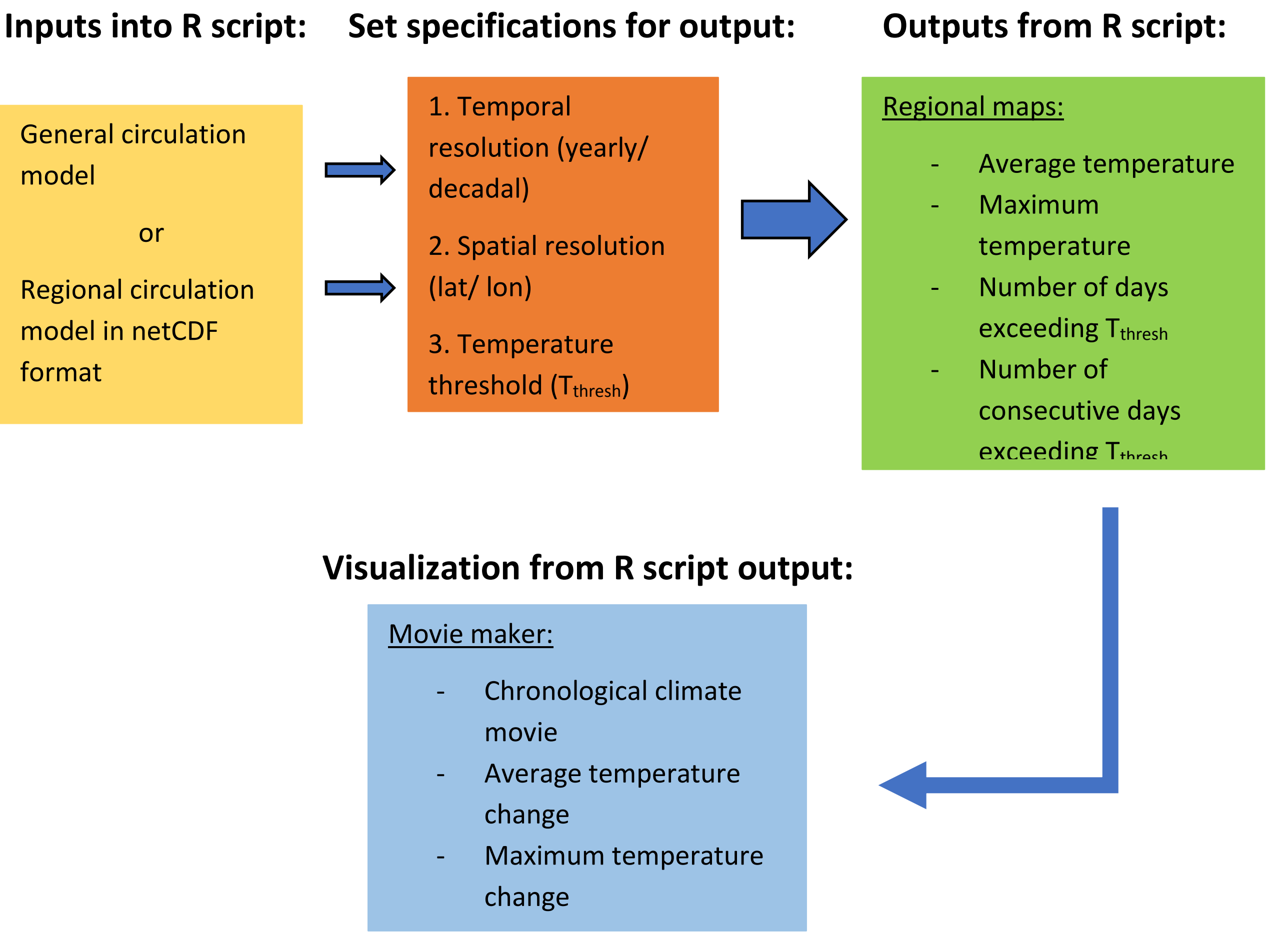


Figure 4. A conceptual framework of the dynamic spatial - temporal interrogation tool. The tool allows for various climate models to be interrogated through specific analyses in both space and time. The output products can be imported into a movie maker for visualization or further analyses.

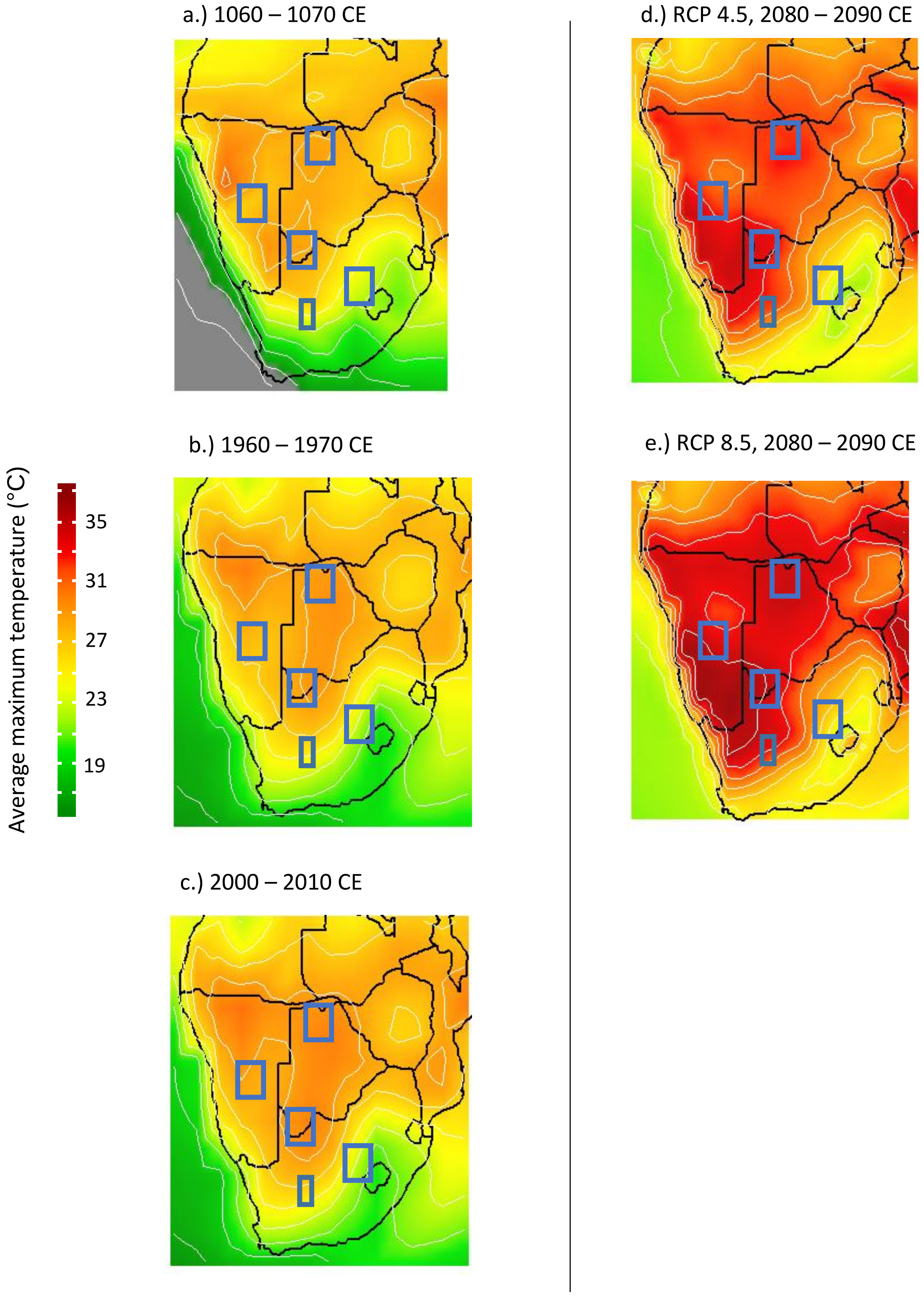
Results

Temperature variability

Both the modern and future climate simulations are characterised by yearly variability in T_{max} whereas historical climate simulations (gap in the original dataset between 1450 – 1500 CE) are represented as decadal variability in T_{max}. The temporal discrepancy accounts for lower variability in the historical dataset relative to the modern and future years (Fig. 5). The modern data reveals 0.11 – 0.97 °C change in T_{max} across all five sites across southern Africa (Table 1) from 2000 – 2010 relative to 1960 – 1970, with central Namibia having the highest increase in T_{max} and the Highveld grasslands, South Africa having the smallest. Under the RCP 8.5 future climate change projections there is a 3.1 – 5.3 °C increase in T_{max} for 2080 – 2090 relative to 1960 – 1970, consistent with the 3 – 5 °C increases predicted by Engelbrecht et al. (2011). Following the same warming trends revealed in the modern climate data the highest projected increase in T_{max} is in the southern Kalahari Desert region with the smallest increase occurring over the Highveld grasslands of South Africa (Fig. 6). The last millennium (1050 – 1850 CE) climate simulations reflected lower levels of decadal variability relative to modern (1850 – 2013 CE) and future (2076 – 2100 CE) climate simulations (Fig. 5). Climatic conditions of both modern and future simulations represent conditions not experienced within the past 1000 years across southern Africa (Fig. 5 and 6).

Table 1. Coordinates of the five time series locations extracted from the visual interrogation tool for climate models.

Location	Timeframe	Latitude (degrees south)	Longitude (degrees east)
Northern Botswana	Past	-18.0 to -19.9	22.5 to 26.3
Northern Botswana	Present	-18.1 to -19.9	22.5 to 24.4
Northern Botswana	Future	-18.4 to -20.3	22.5 to 25.0
Central Namibia	Past	-21.8 to -23.7	15.0 to 18.8
Central Namibia	Present	-21.9 to -23.8	16.9 to 18.8
Central Namibia	Future	-21.2 to -23.1	16.3 to 18.8
Highveld grasslands	Past	-27.5 to -29.4	26.3 to 30.0
Highveld grasslands	Present	-27.6 to -29.5	26.3 to 28.1
Highveld grasslands	Future	-27.8 to -28.7	26.3 to 28.8
Southern Kalahari	Past	-25.6 to -27.5	18.8 to 22.5
Southern Kalahari	Present	-25.7 to -27.6	20.6 to 22.5
Southern Kalahari	Future	-25.9 to -27.8	20.0 to 22.5
Nama Karoo	Past	-29.4 to -31.3	20.6 to 24.4
Nama Karoo	Present	-29.5 to -31.4	21.6 to 23.5
Nama Karoo	Future	-30.6 to -31.6	21.3 to 23.8



a.) 1060 – 1070 CE

b.) 1960 – 1970 CE

c.) 2000 – 2010 CE

d.) RCP 4.5, 2080 – 2090 CE

e.) RCP 8.5, 2080 – 2090 CE

Figure 5. Average daily maximum temperature (°C) across southern Africa under past (a: 1060 – 1070 CE), present (b: 1960 – 1970 CE and c: 2000 – 2010 CE) and two future climate change scenarios (d: RCP 4.5, 2080 – 2090 CE and e: RCP 8.5, 2080 – 2090 CE). Blue squares represent regions of averaged time series extractions.

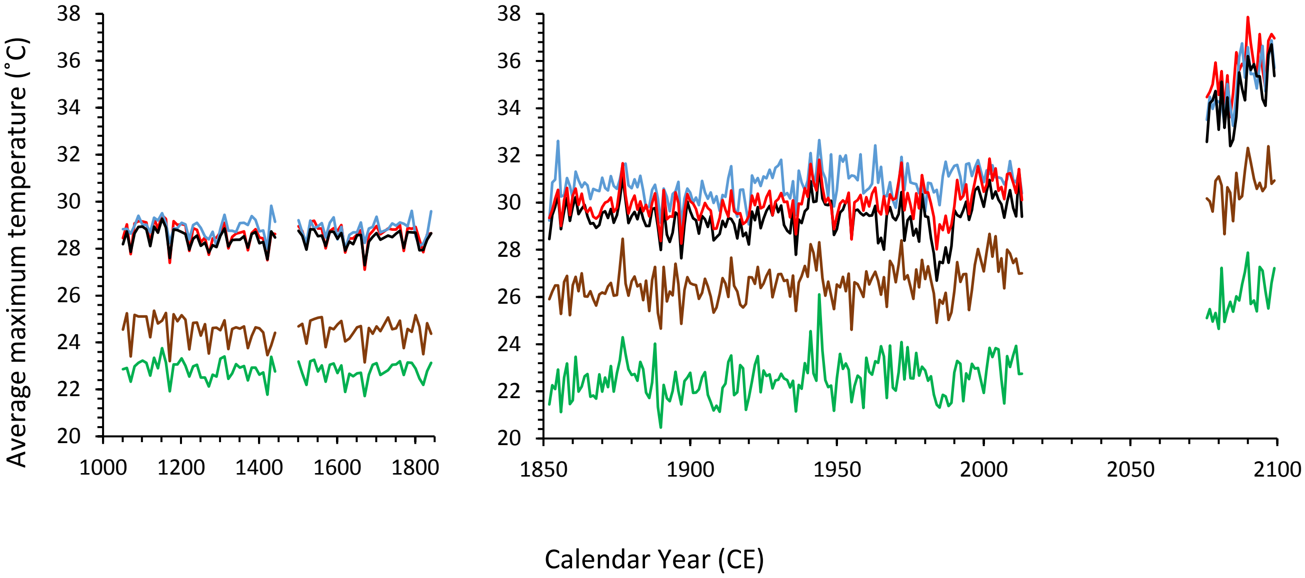


Figure 6. Yearly averages of modelled daily maximum temperature averaged over northern Botswana (blue), central Namibia (black), Highveld grasslands (green), southern Kalahari (red) and Nama Karoo (brown) for the last millennium (1050 – 1850 CE), modern (1850 - 2013 CE) and a future (2076 - 2100 CE) RCP 8.5 climate change scenario.

Discussion

Temperature variability

The data reveal large-scale temperature variability over a historical 1000 – year period and recent years with even more dramatic changes under two future climate change scenarios (RCP 4.5 and RCP 8.5). Both the modern and future climate simulations are characterised by yearly variability in daily maximum temperatures whereas historical climate simulations represent decadal variability in daily maximum temperatures. The temporal discrepancy accounts for lower variability in the historical dataset relative to the modern and future years (Fig. 6). Consistent with literature on southern Africa’s climate my data show that warming has already occurred across southern Africa (Engelbrecht et al., 2015; Kruger & Sekele, 2013; Kruger & Shongwe, 2004; van Wilgen et al., 2016). The rate at which this warming is occurring differs across the region. The modern climate models show the greatest rate of warming over central Namibia, however future climate models suggest that the greatest rate of warming will occur over the southern Kalahari Desert region. The rapid rate of warming predicted to occur over the southern Kalahari Desert region (approximately 0.5 ˚C per decade) is consistent with the projections of Moise & Hudson (2008). Under low mitigation strategies (RCP 8.5) this area is projected to be 5.3 °C warmer by the end of the century relative to average temperatures during 1960 – 1970. Warming is projected to be slower in the Highveld grassland ecoregion of South Africa, where modern average temperatures are 0.3 °C lower than the last millennium and predicted to only increase by 3.1 °C by the end of the century under low mitigation strategies. These dramatic changes in climate relative to historical climate variability will likely impact future ecological processes (Bellard et al., 2012). The non-linear nature of climate warming across southern Africa may be beneficial to ecological processes responding to climate change. For instance, species may respond by shifting from rapidly warming habitats to habitats characterised by more moderate rates of climate warming (Parmesan, 2006).

A hotter climate regime by the end of the century will have severe implications for biodiversity, conservation, and socio-economics. The projected climate changes in both RCP scenarios examined are anticipated to be major drivers in local extinctions (Beaumont et al., 2011; Hughes, 2000). In response to changes in climate, organisms can theoretically adjust their physiology, behaviour, morphology and/or geographic distribution, although their capacity for such adjustments may be constrained by biotic and/or abiotic factors (Hughes 2000; Pearson & Dawson, 2003; Parmesan, 2006). One potential constraint is the rate and extent of temperature variability occurring in extreme environments (McKechnie & Wolf, 2010). Analyses of long-term climate data reveal that species are already responding to changes in temperature through their physiology (Hughes, 2000; Parmesan, 2006), distribution (Pearson & Dawson, 2003), phenology (Parmesan, 2006; Socolar et al., 2017) and behaviour (Cunningham et al., 2013; du Plessis et al., 2012). The levels of warming to which these species responses have occurred is only a fifth or less than the predicted warming for the end of the century (Hughes, 2000).

Conclusion

Using a visual interrogation tool to analyse past, present and future climate models allow for easier identification of areas prone to extreme versus subtle temperature variability. Climate change can thus be viewed in both spatial and temporal dimensions. For example, time series data can be extracted from areas that are shown to experience extreme temperature variability under past, present and future climates and the rate at which this is happening can be analysed. This in turn can feedback into ecological and/ or economic response modelling to climate change. For instance, temperatures in excess of physiologically tolerable limits can be mapped to show the exposure of heat stress risk in a model animal. Southern Africa is vulnerable to extreme temperature conditions in the present and likely future. More work needs to done on the biological and socio-economic consequences of rapid warming to better inform policy – and decision makers in all relevant sectors.

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Chapter III: Acute and chronic heat stress risk in Kalahari Desert birds under past, present and future climates.

Introduction

Interactions between organisms and their physical environments give rise to selection pressures shaping their distribution, physiology and morphology over time. In particular, temperature affects biological processes at levels of organization from cells to ecosystems (Dell, Pawar, & Savage, 2013). Predictions for average air temperature (T_a) change over sub-Saharan Africa describe the western part of the continent as experiencing 5 – 6 ˚C warming by 2070 – 2100 (Engelbrecht et al. 2011), with the southern Kalahari Desert region currently experiencing the fastest rate of warming which is predicted to continue in the future (Moise & Hudson, 2008). Together with increased average T_a, the frequency and intensity of heat waves are predicted to increase (Engelbrecht et al., 2015). Providing better evidence of large-scale temperature changes over time in combination with species responses will greatly enhance our predictive capacities for heat stress risk and the associated conservation actions and management planning needed (Pacifici et al., 2015; Willis et al., 2010).

The direct effects of high T_a on birds can be thought of as representing a continuum of time scales ranging from 1.) acute heat stress effects over minutes to hours (Albright et al., 2017), 2.) chronic, sublethal heat stress effects over days to weeks (Cunningham, Martin, & Hockey, 2015; du Plessis et al., 2012) to 3.) changes in morphology (e.g. decreasing body size), phenology and / or distribution over time scales of years to decades (Porter, 2000; Gardner et al., 2016). Birds are particularly vulnerable to warming because of their predominantly diurnal lifestyle, small size, and high mass-specific energy and water balance requirements (McKechnie & Wolf, 2010; Tieleman & Williams, 1999).

Acute heat stress

When T_a approaches or exceeds T_b the primary avenue of heat dissipation for birds is evaporative heat loss (Dawson & Whittow, 2000). When $T_a > T_b$, evaporative water loss (EWL) in small birds can exceed 5 % of their body mass per hour, even when in fully sheltered microsites and inactive (McKechnie & Wolf, 2010; Wolf & Walsberg, 1996). This produces a fundamental trade-off between two closely related threats, hyperthermia and dehydration, during extremely hot weather (Albright et al., 2017; Whitfield et al., 2015). Modelling the threat of lethal hyperthermia uses data on heat tolerance limits (the highest air temperature at which a bird can defend sublethal body temperature). Recently, measurements of heat tolerance limits have become available for several avian species showing that, under current conditions, maximum air temperatures in southern Africa rarely approach and seldom exceed these limits (McKechnie, Smit, et al., 2016; McKechnie, Whitfield, et al., 2016; McKechnie, Hockey, & Wolf, 2012; McKechnie & Wolf, 2010; O'Connor et al., 2017; Whitfield et al., 2015). However in other parts of the world these thresholds are being exceeded at an alarming rate. For instance, Death Valley, California has recently experienced the warmest month (July 2018) on record, with four consecutive days of approximately 53 °C (O'Connor, 2018), an air temperature exceeding the heat tolerance limits of most Northern Hemisphere passerines investigated to date (Smith et al., 2017).

Under extremely hot conditions where birds avoid lethal hyperthermia via evaporative cooling the risk of death can be modelled by predicting the time taken to deplete body water and become lethally dehydrated (Albright et al., 2017; McKechnie & Wolf, 2010). Albright et al. (2017) examined the effects of heat waves on EWL and survival for desert passerines of the southwestern United States. These authors found that increasing T_a and frequency of heat waves have potentially devastating impacts on the survival of small desert passerines, and important consequences for their water balance, daily activity and geographic distribution. For instance, Lesser Goldfinches (9.7 g) will experience a significant risk of lethal dehydration increasing from an average of 13 days per year currently to 44 days per year by the end of the century (Albright et al., 2017). In the Sonoran Desert, these birds are predicted to experience high risk of lethal dehydration for essentially the entire summer season, and parts of spring and autumn. These authors additionally reported that increases in T_a pose a particularly severe threat to species whose ranges are confined entirely to desert habitats. Similarly in an earlier study, McKechnie and Wolf (2010) found the risk of avian mortality to increases for desert birds during extreme heat waves due to increased avian thermoregulatory water requirements under these conditions.

Chronic heat stress

Small changes in average T_a have the potential to incur sublethal fitness costs to birds occurring in arid environments. These sublethal fitness costs, although less dramatic than mortality events because of lethal dehydration or hyperthermia, have the potential to result in an overall decrease in the long-term survival of a species (du Plessis et al., 2012; Ridley & Raihani, 2007). For example, du Plessis et al. (2012) demonstrated that foraging efficiency (but not effort) decreased with increasing T_a in a habituated population of Southern Pied Babblers (*Turdoides bicolor*) occurring in the southern Kalahari Desert in South Africa. These authors found that daily maximum temperatures exceeding 35.5 °C resulted in babblers not gaining enough body mass during the day to counteract overnight mass loss [approximately 4% of body mass (M_b)]. At temperatures approaching 40 °C these birds were losing mass during the day as a consequence of compromised foraging efficiency. These environmental conditions do not directly result in mortality events, but impose fitness costs as the number of consecutive days with T_a above the threshold increase (Cunningham, Kruger, et al., 2013). Additional thermoregulatory trade-offs at high T_a’s include nestling provisioning effort (Cunningham, Martin, et al., 2013) and incubation effort (Oswald et al., 2008). These thermoregulatory trade-offs at high T_a values have been reported for Southern Yellow-billed Hornbills (*Tockus leucomelas*) and Common Fiscals (*Lanius collaris*), and impose various sublethal fitness costs including reduced breeding success, decreased nestling provisioning rates and offspring development (Cunningham, Kruger, et al., 2013).

Under hot conditions where birds trade-off thermoregulation with foraging, breeding or nestling provisioning, the risk of sublethal fitness costs can be modelled as the number of consecutive days required to decrease body condition (du Plessis et al., 2012) and compromise breeding success (Ridley & Raihani, 2007). Models of chronic heat stress risk are complicated by various temperature thresholds (T_{thres}) which may exist within a single species affecting various fitness variables (Cunningham, Kruger, et al., 2013; Cunningham, Martin, et al., 2013). For instance, Common Fiscals have multiple temperature thresholds (T_{thres}) where 1.) fledging body mass is compromised (T_{thresh} = 33 °C), 2.) tarsus length is significantly reduced (T_{thresh} = 37 °C) and 3.) fledgling is delayed (T_{thresh} = 35 °C). To address this Cunningham, Kruger, et al., (2013) suggested that either the lowest defined T_{thresh} value for the species, the T_{thresh} with the greatest slope of decline in fitness once exceeded or the T_{thresh} affecting a life-history stage known to adversely influence population dynamics in the species should be used.

Comparisons between acute and chronic heat stress risk, have not, to the best of my knowledge, been investigated for species occurring in arid environments. Here I investigated both the risk of acute and chronic heat stress for Kalahari Desert birds under past, present and likely future climates. I aimed to use this information to understand the importance of acute versus chronic heat stress risk for arid-zone birds currently and in the likely future.

Research questions

I aimed to map acute and chronic heat stress risk in southern African arid-zone birds under past, present and future climates, and evaluate their relative importance in determining species' persistence in arid habitats in coming decades. Specifically, I aimed to answer the following questions:

a. What are the environmental conditions associated with acute and chronic heat stress risk and in which areas do they occur in the past, present and likely future?
b. How will future climate change scenarios and the associated risk of acute and chronic heat stress determine future species distributions?

Methods

Study area

Data on thermal physiology and behaviour are available for several species inhabiting the Kalahari Desert of southern Africa. The area is dominated by arid savanna vegetation, dry riverbeds and dune landscapes (Whitfield et al., 2015). The region is characterised by cool, dry winters and hot summers and receives a mean annual rainfall of 215.5 ± 13.0 mm, with average daily summer maximum air temperatures of 34.7 ± 0.05 °C (data from October to March, 1960–2015, Twee Rivieren, South African Weather Service) (van de Ven et al., 2016). The southern Kalahari Desert region is a particularly vulnerable area experiencing rapid rates of warming. For example, the rate of warming over the Kgalagadi Transfrontier Park is approximately 0.039 °C year^{-1} ± 0.007SE, where annual average maximum temperatures have increased by 1.95 °C since 1960 (Moise & Hudson, 2008; van Wilgen et al., 2016).

Thermal physiology data – acute heat stress

Rates of evaporative water loss for eleven Kalahari bird species were obtained from published literature (Table 3). In brief, these measurements were obtained during the day following the protocol described by Whitfield et al. (2015), who exposed birds to increases in T_a using a stepped profile with 5 °C increments at T_a values between 25 and 40 °C, and 2 °C increments at T_a between 40 and 54 - 58 °C. Birds spent a minimum of 10 minutes at each T_a, averaging approximately 30 minutes. Measurements were terminated when a bird: 1.) was obviously stressed (agitated jumping, pecking, wing flapping or any other escape behaviour) or 2.) showed signs of distress such as loss of balance, coordination or dramatic decrease in EWL and/ or uncontrolled increase in T_b to > 45 °C. In the latter scenario, an individual bird was considered to have reached its thermal endpoint (the T_a

associated with the onset of these heat stress signs) (Whitfield et al., 2015). All subsequent papers published in the "Avian thermoregulation in the heat" series followed the same protocol established by Whitfield et al., (2015) and are this comparable among studies.

Body mass data – chronic heat stress

Data for various sublethal fitness cost variables in three arid-zone bird species occurring in southern Africa were obtained from published literature (Table 2). Behavioural variables were analysed in independent studies in relation to maximum air temperature (T_{max}). The variables listed under the "Foraging" column have been suggested to be the mechanisms driving the subsequent changes in both body condition and breeding success (Table 2) (du Plessis et al., 2012; Ridley & Raihani, 2007).

Table 2. The sublethal fitness costs measured in various studies in the southern Kalahari Desert for three arid-zone bird assemblages. Variables driving the changes in breeding success and body condition are indicated in grey.

	Sublethal fitness costs		
	Foraging	**Body condition**	**Breeding success**
Southern pied babbler (*Turdoides bicolor*)	Foraging efficiency (mass of food gained per unit time) Thermoregulatory behaviour (panting, wing-drooping) (du Plessis et al., 2012)	Overnight mass loss versus diurnal mass gain (du Plessis et al., 2012)	
Southern yellow-billed hornbill (*Tockus leucomelas*)	Foraging efficiency (mass of food gained per unit time) Thermoregulatory behaviour (panting, wing-drooping) (van de Ven, 2017)	Male and female mass gain/ loss as function of air temperature (van de Ven, 2017)	Nest provisioning (van de Ven, 2017) Probability of nestling success (van de Ven, 2017)
Common fiscal (*Lanius collaris*)	Foraging success (successful prey capture per minute spent hunting from each perch) (Cunningham, Martin, & Hockey, 2015)		Nestling body-mass gain Size of fledgling Age of fledgling (Cunningham, Martin, et al., 2013)

Data analyses

Acute dehydration risk: survival time

My methods were adapted from those of Albright et al. (2017), using survival time as an indicator of the probability of death and/or the severity of a high-temperature event. Survival time for each species was estimated as the number of hours where cumulative water loss via evaporation remained less than 15% of M_b. This approach assumes that during the hottest time of day birds are resting in deep shade suggesting that 1.) the operative temperature experienced by the bird is equivalent to air temperature and 2.) birds are losing water but not gaining water during this period of inactivity. Mass-specific EWL values and linear regression models were converted to grams per hour values ($g \cdot h^{-1}$). Consistent with the methods used by Albright et al. (2017), I used an ecologically important survival time of ≤ 5 hours of exposure resulting in a moderate risk of lethal dehydration (this is an input variable that can be manipulated in the R code described in Chapter 2, but the forthcoming analysis is based on the ≤ 5 hours of exposure threshold). Survival times under current conditions were estimated using an average diurnal temperature profile calculated from the ten hottest days during the last decade (2000 – 2010 CE), averaged over three regions across southern Africa (southern Kalahari Desert, Central Namibia and Northern Botswana regions), and future survival times from the same curve shifted upwards to account for predicted increases in T_{max} (Appendix B).

Chronic heat stress risk

Temperature threshold limits (T_{thres}) and associated temporal requirements required to induce various sublethal fitness costs were calculated using existing data on three arid-zone bird species (Southern Pied Babbler, Southern Yellow-billed Hornbill and Common Fiscal) (Table 2). Temperature thresholds were defined as the T_{max} above which species experience measurable sublethal fitness costs (Cunningham, Kruger, et al., 2013). Body condition is a key factor influencing breeding potential and has been reported to decreases with increasing T_{max} in some bird species (Table 2). Body condition was used as an indicator for the probability of missed breeding opportunities which extends into fitness costs (Bolger, Patten, & Bostock, 2005; du Plessis et al., 2012; Ridley & Raihani, 2007). I used loss of 15% M_b as an indicator of poor body condition (Levey et al., 1999) and consequently compromised breeding success. To model the risk of chronic heat stress due to compromised body condition the number of consecutive days where $T_{max} > T_{thres}$ were calculated in the R programming environment (R Core Team 2015) using the R Studio (version 3.2.3) interface.

Data analyses and model building

All data analyses were run in the R programming environment (R Core Team 2015) using the R Studio (version 3.2.3) interface. Climate models that best simulate current conditions are increasingly found to be the models projecting the greatest rate of warming for 2100 (Brient & Schneider, 2016; Brown & Caldiera, 2017; Zhai, Jiang, & Su, 2015). Brown & Caldiera (2017) found that observationally informed projections indicate that future warming under unmitigated climate change is likely to be 15% warmer than current model predictions. These authors additionally suggest that climate models representing moderate warming (RCP 4.5) are more likely to represent conditions associated with a moderate-to-high warming scenario (RCP 6.0). The 2015 Paris agreement target to limit global average temperature increases to 2 °C (Millar et al., 2017; UNFCCC,

2015) is becoming increasingly unlikely with approximately 5 % chance of being met by the end of the century (Raftery et al., 2017; Rogelj et al., 2016). Currently several countries are failing to meet their pledges to reduce greenhouse gas-emissions (Climate Action Tracker available at: https://climateactiontracker.org/). Given the evidence of current and likely future warming I used an unmitigated, business-as-usual climate change scenario (RCP 8.5) for end of the century warming projections as the most likely scenario. The calculated survival times, sublethal fitness cost temperature thresholds and bird distribution data (BirdLife International and NatureServe 2013) were incorporated as temperature thresholds into the visual interrogation tool according to the methods described in Chapter 2 for each species respectively (e.g. online repository 2, acute: https://drive.google.com/file/d/1YEJjzOf2M-ozOyAjl1Ak7QEF6_K4AN1z/view?usp=sharing; online repository 3, chronic: https://drive.google.com/file/d/1YTOQHHuzdoXlSxxMdrB5Y8yK6J9LzV26/view?usp=sharing). Species distribution data were cross referenced against the Southern African Bird Atlas Project data and adjusted accordingly (available at: http://sabap2.adu.org.za/; Harrison, Underhill & Barnard, 2008).

Results

Acute heat stress risk: the relationship between air temperature and evaporative water loss

Of the eleven arid-zone species, passerines are predicted to experience moderate risk of lethal dehydration at lower daily maximum T_a than non-passerines occurring in similar geographic areas (Table 3).

Table 3. Acute heat stress risk values for desert birds calculated according to the survival time methods described by Albright et al. (2017). Daily maximum air temperatures associated with a moderate risk of lethal dehydration was calculated according to temperature profiles of the hottest days between 2000 and 2010. Passerine birds are indicated as grey shaded rows and non-passerines as unshaded rows. *Mass-specific EWL linear regression models. Lilac-breasted rollers had two significant inflection points in the EWL versus air temperature relationship (25 °C < T_a < 44.7 °C and *** T_a > 44.7 °C).**

Species	Body mass (g)	EWL linear regression	Moderate T_{max} (˚C)	References
Scaly-feathered finch (*Sporopipes squamifrons*)	10	*EWL = $4.52T_a$ - 172	44	Whitfield et al., 2015
Sociable weaver (*Philetairus socius*)	25	*EWL = $5.05T_a$ – 200	45	Whitfield et al., 2015
White-browed sparrow-weaver (*Plocepasser mahali*)	40	*EWL = $4.02T_a$ - 151	44.5	Whitfield et al., 2015
Burchell's starling (*Lamprotornis australis*)	109	EWL = $0.231T_a$ – 7.110	43	Smit *et al.*, 2018
Namaqua dove (*Oena capensis*)	40	EWL = $0.096T_a$ – 3.629	48.5	McKechnie, Whitfield, et al., 2016
Laughing dove (*Spilopelia senegalensis*)	100	EWL = $0.181T_a$ – 6.797	52	McKechnie, Whitfield, et al., 2016
Cape turtle dove (*Streptopelia capicola*)	153	EWL = $0.235T_a$ – 8.544	52	McKechnie, Whitfield, et al., 2016
Burchell's sandgrouse (*Pterocles burchelli*)	193	EWL = $0.445T_a$ – 17.76	51	McKechnie, Smit, et al., 2016
Rufous-cheeked nightjar (*Caprimulghus rufigena*)	53	EWL = $0.12T_a$ – 4.600	50	O'Connor et al., 2017
African cuckoo (*Cuculus gularis*)	110	EWL = $0.238T_a$ – 8.930	50	Smit et al., 2018
Lilac-breasted roller (*Coracias caudatus*)	95	EWL = $0.039T_a$ – 0.414 ** EWL = $0.337T_a$ – 13.739 ***	48.5	Smit et al., 2018

Acute heat stress risk: spatiotemporal dynamics

Past climatic conditions across southern Africa were less variable than those of both current and future climate simulations. The environmental conditions experienced by the eleven arid-zone species during the last millennium (1050 – 1850 CE) were not likely to induce lethal dehydration. The spatial pattern revealed for lethal dehydration risk among the modelled species is variable, such that some species have increasingly been exposed to a moderate risk of lethal dehydration in recent decades across southern Africa (Table 3). Several of the modelled bird species never experience survival times of less than five hours and are not likely to experience these conditions before the end of the century. All modelled passerine species occasionally experience conditions associated with moderate risk of lethal dehydration for 10 or less days per year ($d \cdot y^{-1}$) during recent years (2000 – 2010 CE) (Fig. 7 and Table 4). These conditions are expected to continue over much larger geographic areas and more frequently under a high risk future climate change scenario (RCP 8.5, 2080 – 2090 CE).

Table 4. Maximum temperatures for three locations across southern Africa under past (1060 – 1070 CE), present (2000 – 2010 CE) and a high risk future climate scenario (RCP 8.5, 2080 – 2090 CE)

	T_{max} (°C)		
Location	**1060 – 1070**	**2000 – 2010**	**2080 – 2090**
Central Namibia	35.0	40.9	45.5
Northern Botswana	36.1	45.6	46.2
Southern Kalahari Desert region	35.4	40.9	45.6

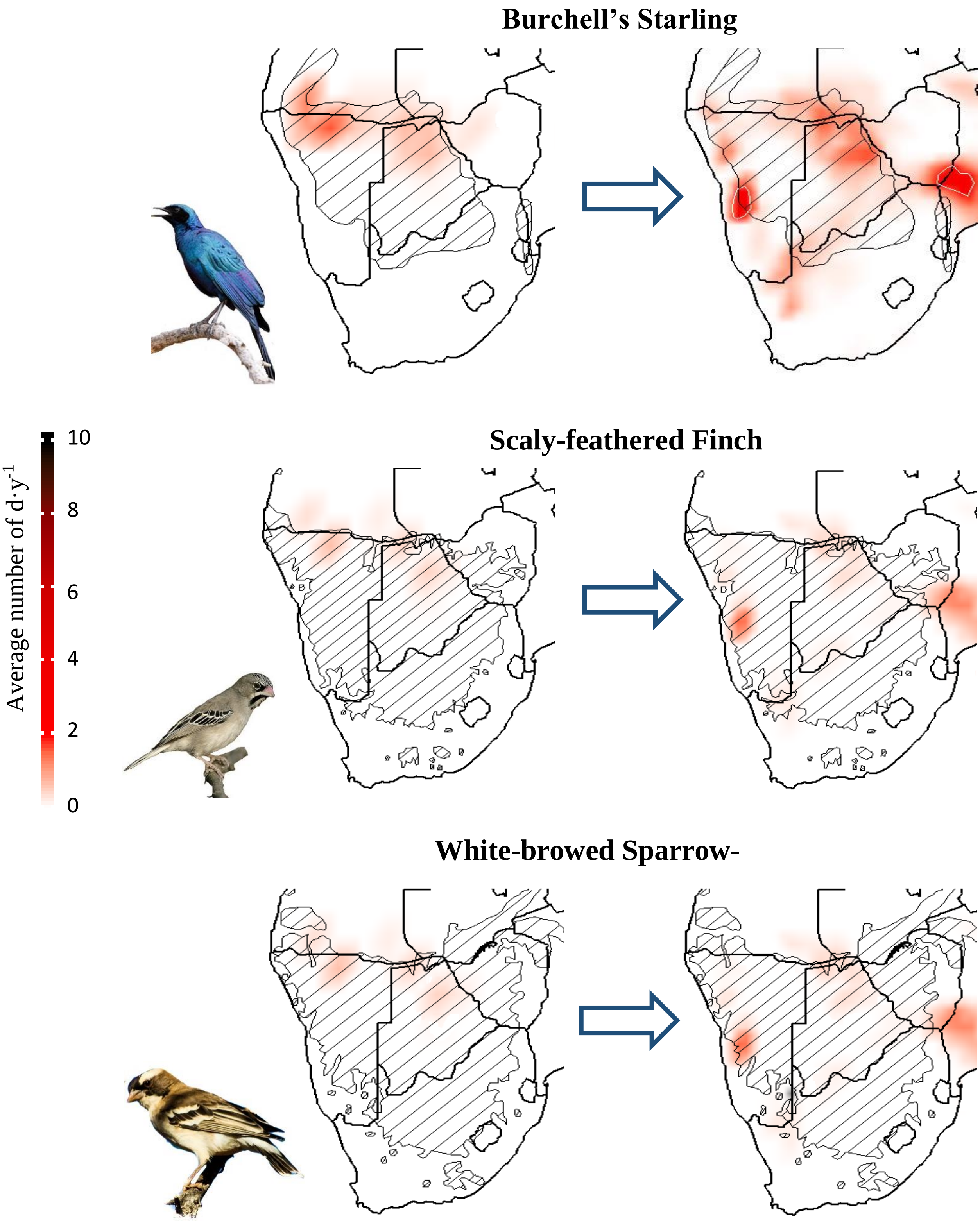

Figure 7. Average number of days per year with moderate dehydration risk (i.e., survival time of < 5 hours) across southern Africa for three arid-zone bird species (Burchell's Starling, Scaly-feathered Finch and White-browed Sparrow-weaver) under current (2000 – 2010) and a high risk future scenario (RCP 8.5; 2080 – 2090). Species ranges indicated with cross-hatching.

Chronic heat stress risk: sublethal fitness costs

Southern Pied Babblers and Southern Yellow-billed Hornbills are increasingly exposed to environmental conditions where foraging efficiency is not sufficient to counteract their overnight mass loss (Table 2). The number of consecutive days per year where $T_a \geq 35.5$ °C during austral summer in the southern Kalahari Desert region was 3.5 days between 2000 and 2010 (Fig. 8 and 9). These conditions are likely to increase to approximately 29 days per year by 2080 – 2090 under a high risk climate change scenario (RCP 8.5, Fig. 7 and 8), resulting in poor body condition for a large proportion of the breeding season. The number of consecutive days where $T_a \geq 38.5$ °C (conditions of no diurnal mass gain in non-breeding Pied Babblers with a net overnight mass loss of 4% M_b) during austral summer in the southern Kalahari Desert region was approximately zero days per year between 2000 and 2010 (Fig. 8 and 9). These conditions are likely to increase to approximately 20 consecutive days per year by 2080 – 2090 under a high risk climate change scenario (RCP 8.5, Fig. 8 and 9), resulting in severe, and likely lethal, body mass loss over a large proportion of the summer. For Common Fiscals the lowest T_{thresh} exposing fledglings to the risk of chronic heat stress risk is at 33 °C ($T_{thresh1}$) above which fledgling body mass is compromised and at temperatures above 35 °C fledging is delayed ($T_{thresh2}$) (Cunningham, Martin, et al., 2013). The number of consecutive days where $T_{max} > T_{thresh1}$ has increased during recent decades with close to 10 consecutive days per breeding season routinely experiencing $T_{max} > T_{thresh1}$ between 2000 and 2010 in the southern Kalahari Desert region (Fig. 8 and 9).

Chronic heat stress risk: spatiotemporal dynamics

Spatially, all three arid-zone species have been exposed to sublethal fitness trade-offs at least occasionally over recent decades (Fig. 8). During the last millennium air temperatures seldom exceeded threshold temperatures for more than a day (Fig. 9). Common Fiscals are the only modelled species to have experienced heat stress ($T_{max} > T_{thresh1}$) for more than one consecutive day (e.g. ± 3 days in Northern Botswana and ± 2 days in Central Namibia) during the under past climatic conditions (1060 – 1070, Fig. 9). Currently there are no areas in which species are experiencing more than 10 consecutive days where $T_{max} > T_{thresh}$, however these conditions are likely to increase by approximately 830% for Southern Pied Babblers and Common Fiscals ($T_{thresh2}$), and 283% for Common Fiscals ($T_{thresh1}$) in the southern Kalahari Desert region, under a high risk climate change scenario (RCP 8.5, 2080 – 2090). Under both a high (RCP 8.5) and moderate (RCP 4.5) climate change scenario conditions of chronic heat stress are likely to persist over the majority of the ranges for Southern Pied Babblers, Southern Yellow-billed Hornbills and Common Fiscals (with the exception of the Drakensberg Mountain Range and along the coastline of South Africa) (Fig. 8 and Appendix C).

The probability of a Southern Yellow-billed Hornbill nestlings success falls below 50% when the average $T_{max} > 35$ °C during the nesting period (van de Ven, 2017), a condition not likely under current climates in the southern Kalahari Desert region (Table 5). Under unmitigated climate change this region is likely to experience $T_{max} > 35$ °C throughout the entire austral summer season by 2080 – 2090 (Table 5).

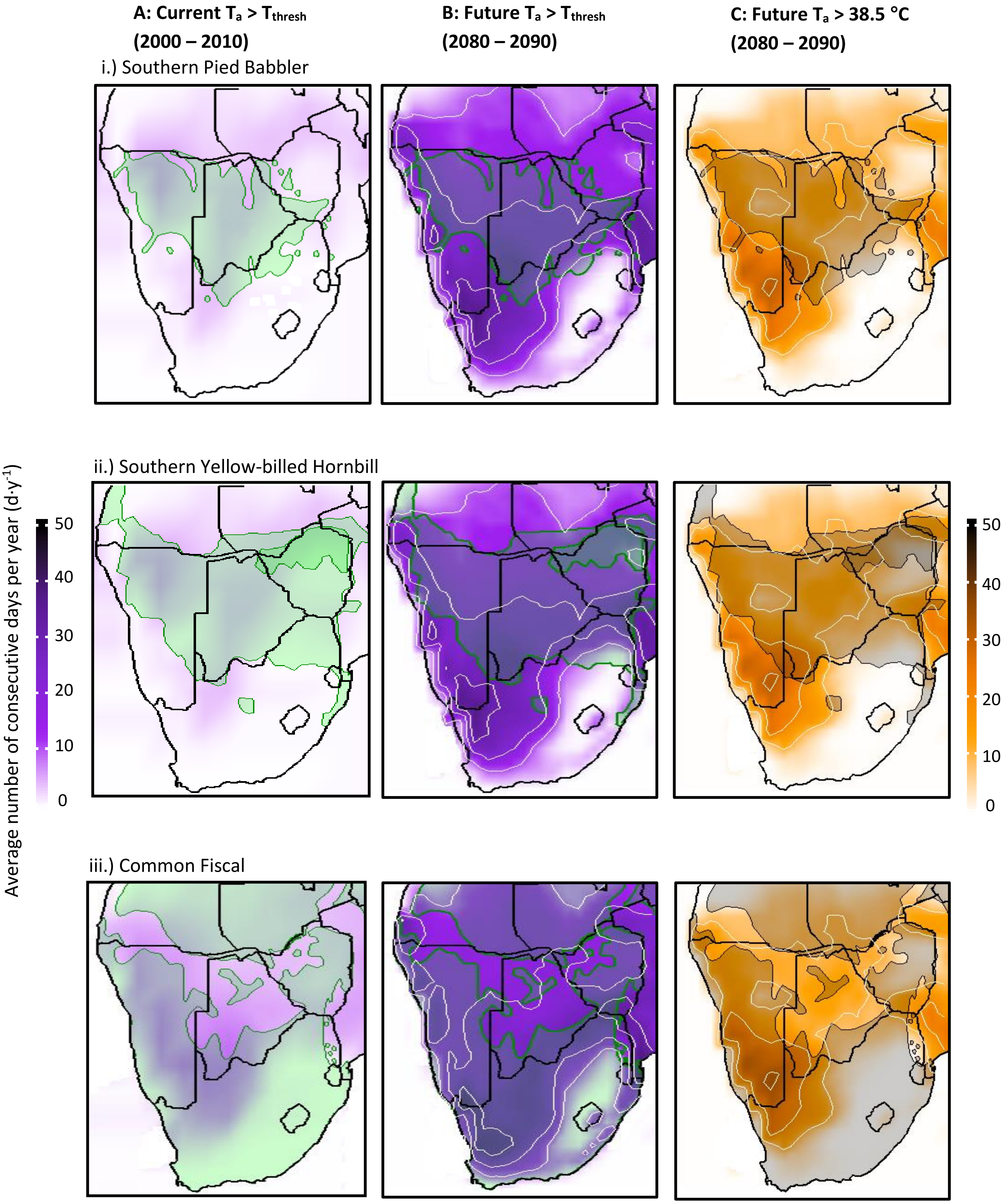

Figure 8. Average number of consecutive days per year where three arid-zone bird species [i: Southern Pied Babbler (T_{thresh} = 35.5 °C), ii: Southern Yellow-billed Hornbill (T_{thresh} = 35 °C) and iii: Common Fiscal T_{thresh} = 33 °C)] are exposed to conditions of chronic heat stress risk under current (A: 2000 - 2010) and a high risk future scenarios (RCP 8.5; B: $T_a > T_{thresh1}$, 2080 – 2090 and C: T_a > 38.5 °C 2080 – 2090). Species ranges indicated in green and grey respectively.

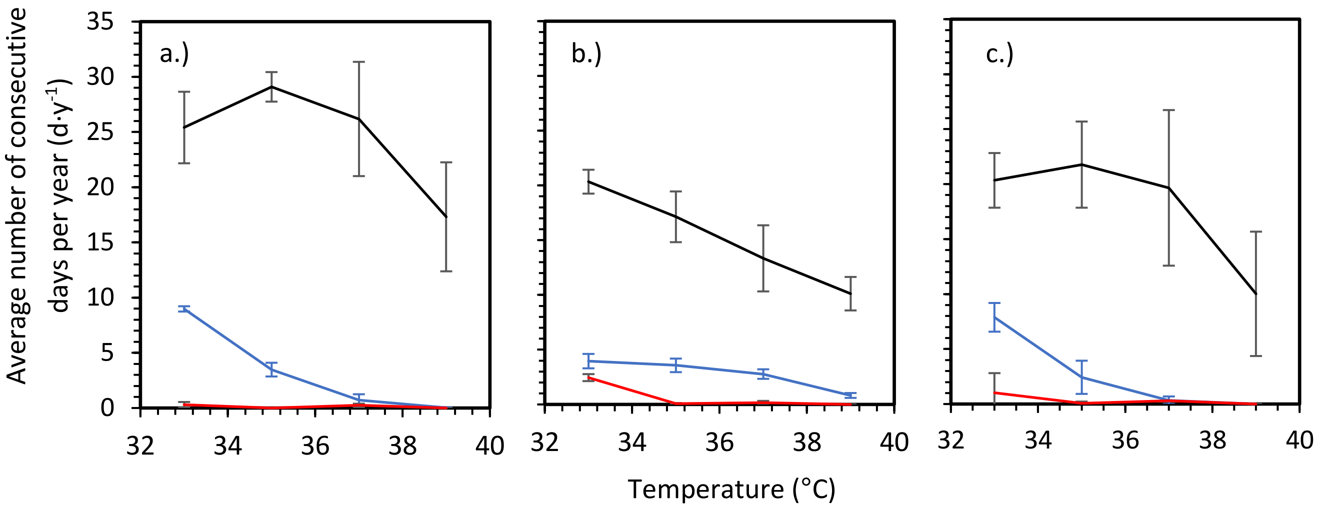

Figure 9. Average (± SD) number of consecutive days per year as a function of maximum air temperature (T_{max}) under past (red, 1060 – 1070 CE), present (blue, 2000 – 2010 CE) and future (black, 2080 – 2090 CE) climate scenarios over three regions (a: Southern Kalahari Desert region; b: Northern Botswana and c: Central Namibia).

Table 5. Average maximum temperatures for three locations across southern Africa under past (1060 – 1070 CE), present (2000 – 2010 CE) and a high risk future climate scenario (RCP 8.5, 2080 – 2090 CE)

		Mean T_{max} (°C)	
Location	**1060 – 1070**	**2000 – 2010**	**2080 – 2090**
Central Namibia	28.6	28.7	34.1
Northern Botswana	28.8	29.6	34.9
Southern Kalahari Desert region	29.0	29.7	35.4

Discussion

Environmental conditions associated with acute and chronic heat stress risk have not, until recently, been routinely experienced by desert birds in southern Africa. During the Medieval Warm Period (before 1000 – 1300 CE) average T_{max} approached current average T_{max} but maximum air temperatures seldom exceeded T_{thresh} for acute and chronic heat stress. In recent decades temperatures have increased above tolerable thresholds for some species resulting in risks of lethal dehydration, and/ or sublethal fitness costs (e.g. compromised foraging efficiency, breeding success and nestling provisioning rates) (Fig. 7 and 8). Towards the end of the century these conditions are expected to increase in severity, frequency and geographic extent under both a moderate and high risk climate change scenario (RCP 4.5 and RCP 8.5).

Acute heat stress risk

The spatial patterns for lethal dehydration risk in arid-zone birds of southern Africa are variable. All species are currently exposed to increasingly high air temperatures which are predicted to further increase under future climate change. However, not all species are likely to experience lethal dehydration as a direct result of high temperatures presently or by the end of the century. All passerines modelled in the present analysis experience some degree of acute heat stress risk under current conditions, with the threat increasing in frequency, severity and geographic area under a high risk climate change scenario (RCP 8.5) by the end of the century. This is most obvious for Burchell's Starling which will experience approximately 6 – 10 $d \cdot y^{-1}$ over a large proportion of their range as well as the surrounding edges of their range [e.g. west coast of Namibia due to earlier and more frequent east winds over short-time scales (Liebenberg-Enslin et al., 2017)]. Similarly Scaly-feathered Finches and White-browed Sparrow weavers will be exposed to an increase in the number of heat stress days within and around their ranges. Given these predictions the likelihood of persistence within and movement out of the modelled species ranges may become constrained by temperature.

Where these environmental conditions are experienced, birds are exposed to severe constraints on water balance, daily activity and potentially geographic distribution. At high T_a values small birds tend to select cool microhabitats and reduce activity. Under these high temperature conditions both foraging effort and water intake (i.e. drinking) decrease and dehydration tolerance limits are approached rapidly. The depletion of body water is exacerbated by decreased activity, foraging and water intake (Albright et al., 2017). A key assumption here is that birds seek out shaded microsites during the hottest part of the day. For species such as the Rufous-cheeked nightjar this is often not the case. When these birds roost in the sun, and hence experience operative temperatures far above air temperature, their time to dehydration shortens rapidly, likely decreasing the T_{thresh} associated with acute risk of lethal dehydration (O'Connor, Brigham, & McKechnie et al., 2018). My models may underestimate of the risk of acute heat stress for active individuals or individuals roosting in the sun. The combined effects of high T_a and species behaviour during the hottest time of day suggest that arid environments such as the Kalahari Desert may experience substantial loses of avifauna species numbers and diversity under unmitigated climate change scenarios.

Although phylogenetic variation in avian thermoregulation still remains largely unclear, among those taxa for which data exist, passerines are generally less efficient at evaporative cooling compared to taxa such as caprimulgids and columbids (McKechnie, Whitfield, et al., 2016; O'Connor et al., 2017; Smit et al., 2018). One mechanism birds use to reduce total EWL is through hyperthermia, whereby body temperature (T_b) increases 2 – 4 °C above normal (Tieleman & Williams, 1999). The maximum T_a at which birds can maintain T_b below lethal limits (heat tolerance limit, HTL) varies considerably across taxa (Whitfield et al., 2015; O'Connor et al., 2017; Smit et al., 2018). In numerous bird species these HTL are being approached and even exceeded. For example, the HTLs of several passerines (Smith et al., 2017) were exceeded in July 2018 when T_a values in Death Valley, California peaked at 52.8 °C for four consecutive days (O'Connor, 2018). This illustrates that birds experience the risk of lethal hyperthermia and/ or dehydration at high T_a values. In southern Africa these limits are rarely being approached currently and are unlikely to be exceeded under future climate change.

The available literature on hyperthermia in free-ranging birds shows that T_b under laboratory conditions and that of free-ranging birds are approximately equivalent, which suggests that models of dehydration risk from laboratory EWL data accurately represents those of free-ranging birds (McKechnie, Whitfield, et al., 2016; Thompson, Cunningham & McKechnie, 2018; Whitfield et al., 2015). My model uses maximum T_a as an indicator of heat stress, however this is a minimum measure of heat stress and a likely underestimate of the thermal exposure to hot arid environments. Birds typically experience air temperatures greater than instrumentally recorded T_a due to radiative and convective heat fluxes. Additionally, birds modelled for acute heat stress were inactive and at rest. The activity of the bird is likely to increase metabolic heat production and place an additional element of heat stress possibly lowering their thermal tolerance thresholds (Smit et al., 2016). At high T_a birds reduce their activity which in turn reduces their foraging and water intake intensifying risks associated with acute heat stress and lethal dehydration (Albright et al., 2017).

Here I present a conservative, baseline model of the risk of lethal dehydration to Kalahari birds. The risk of mass mortality via lethal dehydration for the species modelled here will remain relatively low (< 10 $d \cdot y^{-1}$) compared to desert birds in the southwestern United States (> 50 $d \cdot y^{-1}$, e.g. Albright et al., 2017) under future climate change scenarios. Given the combined effects of high T_a values my model suggests that desert environments may still experience considerable losses of avifauna and diversity under unmitigated climate change scenarios. For instance, threatened species with small populations or long generation times may not be able to recover from mass mortality events due to heat waves (Saunders, Mawson & Dawson, 2011).

Chronic heat stress risk

My models reveal that arid-zone birds are occasionally exposed to the risk of chronic heat stress currently but this risk will dramatically increase in severity and geographic extent under future climate change scenarios across southern Africa. For example, in Common Fiscals the risk of significantly reduced fledgling body mass will increase by approximately 280% and the risk of delayed fledging by approximately 830% by the end of the century (RCP 8.5, 2080 – 2090) relative to present day conditions (2000 – 2010). Successful fledging of chicks has been demonstrated to be negatively affected by mean T_{max} during the nesting phase, such that the probability for Yellow-billed Hornbills falls below 50% when $T_{max} > 35$ °C (van de Ven, 2017). I found that these conditions are likely to occur within certain areas of their range (e.g. southern Kalahari Desert region) where the north and north western regions of their range will approach an average $T_{max} > 35$ °C throughout the austral summer by the end of the century (e.g. Northern Botswana and Central Namibia).

Increased average T_a values influences several fitness related components through lost opportunity costs (Cunningham, Martin & Hockey, 2015). I found that four consecutive days of $T_{max} =$ 38.5 °C resulted in 15% M_b loss for non-breeding Pied Babblers indicating poor body condition (Levey et al., 1999). Offspring development was demonstrated to be directly linked to post-fledgling care by Ridley & Raihani (2007). These authors showed that independent of rainfall adult Southern Pied Babblers that cared for their young for longer periods had offspring with higher body mass and foraging efficiency at 6 months of age and these effects persisted into adulthood. Nestling provisioning rate is linked to adult body condition (Weimerskirch, Prince & Zimmermann, 2000) which in turn relates to foraging efficiency and T_a (Cunningham, Martin, et al., 2013; Ridley & Raihani, 2007). Provided the relationship between T_a and body condition is consistent for both breeding and non-breeding individuals, breeding opportunities are likely to decrease in Southern Pied Babblers as a result of poor body condition at high T_a values. Under current climate (2000 – 2010) these conditions are not likely to occur across the species range, however under future climate change these conditions will frequently be experienced with an averaging of 20 consecutive days per year where $T_{max} > T_{thresh}$ in the southern Kalahari Desert region. Similarly male Yellow-billed Hornbills require less than four consecutive days of $T_{max} = 37.9$ °C to lose 15% M_b. These conditions are not likely to occur currently but are expected to increase in frequency to an average of approximately 23 consecutive $d \cdot y^{-1}$ where $T_{max} > T_{thresh}$ in the southern Kalahari Desert region by 2080 – 2090. The ability for these birds to maintain body mass under future conditions is not likely. For instance, Gardner et al. (2016) found that White-plumed Honeyeaters frequently exposed to $T_{max} >$ 35 °C were in poorer condition, less likely to be recaptured and probably died. Little is known about lethal limits for loss of body mass over time scales of days to weeks but mass loss to this extent is likely to be lethal (Gardner et al., 2016; Wolf, 2000), resulting in drastic consequences for the survival of birds in arid zones such as the southern Kalahari Desert.

Future breeding success in birds correlates with both body mass at fledging and adult body condition (Ghalambor & Martin, 2001; Ridley & Raihani, 2007; Weimerskirch et al., 2000). It has been reported that birds are likely to abandon their clutches if their body condition becomes compromised due to factors such as reduced foraging efficiency (Amat & Masero, 2004; Ridley & Raihani, 2007). Under both a high and moderate climate change scenario, the species modelled here will experience conditions of chronic heat stress across the majority of their ranges. Species resilience to future climate warming is unlikely to be improved through behavioural thermoregulation (Cunningham, Martin & Hockey, 2015). Given the expected increases in frequency and extent of high temperatures (Engelbrecht et al., 2015) and the inability to maintain body condition at these temperatures, successful breeding attempts are likely to decrease by the end of the century in desert birds even if radiative forcing and greenhouse gas emission are stabilized (RCP 4.5, e.g. Southern Pied Babblers and Southern Yellow-billed Hornbills).

Implications for conservation

My results suggest that under historic climatic conditions the distributions of southern African arid-zone birds were not directly limited by high air temperatures. Instead, biotic or abiotic niche constraints likely limited their distribution (e.g. vegetation type, precipitation and food availability) (Crowe & Crowe, 1982). Under current conditions arid-zone bird species are beginning to experience heat stress, but under unmitigated climate change they will experience these conditions much more frequently across their ranges. This suggests that the future distribution of arid-zone bird species will be directly determined by high temperature as well as the historical biotic and/or abiotic factors.

Birds need to make coordinated physiological and behavioural adjustments when air temperatures increase to avoid heat stress risks and increase survival probabilities (Xie, Romero, Htut, & McWhorter, 2017). In arid- to semi-arid environments such as southern Africa these adjustments become critically important given the limited availability of food, water (Williams & Tieleman, 2005) and thermally buffered refugia available (Cunningham et al., 2015; Sears, Raskin, & Angilletta, 2011). In this study I have included arid-zone birds with body masses ranging from 10 g (Scaly-feathered Finch) to over 200 g (Southern Yellow-billed Hornbill), covering the body mass range of most birds in the southern Kalahari Desert. Assuming the thermal physiology and thermoregulatory trade-offs of the modelled species here are representative of most species occurring in the southern Kalahari, this area is likely to lose an enormous proportion of its avifauna by 2100 CE. My model assumes zero physiological and / or behavioural flexibility, a scenario which is unlikely. The effects of plasticity will increase the threshold temperatures at which birds experience heat stress. When exposed to changing climates birds have the potential to display adaptive physiological responses (Noakes, Wolf, & McKechnie, 2016). Our understanding of the exact evolutionary process driving intraspecific variation in avian thermoregulation in response to high T_a is limited and future research should aim to better understand these responses.

For the species modelled here, the risk of mass mortality events will remain relatively low ($< 10\ d{\cdot}y^{-1}$) in the Kalahari Desert compared to those predicted for the southwestern United states ($> 50\ d{\cdot}y^{-1}$, e.g. Albright et al., 2017) under future climate change scenarios. Despite the low risk of mortality modelled here, the risk of acute heat stress will be exacerbated by the effects of chronic heat stress and other environmental changes (Albright et al., 2017). A key finding of this study is that the subtle, chronic effects of heat stress are major threat to future avifauna in the Kalahari Desert. These chronic, sublethal effects are going to be more important in terms of species persistence than the risk of acute mortality events under future climate change. All three species modelled here are predicted to experience reduced foraging efficiency and / or compromised body condition which is likely to negatively influence breeding success across the majority of their ranges by the end of the century under unmitigated climate change. For instance, I predict that several unsuccessful breeding attempts will occur throughout the breeding season for consecutive years towards the end of the century resulting in large losses of biodiversity across arid environments such as the Kalahari Desert.

Given the rapid rate of climate change and the severe risk of chronic heat stress demonstrated in this study I suggest that future research should focus on detailed species-specific studies which will identify threshold temperatures at which various fitness components become compromised. Behavioural and to a lesser extent physiological adjustments may not be enough to ensure the survival and reproduction of desert birds under unmitigated climate change by the end of the century. Knowledge of species-specific behavioural and, to a lesser extent, physiological responses can greatly benefit conservation managers and policymakers to make informed decisions about the extreme consequences of high air temperature on arid-zone fauna. Conservation managers and policy makers need to urgently make decisions and policies which include adaptive planning, management and action to avoid these enormous loses to biodiversity in arid zones.

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Chapter IV: General discussion

Overview

Birds are predominantly diurnal, small sized and have high energy and water balance requirements which makes them susceptible to high temperatures and extreme warming events (McKechnie & Wolf, 2010; Tieleman & Williams, 1999). Southern Africa in particular is vulnerable to extreme temperatures presently and in the likely future (Davis-Reddy & Vincent, 2017; Engelbrecht et al., 2015; Kotir, 2011). The projected warming over this region will be approximately 4 – 6 °C higher by 2071 – 2100 than the average temperatures between 1960 and 1990 (Engelbrecht et al., 2015). These predictions propose that birds will be experiencing increased physiological stress to maintain homeostasis, and could result in mortality events when homeostasis is disrupted and body temperatures exceed tolerable thresholds (McKechnie & Wolf, 2010). Although mass mortality events have been reported in the literature (McKechnie, Hockey, & Wolf, 2012; McKechnie & Wolf, 2010) acute lethal dehydration has been infrequent under current conditions but will increase in severity, frequency and extent by the end of the century (Albright et al., 2017). The effects of subtle, chronic heat stress (e.g. compromised body condition) have been reported more frequently under current conditions (Cunningham, Martin, Hojem, & Hockey, 2013; du Plessis et al., 2012; van de Ven, 2017) and will increasing dramatically under future warming.

My study introduces a spatial – temporal dynamic interrogation tool for the visualization and analysis of past, present and likely future climates in southern Africa. I have demonstrated that this tool identifies areas characterised by extreme versus subtle temperature variability at both a spatial and temporal scale. Such an approach can feed back into ecological response models under future climate change scenarios (e.g. Kearney & Porter, 2009; Kearney et al., 2009). I have demonstrated that the interaction between climate change, extreme climatic events and species responses over various time scales can result in dramatic ecological consequences, a key component in various vulnerability assessment frameworks (Williams et al., 2008; Foden et al., 2018). This contributes to the growing body of literature on trait-based assessments of species vulnerability to climate change impact. I demonstrated this using both physiological and behavioural responses of arid-zone bird species to temperature. At a broad scale birds typically respond to short-term (typically minutes to hours) extreme temperatures resulting in acute heat stress (Albright et al., 2017), medium-term exposure (typically days to weeks) of mild to high temperatures resulting in chronic heat stress (Cunningham, Martin & Hockey, 2015; du Plessis et al., 2012) or to long-term changes over years to decades resulting in morphological or physiological changes (Porter, 2000).

I mapped the exposure of eleven arid-zone bird species to acute heat stress and three arid-zone bird species to chronic heat stress. I found that over the last 1000 years southern African arid-zone bird species have likely not experienced conditions of acute or chronic heat stress. In recent decades the risk of both acute and chronic heat stress increased and are predicted to dramatically increase in frequency, severity and geographic extent by the end of the century.

Limitations of the study: dynamic spatial-temporal interrogation tool

One of the major limitations of the dynamic spatial-temporal interrogation tool relates to computational resources. The higher the resolution of the climate model used the more computation resources required to read in the data frame, subset the data, interrogate and analyse the data and build the model output. The dynamic spatial – temporal tool designed here can be applied to various climate models, however new climate models need to be defined according to the spatial and temporal resolution. The use of multiple climate model ensembles would strengthen the predictive capacity of the application output, however currently the model cannot sustain multiple models due to limited computational resources and the time required to run them on a desktop-level computer. Shifting to a mainframe will improve the computational strength and ability to run multiple climate model ensembles.

Limitations of the study: acute and chronic heat stress risk application

A potential limitation to my modelling approach is the use of summer months only. The body condition of birds prior to breeding is closely correlated with environmental conditions during winter and is likely to influence reproductive performance (Drent & Daan, 2002). I used existing data from individual birds occurring within the southern Kalahari Desert region, however same-species individuals from different populations have been demonstrated to vary in their thermoregulatory abilities (Angilletta et al., 2010). For example, Noakes, Wolf, & McKechnie (2016) found that White-browed Sparrow-weavers (*Plocepasser mahali*) from arid environments had significantly higher evaporative cooling capacities and overall heat stress tolerances than populations from more mesic environments. Including individuals from mesic environments could improve our understanding of the overall threat climate change has for the avifauna of southern Africa. Additionally, comparisons can be made between arid and mesic same-species in terms of the behavioural and physiological adjustments in response to environmental conditions experienced. These comparisons may reveal that performance of birds in mesic environments become compromised due to factors such as increased humidity relative to arid zones (Gerson et al., 2014).

Avoidance of extreme temperatures to balance water and energy budgets is critically important to the survival of a species but may lead to lost opportunity costs including compromised foraging efficiency (du Plessis et al., 2012), breeding success (Jenouvrier, 2013; Ridley & Raihani, 2007) and nestling provisioning rates (Cunningham et al., 2013). These behavioural adjustments therefore lead to sublethal fitness costs, however under climate change scenarios arid-zone birds will experience additional pressures compromising their fitness. For example, the decrease in food availability may decrease foraging efficiency exacerbating the effects of high T_a on foraging (Cunningham, Martin & Hockey, 2015; du Plessis et al., 2012). The species modelled here and their food sources rely on rainfall which influences food availability, breeding success and adult body condition (Cunningham et al., 2013; Ridley & Raihani, 2007). This becomes critically important under climate change as rainfall is predicted to become more scare and variable in desert systems (Engelbrecht et al., 2011) resulting in decreased food availability which will exacerbate the effects sublethal fitness costs. These additional pressures have not been included in my model which will likely result in more severe chronic heat stress effects over shorter time periods.

Future research suggestions

My study introduces a dynamic spatial – temporal tool which investigates and analyses climate change and respective biological responses and risks associated with climate change. Existing data on species responses to temperature can be used by this tool to show exposure to temperatures in excess of physiologically tolerable thresholds (Albright et al., 2017). Additionally, information about the spread and outbreak of disease in response to temperature could be analysed to predict the probability of an outbreak under climate change scenarios. For example, Rift Valley fever and dengue have undergone range expansions with increased temperatures in Africa (Anyamba, Linthicum, & Tucker, 2001; Martin et al., 2008). The spread of these pathogens could however relate to other environmental factors such as land use change or increased drug resistance (Harvell et al., 2002). Infectious diseases tend to have a nonlinear relationship with temperature and are able to evolve and adapt rapidly under changing environmental conditions (Harvell et al., 2002). Therefore a better understanding of disease – temperature associations and their adaptive capacity are need to in order to effectively predict disease responses under climate change using this spatial – temporal tool.

My findings have also highlighted key conservation and management implications for arid-zone species in the southern Kalahari Desert region. For example, the need to maintain and conserve thermally buffered zones (e.g. vegetation cover) and free water bodies may become of critical importance in arid environments where small bird species face the risk of acute and chronic heat stress (Albright et al., 2017). Subsequently the maintenance and conservation of more thermally moderate environments should become a priority for conservation managers and policy-makers to buffer the impacts of extreme temperatures. Thus the need for better understanding into the direct effects of high T_a values in arid through to mesic environments is urgent for the conservation of avifauna regionally and globally where threatened species responses should be prioritised.

Conclusion

This study describes a novel approach to modelling species responses to climate change using a dynamic spatial-temporal interrogation tool. I aimed to determine the degree of temperature variability experienced in the past, present and likely future across southern Africa and how our understanding of past climate variability contribute to predictions of future species responses under climate change scenarios. I found that over the last millennium and recent years southern Africa has experienced large scale temperature variability which is predicted to dramatically increase under climate change scenarios (RCP 4.5 and RCP 8.5) (Chapter 2). The rate of warming currently and in the likely future is non-linear across southern Africa, with Namibia currently warming most rapidly but under future climate change the southern Kalahari Desert region will warm the most (Chapter 2). The rapid rate at which climate is changing may be a potential constraint to species responses (McKechnie & Wolf, 2010). In chapter 3 I investigated heat stress as a potential determinant of arid-zone bird distribution. I aimed to determine: 1.) the environmental conditions associated with acute and chronic heat stress risk and the areas in which they occur in the past, present and future and 2.) how future climate change scenarios and the associated heat stress risk will determine future species distributions. I found that the environmental conditions associated with both acute and chronic heat stress risk have until recently not been routinely experienced by arid-zone birds of southern Africa. Recently temperatures have exceeded above tolerable threshold limits for certain arid-zone birds species resulting in risks of lethal dehydration, and/ or sublethal fitness costs (e.g. compromised foraging efficiency, breeding success and nestling provisioning rates) (Fig. 7 and 8). I predict that by the end of the century these conditions are will increase in severity, frequency and geographic extent under a both a moderate and high risk climate change scenario (RCP 4.5 and RCP 8.5). My results suggest that more studies should focus on the direct effects of high T_a values within arid-zone species. For example, future work should attempt to understand both the behavioural and physiological of threatened species occurring in arid areas.

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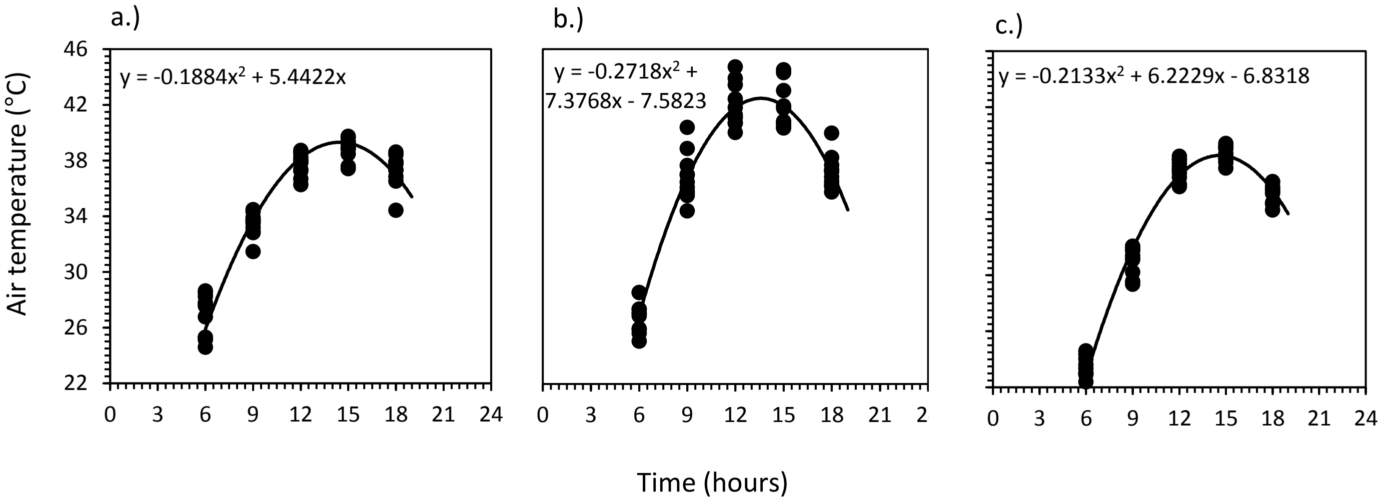
Appendices

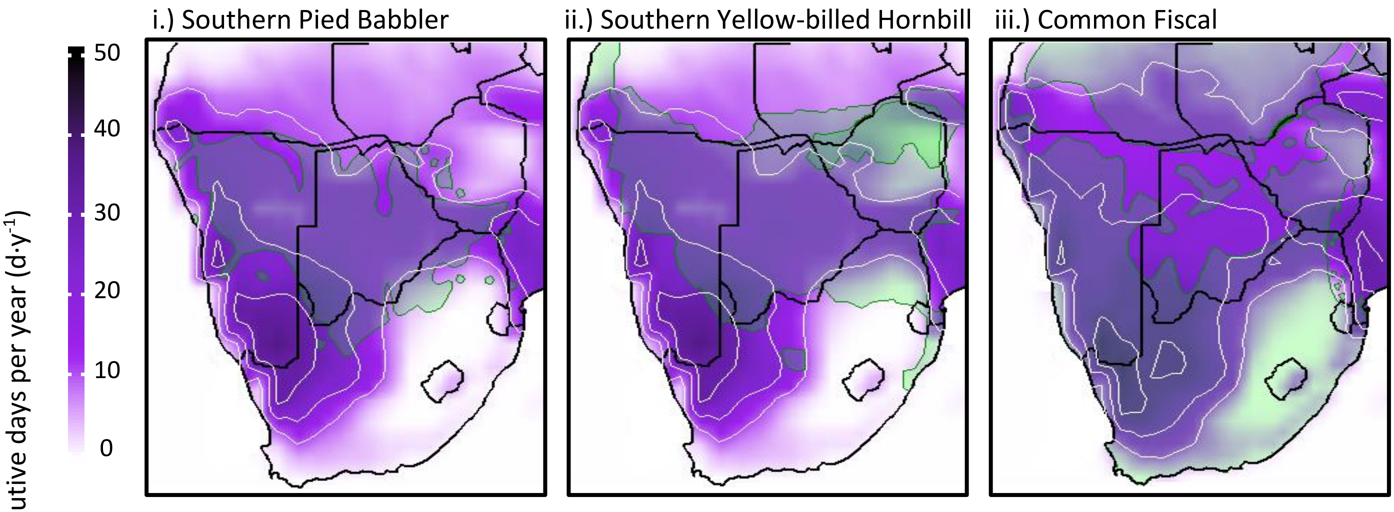
Time period	Air temperature	Online resource
Modern	Average	https://drive.google.com/file/d/1ZcwWwBGy515Dz7s_Y_lPQ3seH7wjZxTT/view?usp=sharing
Modern	Absolute maximum	https://drive.google.com/file/d/1eLszIqJsd4IQOUi23lPCky-kpS7NEoAK/view?usp=sharing
Future RCP8.5	Average	https://drive.google.com/file/d/1lb3MKB2-icGcUabVsU9dO67hX3ew35f_/view?usp=sharing
Future RCP8.5	Absolute maximum	https://drive.google.com/file/d/1XdB-ZaSlunkz9prXsSvw373sW614URRt/view?usp=sharing
Future RCP4.5	Average	https://drive.google.com/file/d/1ZbHcZ_Uz2HwRzCrLpym7uVXn7ES7TC7f/view?usp=sharing
Future RCP4.5	Absolute maximum	https://drive.google.com/file/d/1VQLg1fzrrKCz4zoqjvRKSxL9Y2ZAV-To/view?usp=sharing

Appendix A. The references to an online resource with the climate movies constructed to visualize changes in average and absolute maximum summer air temperatures over the last millennium (decadal), modern years and likely future conditions, using Windows Movie Maker (Version 2012, Build 16.4.3528.0331).

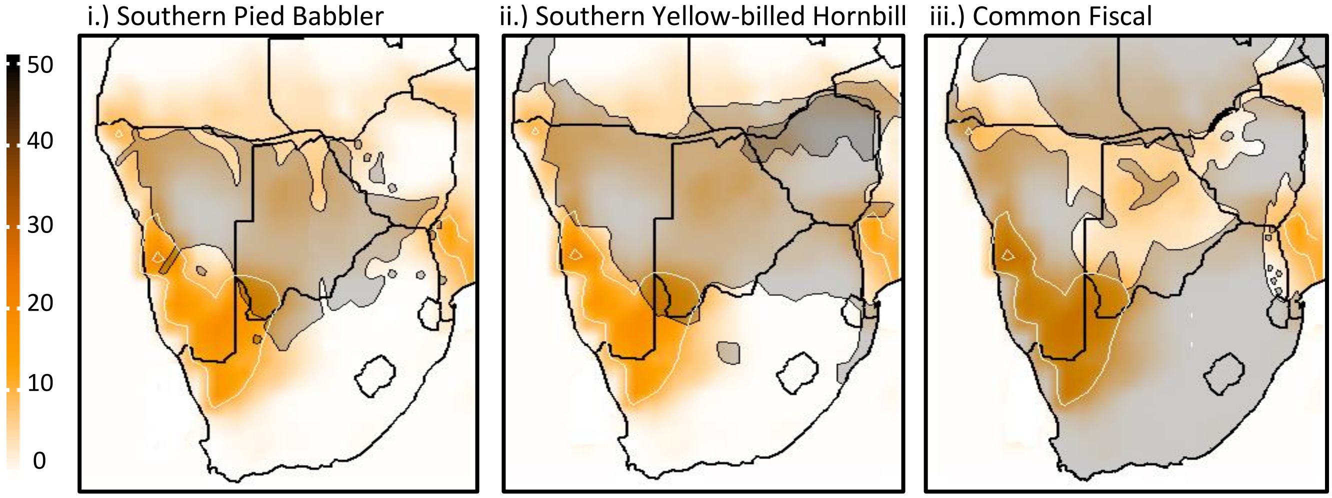


Appendix B. Three-hourly air temperature data from the hottest day between 2000 and 2010 over three regions across southern Africa (a: southern Kalahari Desert, b: central Namibia and c: northern Botswana). A polynomial regression model was fitted to the data from 06:00 to 18:00.

A: $T_a > T_{thresh}$ (2080 – 2090)



B: T_a > 38.5 °C (2080 – 2090)



Appendix C. Average number of consecutive days where three arid-zone bird species [i: Southern Pied Babbler (T_{thresh} = 35.5 °C), ii: Southern Yellow-billed Hornbill (T_{thresh} = 35 °C) and iii: Common Fiscal T_{thresh} = 33 °C)] are exposed to conditions of chronic heat stress risk under a moderate climate change scenario (RCP 4.5; A: Ta > $T_{thresh1}$, 2080 – 2090 and B: Ta > 38.5 °C 2080 – 2090). Species ranges indicated in green and grey respectively.