AN INTEGRATIVE APPROACH TO UNDERSTANDING VULNERABILITY OF AN ALPINE RANGE-RESTRICTED BIRD TO CLIMATE WARMING

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SUMMARY

Understanding species' vulnerability to climate change requires an integrative ecological approach involving, at minimum, physiology, behaviour, reproductive success, and limitations on dispersal. In this thesis I determined potential negative effects of increasing temperatures on behaviour, reproduction, and ability to disperse in an alpine-restricted bird, the Cape Rockjumper *Chaetops frenatus* ("Rockjumper"). Here I provide a comprehensive ecological set of data for understanding the link between Rockjumper population declines and warming habitats.

I tested whether Rockjumper microsite-use at high temperatures resulted in decreased time spent on important behaviours, such as foraging. I found Rockjumpers made increased use of rock-shade as air temperature increased and so spent less time panting, but birds in rock-shade foraged less. Birds may be constrained to foraging in sun at high temperatures to sustain energy or water requirements, despite risks of high thermal load, or else face lost foraging opportunities by remaining in rock-shade.

I determined if adult nest attendance and causes of nest failure were related to high temperatures. I filmed nests over two breeding seasons to examine temperature-effects on adult time in nests, provisioning rate, and resultant nestling daily mass gain. The only temperature effect I found was decreased percent daily change in body mass for older nestlings at hotter temperatures. I also examined causes of nest failure over three breeding seasons in relation to nest concealment and habitat openness by observing failure/success. Nests in more open territories (i.e. early post-fire habitat) had greater success, and the main cause of predation came from Boomslang *Dispholydus typus*. Importantly, the probability of Boomslang predation increased significantly at hotter temperatures. These findings show there may be direct negative effects of increasing temperatures on reproductive success and population recruitment, and so hotter temperature during the breeding season may be at least partly responsible for observed population declines.

Lastly, I examined genetic structure of populations across mountain ranges separated from one another by lowland habitat unsuitable for Rockjumpers. I predicted I would find little evidence for dispersal between mountain ranges separated by unsuitable lowland habitat, but instead found Rockjumpers show little evidence for inbreeding. I also found evidence for a past bottleneck event or founder effect, and little overall genetic diversity (possibly as their specialized niche exerts selective pressure). Low diversity may limit Rockjumpers' ability to adapt to a changing environment.

Adult physiological and behavioural thresholds to increasing temperatures are often used to create predictions of climate change effects. My past physiological research and current behavioural research suggest no particularly strong evidence that temperature-related population declines are driven by poor physiological capacity to tolerate heat or negative behaviour trade-offs. Instead, my current research shows that understanding negative effects of increasing temperatures may require a more in-depth approach involving investigation of fine-scale ecological interactions. No single one of my chapters provides the insight necessary for understanding Rockjumper population declines at warming temperatures. Instead, I show how an integrative approach may be necessary for assessing species' vulnerability to climate change by examining multiple ecological aspects of a single sentinel species, using an alpine species with a narrow thermal range and highly specialized habitat niche.

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PREFACE

FUNDING

This work was supported by a Nelson Mandela University Research Themes Grant to BS, an NRF Thuthuka Grant (no. 106958) to BS, a post-doctoral research grant from the South African National Biodiversity Institute to ATKL, and a grant from the DST-NRF Centre of Excellence at the FitzPatrick Institute for African Ornithology SJC. Funding was also provided directly to this project by an Animal Behavior Society: Student Research Grant to KNO, the Tygerberg Bird Club to KNO, and Birdlife South Africa to KNO.

DISCLAIMER

The chapters of this thesis have been prepared as stand-alone manuscripts. While I attempted to avoid redundancy by removing sections of methods related specifically to my main field site from each chapter and instead referencing previous chapters, at times the text may seem repetitive. In regard to acronyms and initialisms, I have explained their meaning at first use in each chapter summary and main text as opposed to their first use in the thesis, in order to create greater ease of reading.

PUBLICATIONS RESULTING FROM THIS THESIS

In the course of this thesis, one peer-reviewed manuscript has been published based on data from Chapter 2, two have been submitted based on data from Chapters 4 & 5, and one is in preparation for submission based on data from Chapter 3. I also published one popular article based on data from Chapters 3 & 4, and two popular articles based on data from the entire thesis. I was lead author for all publications (peer-reviewed and popular), and was primarily responsible for data collection, concept design, statistical analysis, and supplemental funding.

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Oswald, KN, B Smit, ATK Lee, C L-F Peng, C Brock, and SJ Cunningham. Reduced condition for older nestlings is associated with increasing maximum temperature in a range-restricted alpine bird. *Submitted to Animal Behaviour.*

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Oswald, KN, SE Edwards, ATK Lee, SJ Cunningham, and B Smit. Genetic data shows evidence for a past bottleneck and current dispersal in a sky island endemic. *In Review with Ecology & Evolution.*

Oswald, KN, ATK Lee, SJ Cunningham, and B Smit. The importance of accurate life history data in understanding ecological effects.

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CHAPTER 1: INTRODUCTION

1.1 THE ONGOING IMPACTS OF CLIMATE CHANGE

Evidence of the impact of climate change on the environment has been highlighted by considerable data in the past several decades. The greenhouse effect was first described by Joseph Fourier in 1824, and changing climate was a footnote at the 1972 UN conference on the environment in Stockholm, but arguably the critical importance of climate change was first declared with the Montreal Protocol in 1987. Since then, there have been numerous scientific studies providing evidence the climate is changing at a historically unprecedented rate, with the most recent International Panel on Climate Change declaring not only that air temperatures are shifting toward an overall warmer climate, but also that weather patterns in general are becoming more erratic (IPCC 2014). While land-use modification has been recognized as a secondary key driver in loss of global biodiversity (Ameztegui et al. 2016), climate change remains the main driver of species' distribution shifts (Chen et al. 2011, Bonebrake et al. 2017), changes in population size (Stephens et al. 2016), and changes in species' phenology (Thackeray et al. 2016).

1.2 FYNBOS AND ITS SUSCEPTIBILITY TO CLIMATE CHANGE

For South Africa specifically, climate change will mean an increase in days of extreme heat as well as an increase in the overall occurrence of heat waves, drought, flood, and fire (Easterling et al. 2000a, Easterling et al. 2000b). The southwest corner of South Africa holds a small belt (~90 000 ha) of heathland that is the smallest of the six globally-recognized floral kingdoms — the Cape Floristic Region. The Cape Floristic Region, herein referred to by its local name of Fynbos[1], is one of five Mediterranean-type biomes across the planet, all considered biodiversity hotspots, and all areas of high conservation concern due to climate change (Sala et al. 2000, Simmons et al. 2004; see section 1.3). Climate change scenarios for 2050 predict a 51–65 % reduction of the geographical extent of the Fynbos biome (Midgley et al. 2003), resulting in dramatic reductions in specific habitat for the inhabitants of this already rather small area. Projected increases in drought and fire due to climate change will likely result in a stunted successional cycle where the floral community structure does not advance past the early successional stage (Leadley 2010). The historically stable climate of the Fynbos is partially responsible for the remarkable floristic diversity of the

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[1] although "Fynbos" more specifically refers to only the dominant heathland of the Cape Floristic Region, for the sake of simplicity within this thesis the terms Fynbos and Cape Floristic Region are considered generally interchangeable.

region (Cowling et al. 2015), and so any major change in climatic patterns is likely to have adverse effects on plants and their dependent species. However, the effects of more frequent fires on the Fynbos ecosystem are as yet undetermined, for while the Fynbos thrives on a frequent fire regime (Van Wilgen et al. 2010, Keeley et al. 2011, Keeley 2012), introduced non-native species often dominate post-fire communities in areas of Fynbos with bordering plantations (Van Wilgen et al. 2010). These changes will likely result in negative impacts to biodiversity.

1.3 FYNBOS BIODIVERSITY

The five Mediterranean biomes are the Mediterranean Basin, the Chaparral in the southwestern United States, the Matorral in southern Chile, the Mallee in southwestern Australia, and the Fynbos in southwestern South Africa. Altogether these five biomes cover 2 % of the Earth's land area but support 20 % of the Earth's plant diversity (Cowling et al. 1996). While overall animal diversity is low in Mediterranean biomes, all five have proportionally high levels of endemism across taxa (Cowling et al. 1996, Myers et al. 2000), with some future climate scenarios predicting complete extinction of many of these specialist species (Leadley 2010). The Fynbos is particularly susceptible to climate change due to its small size and highest proportion of endemism among the five Mediterranean-type biomes (Midgley et al. 2003). The Fynbos is known for its prolific and unique plant communities (close to 6,000 endemic plant species among 12 endemic families and 160 endemic genera; Cowling 1992, Myers et al. 2000). Among terrestrial vertebrates the Fynbos holds one endemic mammal (although six near-endemics; Siegfried 1992), and seven endemic birds (six passerines; Barnes 1998). Of these six passerine bird species, two derive from "ancient lineages" of taxa (Chaetopidae and Promeropidae), with low diversity and high phylogenetic distance from nearest relations, making these species distinctive amongst avian communities (Beresford et al. 2005). Predictive climate change modeling indicates the Fynbos heathlands will shift southward, contracting toward the southern coast of South Africa (Midgley et al. 2003), which will result in correlative contractions of suitable habitat for all the Fynbos' endemics.

1.4 MOUNTAIN FYNBOS –– SOUTH AFRICA'S SKY ISLANDS

Within the Fynbos are two main ecoregions: Lowland Fynbos and Renosterveld ("Lowland Fynbos"), and Montane Fynbos and Renosterveld ("Mountain Fynbos"), often interspersed with small patches of Albany Thicket (Rutherford and Mucina 2006). As the name suggests, areas of Mountain Fynbos exist predominantly at higher elevations on quartzite and sandstone ridges, with the sole exception of a small stretch at lower elevation in the Kogelberg Nature Reserve that stretches down to the Southern Ocean (Richardson et al. 1994; see Chapter 5.3.1 for details). Patches of Mountain Fynbos are separated from one another by areas of Lowland Fynbos and Albany Thicket, but also by stretches of semi-arid Karoo, creating continental "sky islands" — high-elevation habitats separated by ecologically distinct lowland habitat (McCormack et al. 2009). Areas of Mountain Fynbos extend from ~300 km north of the Cape Peninsula, in the Western Cape, to ~100 km west of Port Elizabeth, in the Eastern Cape, of South Africa.

Along with the aforementioned contraction of the Fynbos as a biome, as climate warming progresses Mountain Fynbos will further contract upslope (Simmons et al. 2004), resulting in further isolation of the Fynbos sky islands. Globally, sky islands often harbour distinct populations of plants and animals isolated by both paleo-climatic events and habitat fragmentation on an evolutionarily relevant timescale (Gillespie and Roderick 2002). These populations then become highly specialized to their specific habitat niche, with correspondingly unique ecological traits and specific thermal ranges (Janzen 1967, Reif and Flousek 2012, Mahon et al. 2016, Scridel et al. 2017). Sky islands have large proportions of endemics (Gillespie and Roderick 2002), with little opportunity to undergo range shifts as their current habitats continue to warm (Kupfer et al. 2005). Alpine species are also useful in studying climate change as they can show responses at relatively low changes in temperature, likely due to their highly specialized and thermally-restricted nature (Reif and Flousek 2012, Mahon et al. 2016, Scridel et al. 2017). This is especially true for those species which can be defined as climate relicts, a species isolated due to changes in their distribution resulting from changing climate, as is particularly the case for many sky island inhabitants (Woolbright et al. 2014). Birds whose ranges are restricted to mountains (which would include sky island endemics) may be most useful as case studies for climate change responses, and so Scridel et al. (2018) pinpoint long-term studies on population persistence in alpine birds as a gap in current ecological research.

1.5 CAPE ROCKJUMPERS AS SENTINEL FOR A CHANGING WORLD

The Cape Rockjumper *Chaetops frenatus* (hereafter "Rockjumper") is found solely in South Africa's Mountain Fynbos sky islands (Lee and Barnard 2016) — while a single population exists at low elevation east of Cape Town, this habitat is consistant with alpine Fynbos vegetationa and climate despite its lower elevation (see Chapter 5.3.1). Rockjumpers, one of the Fynbos' six endemic passerines, may serve as an indicator species not only for biodiversity loss in the Fynbos, but also an indicator for how similarly range-restricted species worldwide may respond to climate warming. Rockjumpers fulfill all of the criteria identified for sentinels of the effects of climate change: they occur only on continental sky islands

(McCormack et al. 2009), are likely to be climate relicts (Woolbright et al. 2014), show the high degree of habitat specialization common in mountain endemics (Scridel et al. 2018), and are not able to shift their range should their current habitat become thermally unsuitable (Kupfer et al. 2005). Additionally, Rockjumper populations are currently declining specifically in areas of habitat that experienced statistically significant warming trends over the past three decades, but are not in decline in areas of their habitat where climate has remained stable over this time period (Milne et al. 2015). However, this study was not able to determine how specific populations may be declining, as Milne et al. (2015) used occurrence records from South African Bird Atlas Project’s 1 and 2 (1987–1991, and 2007–present, respectively), where occurrence is presence/absence, and does not account for abundance. Limited suitable habitat and declining populations, combined with a predicted shrinking habitat as climate warming pushes Mountain Fynbos further upslope, led to the placement of Rockjumpers on the IUCN Red List for Endangered Species in 2017 (IUCN 2017).

1.6 BASIC BIOLOGY OF CAPE ROCKJUMPERS

Rockjumpers are medium-sized (~55 g) passerines in family Chaetopidae that defend and maintain territories year-round (Holmes et al. 2002). Previous studies found they have a comparatively low physiological threshold for evaporative water loss (Milne et al. 2015), and may face unsustainable rates of evaporative water loss at high temperatures (Oswald et al. 2018c). As with most ground-foraging birds (and indeed most birds in general), Rockjumpers spend the majority of their time foraging. The main diet of Rockjumpers is arthropods such as Lepidopterans, although they also prey upon amphibians and reptiles (personal observations). They are ground-nesting birds, building open-cup nests under rocky overhangs, made mostly of twigs lined with fur and Proteaceae seed pods (Holmes et al. 2002). Their breeding system is described as facultative cooperative; Rockjumpers are most often found in pairs, but occasionally occur in groups of 3-5 individuals, in which cases the extra-pair individuals are most often male, and often offspring from previous years (personal observations; Holmes et al. 2002). All adults in a territory are involved in incubating, brooding, and provisioning nests (Martin 1964, Holmes et al. 2002), with clutch sizes reported to consist of two eggs (Holmes et al. 2002).

1.7 MAIN STUDY SITE

My primary study site was Blue Hill Nature Reserve, Western Cape, South Africa (33.56S, 23.40E; Figure 1.1). Blue Hill Nature Reserve extends over 2,000 ha of predominantly Mountain Fynbos at elevations of 1,100 to 1,600 masl, with small sections of mixed thicket and Renosterveld, bordered by succulent Karoo. In 2008, upon purchase by the Lee family, the farm was established as a CapeNature Conservancy, a partnership between the landowner and CapeNature — the Western Cape's public institution for biodiversity conservation.

Figure 1.1 Mountain Fynbos with low Restionaceae-dominated vegetation on scree slopes with large quartzite boulders providing suitable habitat for Cape Rockjumpers (*Chaetops frenatus*) at Blue Hill Nature Reserve, Western Cape, South Africa.

At the beginning of this study Rockjumpers were found only in the main southern section of Blue Hill Nature Reserve that had burned in 2012 (~1,800 ha). However, after a fire burned through the northern stretch of older growth Proteaceae in April of 2017 (~200 ha), Rockjumpers occupied and established territories in the newly burned habitat within six months (Figure 1.2), with breeding activity observed in 1–2 of the new territories in the 2017 season.

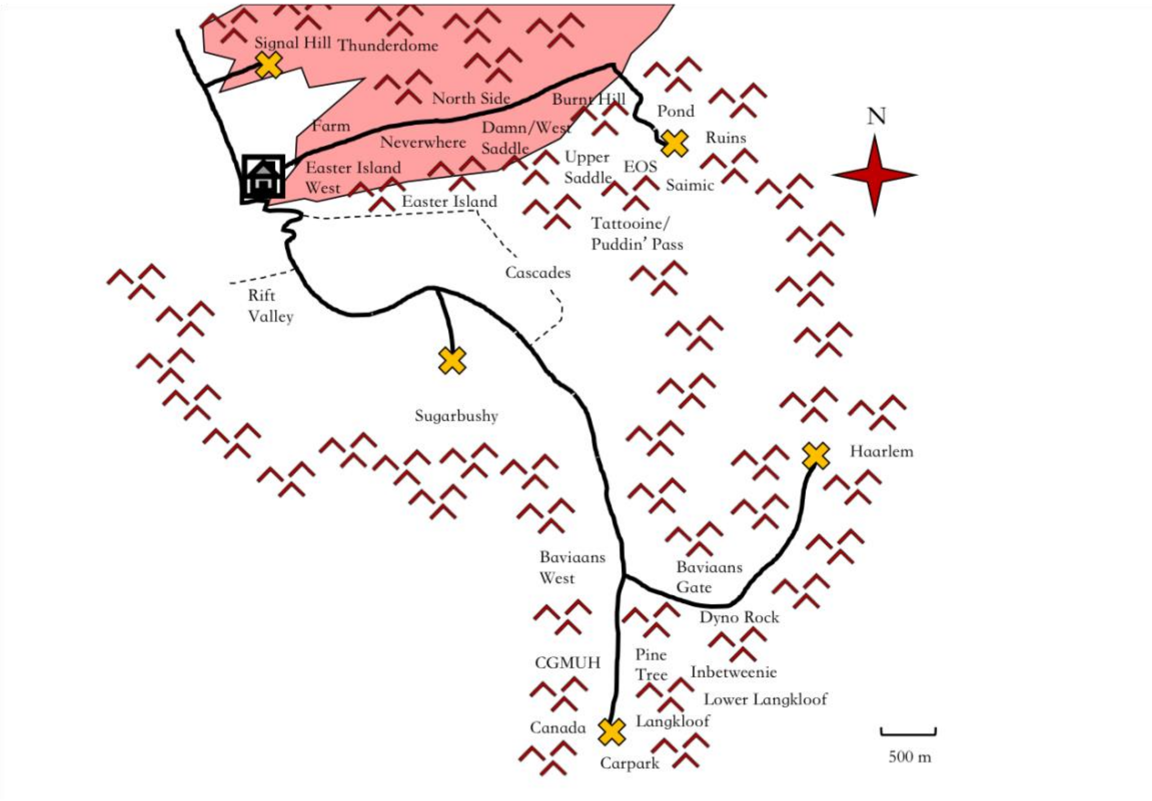

Figure 1.2 Map of Blue Hill Nature Reserve, Western Cape, South Africa, showing general location of individual Cape Rockjumper (*Chaetops frenatus*) territories (N = 29) represented by a name in text. The area burned in the 2017 fire is overlaid in transparent red. Solid black lines indicate roads, dashed lines indicate cleared hiking trails, yellow X's indicate road terminations, house icon indicates the farmhouse, and red chevrons indicate main mountain ridges.

1.8 MAIN OBJECTIVES

In this thesis I aim to determine the mechanism responsible for declining Rockjumper populations that seem to be correlated with increasing temperatures, and extrapolate on what this may mean for Rockjumper overall population resilience. I will use a mechanistic approach by collecting data on their ecology which will include behaviour, reproduction, and current gene-flow patterns and provide an integrated picture of how Rockjumpers are responding to climate change (see Figure 1.3). While my previous research suggested both adult and immature birds may face water constraints at high temperatures (Oswald et al. 2018b, c), it did not find obvious evidence that physiological mechanisms were directly related to current population declines under current temperature regimes. Buckley and Kingsolver (2012) identified three primary mechanisms by which species can respond to climate change: through relocation (spatially or temporally) to occupy similar habitat, through evolutionary adaptation, or through phenotypic plasticity (both behavioural and physiological). As range-restricted alpine endemics, Rockjumpers cannot relocate.

Therefore, I examine their phenotypic plasticity by looking at their behavioural responses to temperature in Chapter 2, having examined their physiology previously. I also examine their evolutionary adaptability by collecting data on their reproductive success in Chapters 3 and 4 and their genetic dispersal capability in Chapter 5. Using this approach, I aim to determine how Rockjumpers will be affected by future climate warming to provide a framework to help understand climate change responses in other such thermally-restricted alpine relicts.

In Chapter 2, I assess how behavioural changes including microsite selection may be used by birds to buffer against warmer temperatures and discuss potential trade-offs arising from these changes. In Chapter 3, I assess how overall parental nest attendance and provisioning change in relation to higher temperatures and precipitation and discuss potential effects this may have on overall breeding success. In Chapter 4, I assess overall reproductive success of Rockjumper nests in relation to nest-site selection (e.g. vegetative cover), and habitat openness (e.g. post-fire habitat stage), I also relate these factors to predation events and temperature. In Chapter 5, I assess the genetic structuring of Rockjumpers from across their range to determine whether gene flow between mountain populations is hindered by inhospitable lowland habitat to see how current and future warming may affect their dispersal. Finally, in Chapter 6, I provide a general conclusion, using the results of the above chapters to present an integrated story of how climate change has affected and will affect Rockjumpers directly and what this may mean for similar species. In Chapter 6, I also use predictive modelling to extrapolate what increasing temperatures may mean for Rockjumpers, given my main findings that high temperature correlates with increased probability of snake predation and reduced mass gain in older nestlings.

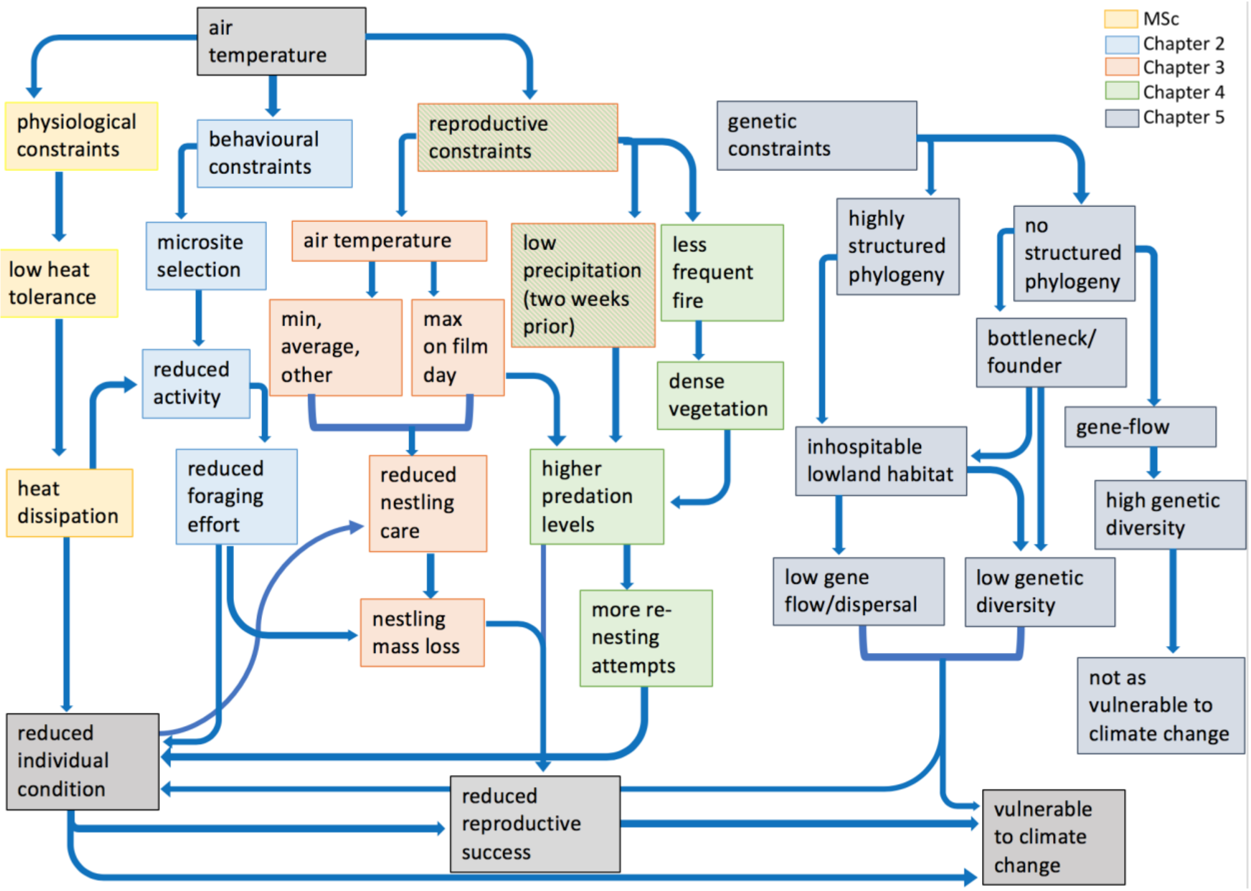

Figure 1.3 Flowchart showing division of topics covered per chapter, with arrows indicating the main relationships and variables covered in this thesis. I have included topics from my MSc (Oswald 2016) where they directly relate to the foundations of chapters in this thesis.

1.8.1 CHAPTER 2: BEHAVIOURAL ADJUSTMENTS TO AIR TEMPERATURE

Short-term behavioural responses to changing temperature can allow individuals to quickly respond to environmental challenges such as inclement weather or changes in food supply. Individuals may be able to reduce the negative impacts of unpredictable events by exploiting this flexibility (Wingfield 2003). Reducing daily energy expenditure and exploiting cooler microclimates are commonly used behavioural mechanisms for coping with high temperatures (Mugaas and King 1981, Sinervo et al. 2010, Gifford and Kozak 2012, Visinoni et al. 2015). Specifically, Huey et al. (2012) found that species in thermally heterogeneous environments use “behavioural buffering” (e.g. seeking thermally favourable microsites) as a mechanism to help maintain body temperature.

For birds, Williams et al. (1995) suggested use of microsites (i.e. behavioural buffering) was the most effective means of water conservation; the alternative of losing heat through evaporative water loss (i.e. by panting) can reduce foraging efficiency (du Plessis et al 2012; van de Ven et al 2019), as well as requiring increased acquisition of water. In turn, interest in behavioural buffering has led to a growing body of work concerning use of behavioural adjustments among birds as a means to cope with high temperatures (Wolf and Walsberg 1996, Hill 2006, Carroll et al 2015a, Cunningham et al. 2015, Martin et al. 2015, Shi et al. 2015, Pattinson and Smit 2017). Indeed, interest in research on behavioural thermoregulation is an area of increasing interest among range-restricted animals across taxa (Monasterio et al. 2009, Dirnböck et al. 2011, Moyer-Horner et al. 2015, Žagar et al. 2015).

I examined Rockjumper behavioural responses to temperature by collecting two years of summer behavioural observations from 10 focal territories. By recording behaviours where they occur in regard to microsite and analyzing this in relation to temperature, I aimed to determine whether Rockjumpers are using behavioural buffering to mitigate heat load at high air temperatures. I assessed the relationship between air temperature and Rockjumper behaviour and whether Rockjumper behaviours changed when using cooler microsites.

1.8.2 CHAPTER 3: CHANGES IN NEST ATTENDANCE RELATED TO AIR TEMPERATURE

Reproduction is affected by both direct and indirect effects of climatic variability; weather can affect not only individual behaviour but can also affect species' reproductive phenology, output, and success (Bradley et al. 1997, Steenhof et al. 1999, Bolger et al. 2005, Borgman and Wolf 2016, Conrey et al. 2016, Martin et al. 2017). Overall nest success or failure can be directly affected by knock-on effects of temperature; for example, changes in adult foraging can result in an inability to adequately provision their young at high temperatures (Cunningham et al. 2013b, Wiley and Ridley 2016). Such decreases can result in a chain reaction of reduced nestling condition (i.e. body mass), reduced fledging success (Cunningham et al. 2013b), and ultimately reduced survival, recruitment, and lifetime fitness (Magrath 1991, Thompson and Flux 1991, Greno et al. 2008, Schwagmeyer and Mock 2008).

In passerine species, offspring are predominantly altricial (i.e. blind, featherless, and helpless when first hatched) and require a large amount of parental attention and care to raise young to successful fledging. Nest attendance, such as cleaning and temperature regulation, may also decrease as temperatures increase, resulting in lowered overall nest success or increased costs incurred by adults (Lloyd and Martin 2004, Hanssen et al. 2005). If Rockjumpers are not able to maintain provisioning rates or nest attendance as temperatures increase, this may result in decreased fledging success.

I collected two seasons of data (2017 and 2018) on nest attendance (i.e. overall time in nest, and provisioning) by parents of nestlings of three different age stages: younger (≤7 days old), middle (8–12 days old), and older (≥13 days old). I recorded video footage from Rockjumper nests over two breeding seasons to determine if increases in daily maximum temperature affected Rockjumper fledging success. I then examined heat dissipation by parents (i.e. panting) in relation to temperature, as well as changes in nest attendance (i.e. provisioning rate, time at nest), and overall nestling condition (i.e. percent daily body mass gain).

1.8.3 CHAPTER 4: NEST FAILURE AND PREDATION AS RELATED TO SITE-SELECTION AND AIR TEMPERATURE

Overall nest success or failure can also be associated with indirect effects such as resource availability, thermal constraints, and predation risk (Carroll et al. 2015a, Carroll et al. 2018). Nest-site selection plays a role in overall success, with previous studies often showing increased vegetative cover results in higher nest success (e.g. Davis 2005), so long as adults still have visibility to see potential predators (Magana et al. 2010). Rockjumper territories contain multiple microsites allowing for choice in nest-sites with a variety of vegetative cover. Additionally, the Fynbos' regular (i.e. 5–7 year) fire regime (Van Wilgen et al. 2010) adds the occasional ability to expand into newly burned habitat.

In general, ground-nesting birds such as Rockjumpers face higher rates of predation compared to species which nest off-ground (e.g. Nilsson et al. 1985, Martin and Li 1992). Rockjumper habitat contains a variety of potential predators including mammals (e.g. Cape Grey Mongooses *Galerella pulverulenta*) and snakes (e.g. Boomslang *Dispholidus typus*, Cape Cobras *Naja nivea*; Holmes et al. 2002). For snakes in particular, warmer temperatures lead to increased overall activity (Hailey 1986) and thus increased predation on passerine nests (Sperry et al. 2008, Cox et al. 2013a). Any factor which increases predation may result in Rockjumpers' inability to maintain recruitment levels.

I collected nest data from 2 nests *ad hoc* in 2016, as well as from two full breeding seasons in 2017 and 2018 (N = 17 and 37 respectively), to identify causes of success or failure. I first examined how overall daily survival rate changed as a result of nest concealment (e.g. vegetative cover directly around the nest), landscape cover (e.g. time since the territory had burned), and daily maximum temperature. I then examined how predation (predominantly by snakes) was related to daily maximum temperature throughout the time nests were active. I expected to find greater nest survival correlated with (1) greater habitat openness, and (2) increased nest concealment, and I expected occurrence of snake predation to be higher on days with warmer temperatures.

1.8.4 CHAPTER 5: GENETIC STRUCTURING OF POPULATIONS

Although generally contiguous (Holmes et al. 2002), many of the mountain ranges inhabited by Cape Rockjumpers *C. frenatus*[2] are disconnected by ~20 km stretches of unsuitable lowland habitat which creates potential dispersal barriers. Maintaining high genetic diversity is important for a species' overall fitness and long-term viability (Roelke et al. 1993, Reed and Frankham 2003, Da Silva et al. 2006) and is one of the main criteria the IUCN has designated for determining whether a species is at risk (Reed and Frankham 2003). Limited dispersal within already structured populations can result in loss of genetic variation and diversity, with reduced dispersal causing re-distribution of genetic variability within only a few generations (Harrison and Hastings 1996). However, species in highly specialized habitats often have low genetic diversity due to selective pressure from their specific niche (Orsini et al. 2013).

The closest relative of *C. frenatus*, the Drakensberg Rockjumper *C. aurantius*, occupies the nearby Lesotho highlands and adjacent Great Escarpment, separated from *C. frenatus* by the Great Karoo plain (~100 to 150 km wide) north of Grahamstown (Hockey et al. 2005). These species are superficially similar in appearance and vocalization. However, they differ in habitat preference, with *C. aurantius* inhabiting Alpine Grassland as opposed to *C. frenatus* preference for Mountain Fynbos (Hockey et al. 2005). The potential dispersal barriers among *C. frenatus* populations, along with a nearby closely related sister-species, present a unique system for studying the links between population genetics and the persistence of small isolated populations as a function of past and present climatic regimes.

I collected *C. frenatus* blood samples from eight distinct mountain localities to examine genetic structuring among Cape Rockjumper populations. I aimed to identify potential dispersal barriers in order to improve understanding of how gene-flow is currently occurring between isolated populations. I also collected blood samples from two localities of *C. aurantius* to use as a main outgroup, as well as using existing samples of the sister family to Chaetopidae, Picathartidae (specifically the White-necked Rockfowl *Picathartes*

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[2] Full scientific names are used both in this section and in Chapter 5 to simplify discussion of the two Rockjumper species.

gymnocephalus) as an additional outgroup. I hypothesized that unsuitable lowland habitat between the geographically distinct mountain ranges would act as a barrier to effective dispersal between populations, resulting in genetic structuring aligned with the topography of the Cape Fold Belt. Geographic genetic structuring, suggesting some populations of *C. frenatus* are genetically isolated from one another, would indicate key areas in need of conservation.

1.9 ETHICS AND PERMISSIONS

Data collection for December 2014 to December 2016 received ethics approval from University of Cape Town: Science Faculty Animal Ethics Committee (2014/V19/AL). Data collection between June 2014 and February 2018 received ethics clearance from Nelson Mandela University: Research Ethics Committee (Animal; A15-SCI-ZOO-007) as well as from the Ethics Committee of the Department of Zoology & Entomology, Rhodes University (RU-DZE-2017-10-028). Capture permits have been received from both Western Cape Province: CapeNature (AAA041-00565), and Eastern Cape Province: Department of Economic Development and Environmental Affairs and Tourism (CRO55/17CR and CRO56/17CR). Birds were ringed with permission from SAFRING (Ringer no: 17059), and competence in blood sampling technique was confirmed by Dr. Tarryn Fick (BVSc, Newton Park Animal Hospital, Port Elizabeth, SA).

CHAPTER 2: BEHAVIOUR OF AN ALPINE RANGE-RESTRICTED SPECIES IS DESCRIBED MAINLY BY INTERACTIONS BETWEEN MICROSITE-USE AND TEMPERATURE.

2.1 SUMMARY

Climate change predictions include increased mean temperatures and increased frequency of heat waves. Short-term responses to high air temperatures can allow animals to conserve water while maintaining a safe body temperature. For birds, cooling is often through evaporative water loss, which can be physiologically costly. Microsite-use is an effective means of conserving water via reducing environmental heat load, so long as there are no negative trade-offs with other necessary functions, such as foraging. I examined behavioural responses to temperature in Cape Rockjumpers *Chaetops frenatus* (hereafter "Rockjumper"), an alpine-specialist bird. I hypothesised that Rockjumper behaviours would be temperature- and microsite-dependent. I collected data on Rockjumper microsite-use (sun, rock-shade), behaviour (activity, foraging, preening, panting), and temperature (air, environmental). Rockjumpers made increased use of rock-shade as air temperature increased. However, birds in rock-shade foraged less. Depending on where their main food source is located, this suggests that when foraging demands are high, birds may be constrained to remain in the sun despite risks of high thermal load, or else may suffer costs of lost foraging opportunities. The relationship between air temperature and heat dissipation behaviour (panting) was also mediated by microsite: birds showed significant increases in panting with increasing air temperature only when located in the sun. The lack of increase in panting for birds in rock-shade suggests that shade-seeking may buffer physiological thermoregulatory costs (i.e. water expenditure). Individuals may therefore be able to mitigate some potential negative effects of high temperatures by making use of cooler microsites, though this could come at a cost to foraging.

2.2 INTRODUCTION

Under climate change, weather patterns are increasingly characterised by warmer overall temperatures and more intense heat waves (Easterling et al. 2000a). One way in which animals may respond quickly to environmental challenges is by using short-term behavioural responses (Wingfield 2003). In general, behavioural responses to temperature have been considered typical of ectotherms (e.g. Huey et al. 1989, Adolph 1990, Huey 1991, Gilman et al. 2008, Gifford et al. 2012, Sears et al. 2016), while endotherms are often assumed to rely primarily on physiological adjustments to regulate their body temperatures (Chamane and Downs 2009, Boyles et al. 2011, Smit et al. 2013). However, when examining potential avenues for mitigating the negative effects of increasing temperatures, Huey et al. (2012) suggested that any terrestrial species in thermally heterogeneous environments could use "behavioural buffering" (e.g. spending more time in cooler microsites) to help maintain body temperature. Indeed, behavioural buffering is a commonly used behavioural mechanism for coping with high temperatures, along with reducing daily energy expenditure, across both ectothermic and endothermic taxa (Mugaas and King 1981, Sinervo et al. 2010, Gifford et al. 2012, Buckley et al. 2015, Visinoni et al. 2015).

Interest in behavioural buffering has led to a growing number of studies focusing on how endotherms use microsites to cope with high temperatures, including both birds (e.g. Wolf et al. 1996, Hill 2006, Cunningham et al. 2015, Martin et al. 2015, Shi et al. 2015, Pattinson and Smit 2017), and mammals (e.g. Hewson 1990, Moyer-Horner et al. 2015; and see review Cain III et al. 2006). Adjusting behaviour in response to weather conditions is vital for maintaining heat balance while also balancing water and energy demands, especially in water-scarce environments (McKechnie and Wolf 2004, Williams and Tieleman 2005, Smit et al. 2013, Xie et al. 2017), and selective microsite-use remains the most effective means of water conservation (Williams et al. 1995). Ground-foraging birds may make particularly dramatic changes in microsite-use in order to manage heat load at high air temperatures (Martin et al. 2015, Van de Ven 2017), as the exposed microsites on the ground in which these birds forage are typically among the hottest in the landscape (Tieleman and Williams 2002b, Carroll et al. 2015b, Pattinson and Smit 2017). Indeed, greater shifts in microsite-use at high temperatures were found for ground-foraging species when compared to arboreal-foraging species (Martin et al. 2015).

Resting in shaded microsites may allow individuals to spend time on other necessary activities, such as feather maintenance (Tieleman and Williams 2002a, Leitão and Mota 2015), but must also be balanced with foraging, reproductive behaviour, and territory maintenance (Thiollay 1988, Wolf 2000, Gilman et al. 2008, Cunningham et al. 2015, Martin et al. 2015, Wiley and Ridley 2016). Alternatively, individuals can maintain body temperature by reducing daily energy expenditure, and thus reduce metabolic heat production (Weathers and Sullivan 1989, 1993, Visinoni et al. 2015, Pattinson and Smit 2017). However, reducing activity may not always be possible, as birds often need to continue foraging at high temperatures to meet individual energy demands (du Plessis et al. 2012, Van de Ven 2017), and also to meet the additional energy demands of offspring during the breeding season (Coe et al. 2015, Cunningham et al. 2015, Edwards et al. 2015, Clauser and McRae 2017).

A recent meta-analysis on the vulnerability of alpine species to climate change identified a research gap in fine-scale ecological studies of mountain specialist birds (Scridel et al. 2018). The Cape Rockjumper *Chaetops frenatus* (hereafter “Rockjumper”) represents one such range-restricted alpine species, inhabiting the upper slopes of the Fynbos mountains in South Africa. Rockjumpers are potential “climate relicts” due to fragmented ranges likely isolated by past climate shifts [see discussion in Woolbright et al. (2014)]. For alpine range-restricted specialists such as the Rockjumper, use of behavioural buffering may be necessary as they cannot shift their range poleward or upward into cooler climates (Gibson et al. 2010, Robin et al. 2015, Freeman et al. 2018). Rockjumpers are currently experiencing decreasing populations especially in parts of their range which show warming trends (Milne et al. 2015). Rockjumpers thus provide an ideal model for investigating whether alpine range-restricted species can use behavioural adjustments to mitigate the negative effects of warming temperatures.

In this study, I assess the relationship between air temperature and Rockjumper behaviour, and whether Rockjumper behaviours changed when using cooler microsites. While the exposed and rocky environment with low vegetation preferred by Rockjumpers lacks variation in vegetation structure that would generally provide thermal buffering (Lee and Barnard 2016); their habitat contains rocks and outcrops allowing patches of deep shade throughout the day. I thus hypothesised that daily activity patterns of Rockjumpers would be highly temperature- and microsite-dependent, due to increasing use of rock-shade for behavioural buffering as air temperatures increase. I observed behaviour of free-living Rockjumpers and predicted that as temperatures increased Rockjumpers would: (1) increase use of rock-shade, (2) become less active, (3) reduce foraging, (4) reduce preening, and (5) increase heat dissipation (i.e. panting or wing-drooping), with significant interactions between microsite and temperature.

2.3 METHODS

2.3.1 STUDY SITE AND SPECIES

This study took place at Blue Hill Nature Reserve ("BHNR") in the Western Cape province of South Africa; BHNR consists primarily of Mountain Fynbos suitable for Rockjumpers. Behavioural data collection occurred between January 2015 and February 2016 on 20 focal families (see below). Rockjumpers are group-living (2–5 adult individuals per territory) birds that maintain and defend year-round territories (Holmes et al. 2002, Oswald 2016a). See Chapter 1 for further details on study site and species.

2.3.2 CAPTURE AND TAGGING OF INDIVIDUAL BIRDS

To ensure identification of individual birds within territories, I caught 33 Rockjumpers from both focal and adjacent territories (N = 12 territories) between October 2014-September 2015, using baited snap traps (spring-loaded 30 cm x 30 cm mesh-covered wire frames baited with beetle larvae *Tenebrionoid* spp.). Ten birds were caught in October-November 2014, and an additional 23 birds were caught between April-September 2015. Birds were ringed with aluminium rings (SAFRING, South Africa), and given a unique combination of three colour rings for identification.

Behavioural data were collected in five Rockjumper territories between 23 January 2015 and 8 March 2015 (“Cohort 1”; N = 15 individual birds; 2–4 adults per territory). To aid locating Rockjumpers in Cohort 1, five of the adults caught during October-November 2014 (one in each of the five separate territories) were fitted with VHF transmitter tags (2.4 g, < 5.0 % average body mass; “M_b”; CTx, Biotrak Ltd., United Kingdom; see below for attachment details). Biotrack tags were programmed to emit radio signals (~150MHz) for 48-hrs every 12 days. Behavioural observations on Cohort 1 began in January 2015, with all ringed and tagged birds still active in their original territory of capture during these observations.

From 12 November 2015 to 21 January 2016, I continued observations on Cohort 1, as well as collecting observations in an additional five territories (“Cohort 2”; N = 20 additional individual birds, 2–3 adults per territory). To aid locating Rockjumpers in Cohort 2, five of the adults caught in July and August 2015 were captured and fitted with similar VHF transmitter tags (3.4 g, < 6.5 % average M_b; LB-2N, Holohill Systems Ltd., Canada) programmed to emit continuous radio signals (~150 MHz). Behavioural observations on Cohort 2 began in November 2015, with all ringed and tagged birds still active in their original territory of capture during these observations.

Tags were attached using leg-loop harnesses with tags resting between the wings and antenna pointing toward the rear (Smith et al. 2011, Vandenabeele et al. 2013). VHF-tagged birds were located during observation sessions using an 8 Mhz radio tracking receiver (SIKA, Biotrack Ltd., UK) and flexible 3-element yagi antenna (Lintec Antennas, UK).

Eighteen of the 33 ringed birds were ringed and released on location within their territories. For the other 15, birds were captured and transported via cloth bag to an on-site field station at BHNR where birds were held in 45x30x45 cm (length x width x height) cages for 24-48 h as part of a separate study on physiology (see Oswald et al. 2018c, b). During this 24-48 h period food was provided *ad libitum*, after which birds were released back at point of capture with no obvious long-term effects (Oswald et al. 2018a). Continued direct observations of Rockjumpers at BHNR have found VHF-tagged birds experienced minimal negative effects, with tag-attachments degrading and detaching in most instances — in addition, one tag was removed when the bird was re-captured in January 2016. I am further convinced that my VHF-tags had minimal negative effects due to two facts: (1) for territories I continued to monitor (N = 5 birds), all five birds were still present and reproductively active in 2017-2018, and (2) a preliminary analysis of activity levels between VHF-tagged and untagged birds (Generalized Linear Mixed-effects Mode,l "GLMM", of activity as a function of tagged or untagged with ID and territory as random effects, see below for more details) found no difference ($Z_{1,2059} = -1.30$, $p = 0.194$).

2.3.3 BEHAVIOURAL OBSERVATIONS

All observations were collected between 8:45–15:15 SAST. From 23 January to 8 March 2015 Cohort 1 birds were followed one day per territory within each 12-day VHF transmission cycle. From 12 November 2015 to 21 January 2016 each group from Cohorts 1 and 2 was followed one day every two weeks. For each observation day I collected behavioural observations from a single territory.

Observational data were collected using teams of two to four persons performing scan samples every five min. Due to the rocky landscape inhabited by Rockjumpers, there were multiple instances where no birds were visible at the time of a scan sample. This may have resulted in an under-representation of some types of microsite-use, as well as periods of inactivity, in my final dataset. Data recorded included (1) ordinal date; (2) time of day; (3) territory designation; (4) sex (m — male; f — female); ID (VHF code, color ring combination, unmarked with no color rings, or unknown); (5) microsite [s — sun; r — rock-shade; o — other (i.e. shade from plants or clouds)]; (6) overall activity ("active" — any movement ≥ five seconds including all behaviours, or "inactive" — no movement ≥ five seconds); (7) breeding stage ("breeding" —

whether birds were observed nest building, incubating, brooding, or provisioning on individual observation days, or “non-breeding” — no breeding activity observed); and (8) behaviours (see below).

Behaviours included: (1) foraging (erratic movement pattern usually leaning forward, moving a few steps and stopping, pecking at plants, etc.); (2) panting (bill observed in an open position for ≥ five seconds); and (3) preening (bill placed among feathers for ≥ five seconds). These behaviours were recorded as “1” for presence or “0” for absence. Distance from birds resulted in an inability to consistently determine whether panting occurred, and so panting was additionally recorded as “no data” when not able to be determined. While wing-drooping (i.e. holding wings away from the body) is a commonly recorded mechanism of heat dissipation among birds (see Tieleman and Williams 2002a, du Plessis et al. 2012, Smit et al. 2013, Edwards et al. 2015, Smit and McKechnie 2015), throughout my observation period I observed no instances of wing-drooping.

The above data were recorded every five min with preference for focal VHF-tagged individuals, but were additionally recorded opportunistically for other individuals within the target territory as well as individuals from adjacent territories (N = 2 additional territories). For each instantaneous scan I recorded behaviours for the focal bird up to 10 sec — and all additional nearby birds up to 20 seconds, after the 5-min mark. Observations were conducted from 20–200 m away from focal birds so as to minimize observer disruption, with birds observed through binoculars (8 or 10 X magnification) and spotting scopes (20 to 60 X magnification).

2.3.4 TEMPERATURE

Air temperature data ("T_{air}") were collected every 30 min by a VantageVue weather station at BHNR (“weather station”; Davis Instruments Corp., USA). The weather station was placed ~2 m above the ground at 1,030 masl, at a distance of 500–5,000 m from observed Rockjumper territories.

To gain an estimate of temperature variation at the microsite level within the landscape, on observation days during the second round of observations (November 2015-January 2016), “black bulb” thermometers were deployed and collected within the focal observed territory (~8:30–15:30 SAST; see below for details). Black bulbs were constructed from two copper hemispheres (diameter 30 mm, thickness 0.9 mm); in each black bulb, one iButton (model DS1921G-F5 ± 0.1 °C, Fairbridge Technologies, Sandton, South Africa) was secured to an iButton retainer (model DS9098P-TRW+, Fairbridge Technologies, Sandton, South

Africa) placed inside the two hemispheres, which were then glued together as a sphere and painted matte black.

Black bulbs integrate ambient temperature, solar radiation, and wind effects to approximate the conditions experienced across different locations (Campbell and Norman 2012, Cunningham et al. 2015). However, as studies have shown using black bulbs as a proxy for operative temperature can have multiple issues (see Bakken et al. 1985, Bakken 1992), I used black bulbs solely as an indication of potential variation in thermal conditions in microsites within a Rockjumpers' environment. On each day of black bulb deployment, before beginning observations I secured three replicate black bulbs within the observed territory in each of two microsite types (i.e. three in “rock-shade” — under rock in full shade, and three in “sun” — on rock surface in direct sun), and collected the black bulbs at the end of the days' observations. Black bulb data were collected from 10 territories on 18 non-consecutive days. Due to logger failure, data were collected in triplicate on N =11 observation days, but in duplicate on N = 7 observation days.

2.3.5 ANALYSES

Rockjumper behaviour: As one of my main objectives was to examine how microsite choice affects behaviour, I used only observations where birds were visible (N = 2 862 scan samples) and microsite was sun or rock-shade (N = 2 059 scan samples), omitting instances of “other” (plant- or cloud-shade; N = 803 scan samples; 28 %). Due to the sparse nature of Fynbos vegetation, there would be large variation in thermal conditions within plant-shade meaning I could not be able to reliably ascertain whether or not any particular patch of plant-shade constituted a true "thermal refuge". Similarly, cloud-shade is temporally unpredictable, and cloudy weather alters the thermal landscape wholesale, rendering comparisons between different microsites less meaningful. Therefore, these data were excluded. For panting analysis, I further subset the data to include only instances where panting was recorded as “1” or “0” (N = 958 scan samples). I used weather station T_{air} data as the “temperature” predictor variable in all analyses, and time of day ("time") was rounded to the nearest 30-min in order to better align with T_{air}.

I created GLMMs using package *lme4* (Bates et al. 2015), with binomial error distribution and Rockjumper individual ID and territory as random effects to explore Rockjumper behaviour and microsite-use data. To understand the influence of microsite-use, T_{air}, time, sex, and breeding stage on activity, foraging, panting, and preening I fitted Gaussian GLMMs with a log link function.

Due to convergence issues, I followed Afshartous and Preston (2011) and transformed categorical variables into numeric sum-to-zero variables [sex (1 female, -1 male), breeding stage (1 breeding, -1 not breeding), microsite (1 sun, -1 rock-shade)]. However, for activity, issues of convergence required microsite be retained as a standard categorical variable. Continuous variables (T_{air}, time) were centered and scaled using the standard *scale* function in R. The coefficient output thus represents the contribution of variables relative to each other. I discuss competing models within 2 AICc of the top model, with model selection carried out using the package *MuMIn* (Barton 2018), and statistical output using *lmerTest* (Kuznetsova et al. 2017). Parameters are discussed based on the magnitude of their coefficients, and their occurrence in the set of top models.

Multicollinearity of variables in the final models was explored using the vif function for the *car* package (Fox and Weisberg 2019), with values < 2.5 in all cases.

Overall microsite-use: To explore whether Rockjumpers were found more often in rock-shade as air temperature increased, I created a GLMM fitting microsite as a function of the potential predictor variable, T_{air}, along with random effects of ID and territory, and a binomial error distribution.

Black bulb temperatures: To assess whether black bulbs recorded different temperatures depending on microsite placement, and to confirm that "rock-shade" microsites were indeed thermally-buffered compared to "sun" microsites, I fitted data to a generalized additive mixed-effects model using *gamm4* (Wood et al. 2017). I additionally included air temperature data (T_{air}) from the weather station for comparison with temperature recoded by the black bulbs. This model explored whether recorded temperature was explained by location (sun, rock-shade, weather station) or time of day, adding territory and date as random effects (N = 10 territories; N = 18 days).

All analyses were performed in the R statistical environment version 3.5.3 (R Core Team 2019) using RStudio version 1.1.463 (RStudio Team 2018). I took $p < 0.05$ as statistically significant.

2.4 RESULTS

2.4.1 MICROSITE-USE

The probability of recording a Rockjumper in rock-shade was higher with increasing T_{air} (coefficient estimate = 0.68, 95 % confidence interval: 0.55–0.81, Z = 10.29, $p < 0.001$), which were cooler than sites in the sun (Figure 2.1; see *Microsite Temperature* results below).

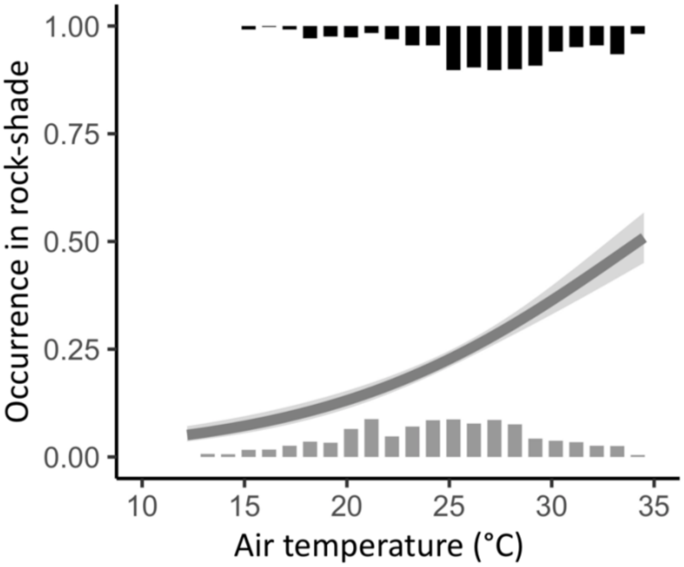

Figure 2.1 Rockjumper location based on microsite (1 = rock-shade, black; 0 = sun, grey) across a range of air temperatures (°C) recorded during behavioural observations on Cape Rockjumpers (*Chaetops frenatus*) during the Austral summer in 2015 and 2016 at Blue Hill Nature Reserve, Western Cape, South Africa. Model fit is GLMM with binomial error structure, logistic regression and shaded 95 % confidence intervals, with histograms indicating number of observations.

2.4.2 ACTIVITY

Rockjumper activity was best explained by microsite-use, with activity recorded more often in the sun compared to the shade (top model coefficient estimate = 4.45, 95 % confidence interval: 3.7–5.3, Z = 11.51, $p < 0.001$); these results were seen across all top competing models (N = 6; Table 2.1). All models also indicated the probability of a bird being recorded as active decreased throughout the day (coefficient estimate = −0.40, 95 % confidence interval −0.67–−0.10, Z = −2.81, $p < 0.01$). Activity was generally lower when breeding (coefficient estimate = −0.64, 95 % confidence interval −1.08–−0.18, Z = −2.80, $p < 0.01$). A decrease in activity at hotter T_{air} was observed, but this response was of low amplitude and not significant (coefficient estimate = −0.23, 95 % confidence interval −0.51–0.04, Z = −1.64, p = 0.100). Interactions were mostly not included in the competing models, and generally not significant if they were.

Table 2.1 Model coefficient summary tables for competing models in top model set (Δ2 AICc; N = 6) explaining activity as a function of the interaction between microsite ("sun" or "rock-shade") and air temperature (T_{air}), the interaction between microsite and breeding stage ("breeding" or "non-breeding"), time of day, and the interaction of microsite and sex ("male" or "female"). Data were collected from Cape Rockjumpers (*Chaetops frenatus*) between January 2015-2016 from Blue Hill Nature Reserve, Western Cape, South Africa. Significant predictors ($p < 0.05$) are in bold.

model	response variable	estimate	std. error	z value	Pr(>|z|)
activity ~ **microsite*breeding** + T_{air} + **time** *DF = 8, logLik = −279.098, AICc = 574.3, model weight = 0.282*	Intercept	1.38	0.36	3.80	**< 0.001**
	breeding	−0.64	0.23	−2.80	**< 0.01**
	sun	4.45	0.39	11.50	**< 0.001**
	T_{air}	−0.23	0.14	−1.64	0.100
	time	−0.40	0.14	−2.81	**< 0.01**
	breeding*sun	0.73	0.38	1.91	0.056
activity ~ **microsite*breeding** + **time** *DF = 7, logLik = −280.468, AICc = 575.0, ΔAICc = 0.72, model weight = 0.197*	Intercept	1.30	0.36	3.63	**< 0.001**
	breeding	−0.63	0.23	−2.81	**< 0.01**
	sun	4.54	0.38	11.86	**< 0.001**
	time	−0.45	0.14	−3.27	**< 0.01**
	breeding*sun	0.69	0.38	1.83	0.068
activity ~ **microsite*breeding** + T_{air} + **time** + microsite*sex *DF = 10, logLik = −277.636, AICc = 575.4, ΔAICc = 1.11, model weight = 0.162*	Intercept	1.36	0.37	3.72	**< 0.001**
	breeding	−0.64	0.23	−2.81	**< 0.001**
	sun	4.85	0.56	8.72	**< 0.001**
	T_{air}	−0.24	0.14	−1.70	0.089
	time	−0.40	0.14	−2.77	**< 0.01**
	female	−0.07	0.15	−0.45	0.652
	breeding*sun	0.78	0.38	2.05	**0.043**
	sun*sex	0.81	0.55	1.48	0.139
activity ~ **microsite** + **breeding** + T_{air} + **time** *DF = 7, logLik = −280.798, AICc = 575.7, ΔAICc = 1.39,, model weight = 0.141*	Intercept	1.36	0.37	3.71	**< 0.001**
	breeding	−0.53	0.22	−2.36	**< 0.05**
	sun	4.65	0.39	11.98	**< 0.001**
	T_{air}	−0.22	0.14	−1.56	0.120
	time	−0.39	0.14	−2.76	**< 0.01**
	Intercept	1.30	0.36	3.55	**< 0.001**

activity ~ **microsite** + **breeding time** *DF = 9, logLik = −282.025, AICc = 576.1, ΔAICc = 1.82, model weight = 0.113*	breeding	−0.53	0.22	−2.40	**0.016**
	sun	4.73	0.37	12.24	**< 0.001**
	time	−0.44	0.14	−3.20	**< 0.01**
activity ~ **microsite*breeding** + microsite*T_{air} + **time** *DF = 9, logLik = −279.085, AICc = 576.3, ΔAICc = 1.99, model weight = 0.104*	Intercept	1.37	0.36	3.78	**< 0.001**
	breeding	−0.64	0.23	−2.80	**< 0.01**
	sun	4.46	0.41	11.09	**< 0.001**
	T_{air}	−0.22	0.15	−1.54	0.125
	time	−0.40	0.14	−2.80	**< 0.01**
	breeding*sun	0.73	0.38	1.92	0.055
	T_{air}*sun	−0.07	0.44	−0.16	0.871

2.4.3 FORAGING

The probability of observing a Rockjumper foraging depended most strongly on microsite use, being lower in rock shade (top model coefficient estimate = 0.37, 95 % confidence interval: 0.24–0.49, Z = 5.65, $p < 0.001$), and with females reducing their foraging to a larger degree than males between microsites (coefficient estimate = 0.21, 95 % confidence interval: 0.00–0.32, Z = 3.67, $p < 0.001$; inset Figure 2.2); these effects were observed in both competing models within 2 AICc of the top model (N = 2; Table 2.2). Breeding birds also had a lower probability of being recorded as foraging (coefficient estimate = −0.24, 95 % confidence interval: −0.40–−0.05, Z = −2.71, $p < 0.01$), with some evidence that this was microsite dependent (coefficient estimate = 0.14, 95 % confidence interval: 0.02–0.25, Z = 2.33, $p = 0.020$). The probability of observing a bird foraging also decreased with increasing air temperature (coefficient estimate = −0.17, 95 % confidence interval: −0.29–−0.05, Z = −2.76, $p < 0.01$), again with some evidence that this was microsite dependent (coefficient estimate = 0.13, 95 % confidence interval: 0.01–0.25, Z = 3.61, $p = 0.037$; Figure 2.2).

Table 2.2 Model coefficient summary tables for competing models in top model set (Δ2 AICc; N = 2) explaining foraging as a function of the interaction between microsite ("sun" or "rock-shade") and air temperature (T_{air}), the interaction between microsite and breeding stage ("breeding" or "non-breeding"), time of day, and the interaction of microsite and sex ("male" or "female"). Data were collected from Cape Rockjumpers (*Chaetops frenatus*) between January 2015-2016 from Blue Hill Nature Reserve, Western Cape, South Africa. Significant predictors ($p < 0.05$) are in bold.

model	response variable	estimate	std. error	z value	Pr(>|z|)
foraging ~ **microsite*breeding** + **microsite*T_{air}** + **microsite*sex** *DF = 10, logLik = -1335.010, AICc = 2690.1, model weight = 0.659*	Intercept	−0.18	0.12	1.53	0.127
	breeding	−0.24	0.09	−2.71	**< 0.01**
	sun	0.37	0.06	5.65	**< 0.001**
	T_{air}	−0.17	0.06	−2.76	**< 0.01**
	female	0.14	0.08	1.83	0.068
	breeding*sun	0.14	0.06	2.33	**0.020**
	T_{air}*sun	0.13	0.06	2.08	**0.037**
	T_{air}*female	0.21	0.06	3.61	**< 0.001**
foraging ~ **microsite*breeding** + **microsite*T_{air}** + time + **microsite*sex** *DF = 11, logLik = −1334.659, AICc = 2691.4, ΔAICc = 1.32, model weight = 0.341*	Intercept	0.17	0.12	1.47	0.143
	breeding	−0.24	0.09	−2.71	**< 0.01**
	sun	0.37	0.06	5.71	**< 0.001**
	T_{air}	−0.18	0.06	−2.87	**< 0.01**
	time	0.04	0.05	0.84	0.402
	female	0.14	0.08	1.77	0.077
	breeding*sun	0.14	0.06	2.32	**0.020**
	T_{air}*sun	0.12	0.06	2.04	**0.041**
	T_{air}*female	0.21	0.06	3.65	**< 0.001**

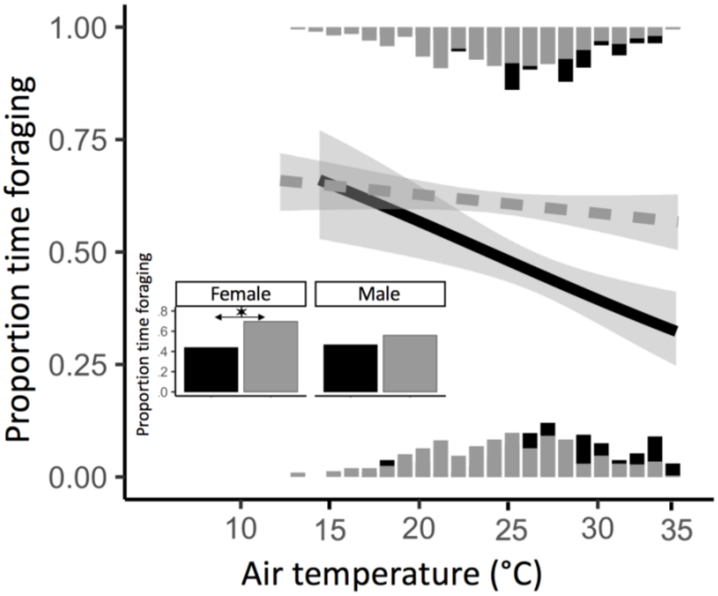

Figure 2.2 Foraging (0 = not foraging, 1 = foraging) based on microsite ("rock-shade" — black, solid line; or "sun" — grey, dashed line) across a range of air temperatures (°C) recorded during behavioural observations on Cape Rockjumpers (*Chaetops frenatus*) during the Austral summer in 2015 and 2016 at Blue Hill Nature Reserve, Western Cape, South Africa. Model fit is GLMM with binomial error structure, logistic regression and shaded 95 % confidence intervals, with histograms indicating number of observations and location ("rock-shade" — black; or "sun" — grey). Inset: bar graphs showing proportion of behavioural scan samples during which free-living Cape Rockjumpers were observed foraging in sun compared to rock-shade ("rock-shade" — black; or "sun" — grey), by male and female. Asterisk denotes significance at $p < 0.05$.

2.4.4 PREENING

The probability of observing a Rockjumper preening was most dependent on breeding and the interaction of microsite and T_{air}, being lower when birds were breeding (top model coefficient estimate = −0.42, 95 % confidence interval: 0.72–0.13, Z = −2.89, $p < 0.01$; inset Figure 2.3), and decreasing at hotter T_{air} in the sun (coefficient estimate = −0.30, 95 % confidence interval: −0.49–−0.10, Z = −2.96, $p < 0.01$; Figure 2.3); these effects were observed in all competing models within 2 AICc of the top model (N = 5; Table 2.3). In most competing models (N = 4) birds were also less often observed preening if female (coefficient estimate = −0.24, 95 % confidence interval: −0.51–0.02, Z = −1.97, $p = 0.048$). A decrease in preening was observed in sun, at hotter T_{air}, and as the day progressed, but these responses were of low amplitude and not significant (sun: coefficient estimate = −0.10, 95 % confidence interval −0.31–0.12, Z = −0.92, $p = 0.360$; T_{air}: coefficient estimate = −0.03, 95 % confidence interval −0.23–0.17, Z = −0.30, $p = 0.765$; time: coefficient estimate = −0.14, 95 % confidence interval −0.29–0.01, Z = −1.80, $p = 0.072$). The interactions of microsite and breeding, and microsite and sex, were included in few competing models (N = 2, N = 1, respectively), but were not significant.

Table 2.3 Model coefficient summary tables for competing models in top model set (Δ2 AICc; N = 5) explaining preening as a function of the interaction between microsite ("sun" or "rock-shade") and air temperature (T_{air}), the interaction between microsite and breeding stage ("breeding" or "non-breeding"), time of day, and the interaction of microsite and sex ("male" or "female"). Data were collected from Cape Rockjumpers (*Chaetops frenatus*) between January 2015-2016 from Blue Hill Nature Reserve, Western Cape, South Africa. Significant predictors ($p < 0.05$) are in bold.

model	response variable	estimate	std. error	z value	Pr(>|z|)
preening ~ **breeding** + **microsite*T_{air}** + **sex** + time *DF = 9, logLik = −651.06, AICc = 1320.2, model weight = 0.308*	Intercept	−2.63	0.24	−10.84	**< 0.001**
	breeding	−0.42	0.15	−2.89	**< 0.01**
	sun	−0.10	0.11	−0.92	0.360
	T_{air}	−0.03	0.10	−0.30	0.765
	time	−0.14	0.08	−1.80	0.072
	female	−0.24	0.12	−1.97	**0.048**
	T_{air}*sun	−0.30	0.10	−2.96	**< 0.01**
preening ~ **breeding** + **microsite*T_{air}** + microsite*sex + time *DF = 10, logLik = −650.14, AICc = 1320.4, ΔAICc = 0.17, model weight = 0.283*	Intercept	−2.62	0.24	−10.80	**< 0.001**
	breeding	−0.41	0.15	−2.84	**< 0.01**
	sun	−0.13	0.11	−1.17	0.243
	T_{air}	−0.03	0.10	−0.30	0.766
	time	−0.15	0.08	−1.89	0.059
	female	−0.18	0.13	−1.41	0.160
	T_{air}*sun	−0.29	0.10	−2.97	**< 0.01**
	female*sun	−0.12	0.09	−1.38	0.168
preening ~ **breeding** + **microsite*T_{air}** + **sex** *DF = 8, logLik = −652.71, AICc = 1321.5, ΔAICc = 1.28, model weight = 0.162*	Intercept	−2.65	0.25	−10.81	**< 0.001**
	breeding	−0.42	0.14	−2.91	**< 0.01**
	sun	−0.08	0.11	−0.78	0.439
	T_{air}	−0.06	0.10	−0.56	0.578
	female	−0.26	0.13	−2.06	**0.040**
	T_{air}*sun	−0.30	0.10	−3.02	**< 0.01**
preening ~ **breeding** + **microsite*T_{air}** + microsite*sex *DF = 9, logLik = −651.91, AICc =1321.9, ΔAICc = 1.70, model weight = 0.132*	Intercept	−2.65	0.25	−10.80	**< 0.001**
	breeding	−0.42	0.15	−2.87	**< 0.01**
	sun	−0.11	0.11	−0.99	0.322
	T_{air}	−0.06	0.10	−0.56	0.574
	female	−0.21	0.14	−1.54	0.123
	T_{air}*sun	−0.30	0.10	−3.03	**< 0.01**
	female*sun	−0.12	0.09	−1.28	0.199
	Intercept	−2.64	0.24	−10.85	**< 0.001**

preening ~ **microsite*T_{air}** + microsite***sex** + time *DF = 10, logLik = −651.03, AICc = 1322.2, ΔAICc = 1.96, model weight = 0.116*	breeding	−0.43	0.15	−2.84	**< 0.01**
	sun	−0.09	0.12	−0.72	0.471
	T_{air}	−0.03	0.10	−0.30	0.762
	time	−0.14	0.08	−1.82	0.069
	female	−0.24	0.12	−1.98	**0.048**
	female*sun	0.03	0.11	0.25	0.799
	T_{air}*sun	−0.29	0.10	−2.94	**< 0.01**

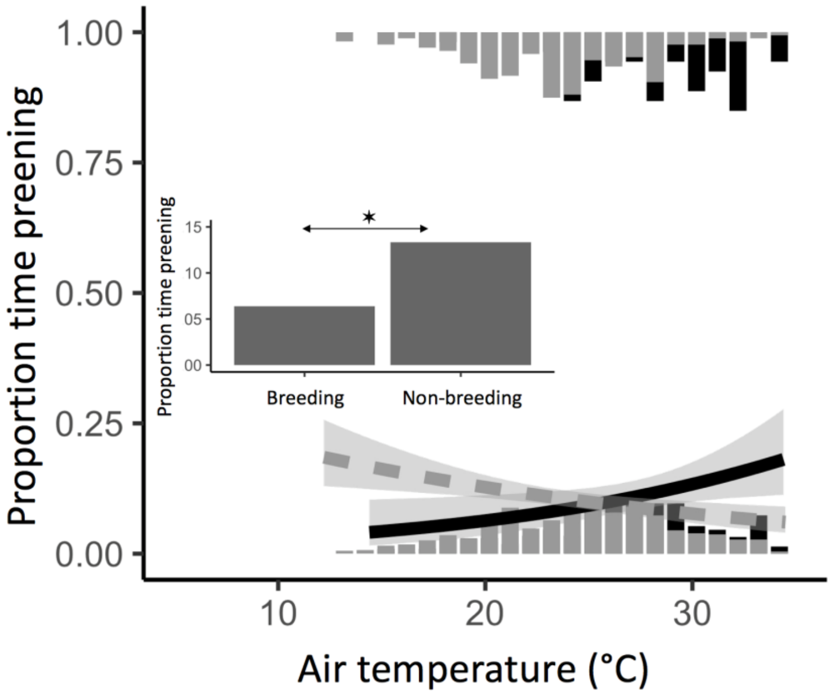

Figure 2.3 Preening (0 = not preening, 1 = preening) based on microsite (“rock-shade” — black, solid line; or “sun” — grey, dashed line) across a range of air temperatures (°C) recorded during behavioural observations on Cape Rockjumpers (*Chaetops frenatus*) during the Austral summer in 2015 and 2016 at Blue Hill Nature Reserve, Western Cape, South Africa. Model fit is GLMM with binomial error structure, logistic regression and shaded 95 % confidence intervals, with histograms indicating number of observations and location (“rock-shade” — black; or “sun” — grey). Inset: bar graphs showing proportion of behavioural observations free-living Cape Rockjumpers spent preening when breeding or non-breeding. Asterisk denotes significance at $p < 0.05$.

2.4.5 PANTING

The probability of observing a Rockjumper panting was most dependent on breeding and the interaction of temperature and microsite, being higher when birds were breeding (top model coefficient estimate = 1.14, 95 % confidence interval: 0.51–1.86, Z = 3.35, $p < 0.001$; inset Figure 2.4), increasing at hotter T_{air} (coefficient estimate = 0.82, 95 % confidence interval: 0.18–1.62, Z = 2.28, $p = 0.023$), and increasing more at hotter T_{air} when in the sun (coefficient estimate = 0.88, 95 % confidence interval: 0.19–1.51, Z = 2.64, $p < 0.01$; Figure 2.4); these results were included in both competing models (N = 2; Table 2.4). Panting depended on time of day in one competing model, where birds were observed panting more often as the day progressed, but the effect was of low amplitude and not significant.

Table 2.4 Model coefficient summary tables for competing models in top model set (Δ2 AICc; N = 2) explaining panting as a function of the interaction between microsite (“sun” or “rock-shade”) and air temperature (T_{air}), the interaction between microsite and breeding stage (“breeding” or “non-breeding”), time of day, and the interaction of microsite and sex (“male” or “female”). Data were collected from Cape Rockjumpers (*Chaetops frenatus*) between January 2015-2016 from Blue Hill Nature Reserve, Western Cape, South Africa. Significant predictors ($p < 0.05$) are in bold.

model	response variable	estimate	std. error	z value	Pr(>|z|)
panting ~ **breeding** + **microsite*T_{air}** *DF = 7, logLik = −166.3664, AICc = 346.8, model weight = 0.717*	Intercept	−4.60	0.75	−6.16	**< 0.001**
	breeding	1.14	0.34	3.35	**< 0.001**
	sun	0.21	0.27	0.76	0.448
	T_{air}	0.82	0.36	2.28	**0.023**
	T_{air}*sun	0.88	0.33	2.64	**< 0.01**
panting ~ **breeding** + **microsite*T_{air}** + time *DF = 8, logLik = −166.317, AICc = 348.8, ΔAICc = 1.86, model weight = 0.283*	Intercept	−4.58	0.74	−6.32	**< 0.001**
	breeding	1.13	0.34	3.31	**< 0.001**
	sun	0.21	0.27	0.78	0.438
	T_{air}	0.78	0.38	2.08	**0.038**
	T_{air}*sun	0.87	0.33	2.63	**< 0.01**
	time	0.07	0.23	0.32	0.753

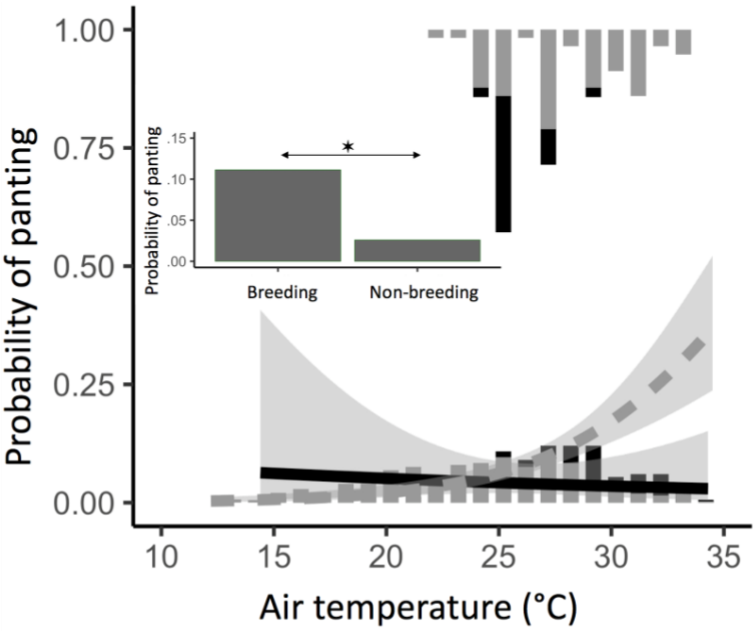

Figure 2.4 Panting (0 = not panting, 1 = panting) based on microsite ("rock-shade" — black, solid line; or "sun" — grey, dashed line) across a range of air temperatures (°C) recorded during behavioural observations on Cape Rockjumpers (*Chaetops frenatus*) during the Austral summer in 2015 and 2016 at Blue Hill Nature Reserve, Western Cape, South Africa . Model fit is GLMM with binomial error structure, logistic regression and shaded 95 % confidence intervals, with histograms indicating number of observations and location ("rock-shade" — black; or "sun" — grey). Inset: bar graph showing proportion of behavioural observations free-living Cape Rockjumpers spent panting when breeding or non-breeding. Asterisks denote significance at $p < 0.05$.

2.4.6 MICROSITE TEMPERATURE

Recorded temperatures (°C) were significantly affected by location, with black bulbs in sun recording temperatures on average 11.75 ± 1.6 °C higher than those recorded by the weather station, and 13.4 °C higher than black bulbs in rock-shade (coefficient estimate = 13.44 ± 0.15, 95 % confidence interval: 13.13–13.74, Z = 86.78, $p < 0.001$), with recorded temperature at all locations increasing throughout the day (coefficient estimate = 1.78 ± 0.05, 95 % confidence interval: 1.68–1.87, Z = 37.76, $p < 0.001$; Figure 2.5).

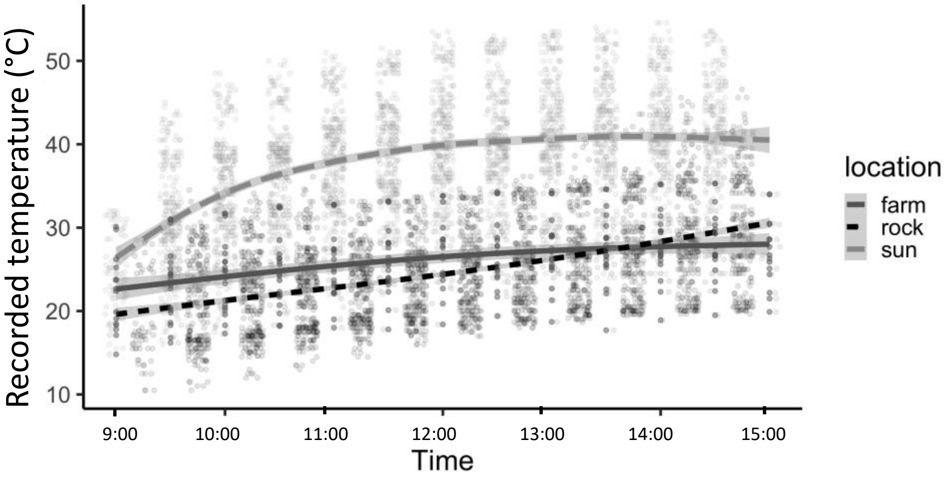

Figure 2.5 Temperature (°C) recorded at Blue Hill Nature Reserve by the weather station (“farm” — medium grey, solid line) and by black bulbs placed in full sun (“sun” — light grey, long dashed line) or full shade (“rock” — black, short dashed line) from 9:00 to 15:00 SAST (N = 18 days) November 2015 to January 2016 at Blue Hill Nature Reserve, Western Cape, South Africa. Data points have been rounded for clearer visualisation (jitter set to α = 0.1), model fit is GAM with shaded 95 % confidence intervals.

2.5 DISCUSSION

Overall, Rockjumpers were observed increasingly more often in rock-shade as T_{air} increased, providing evidence of the potential for behavioural buffering (*sensu* Huey et al. 2012) as a mechanism for dealing with high T_{air} in this alpine species. Both T_{air} and microsite appeared in all top model sets for the behaviours I investigated (panting, preening, foraging, and active/inactive), although T_{air} significantly predicted variation in only two behaviours (foraging and panting). Hotter T_{air} was correlated with reductions in activity and foraging, with the effect of T_{air} on preening and panting possibly mitigated by microsite-use. Preening decreased, and panting increased, only in sun-exposed microsites, suggesting that seeking rock-shade might buffer birds from impacts of temperature on these behaviours. For activity and foraging, I found birds decreased levels of both while they were in rock-shade. This suggests that while any potential direct impact of temperature is mediated by the change in microsite-use, seeking shade might involve a trade-off against foraging or maintaining activity levels. Long-term negative consequences of increasing T_{air} could therefore be mediated by such trade-offs if these threaten the ability of birds to maintain energy and/or water balance. Breeding stage was also a significant predictor variable for all behaviours, and the impact of breeding on behaviour was significantly modified by microsite-use for foraging, preening, and panting. The only behaviour where I found a strong sex-based effect was the interaction of sex and microsite for foraging: females foraged more than males and this extra foraging was done in the sun. Males also preened more than females. It thus seems that overall birds may be able to mitigate the direct effects of high T_{air} through behavioural buffering — that is, by making use of cooler microsites.

2.5.1 INTERACTING EFFECTS OF TEMPERATURE AND MICROSITE USE

My main purpose in placing black bulbs was to examine whether significant temperature variation existed between areas of full sun and those in rock-shade; my black bulb data indicate shaded microsites available within Rockjumper habitat are cooler than areas of direct sunlight (Figure 2.5). Although Rockjumpers made clear use of cooler microsites as T_{air} increased, they continued to maintain foraging in sun while decreasing foraging in rock-shade. I propose four explanations for this observation: (1) food availability in sun is higher than in rock-shade, meaning birds were forced to maintain foraging in sun at expense of thermoregulation, alternatively (2) food availability in sun is higher than in rock-shade, and so birds are able to obtain water from their diet which would offset water loss from panting, (3) birds sought areas with reduced thermoregulatory demands at the expense of overall energy intake when making use of cooler microsites (a foraging-thermoregulation trade-off), or (4) food availability does not differ between sun and rock-shade, but birds were more often observed foraging in sun simply because, on average, a greater area of their territories are in sun than rock-shade. Unfortunately, in this study I was unable to determine food availability per microsite, and so the potential implications of foraging in sun vs. rock-shade at high T_{air} remain unclear.

Non-breeding Rockjumpers were significantly more likely to be observed preening than breeding birds. As in Killdeer *Charadrius vociferous,* where preening was most likely to occur pre-laying (Brunton 1988), preening just before breeding may help Rockjumpers attain or retain mates for the upcoming breeding season by resulting in enhanced plumage (Zampiga et al. 2004, Leitão and Mota 2015). Use of rock-shade also allowed birds to maintain levels of preening even at high T_{air}, and appeared to reduce their evaporative cooling requirements (i.e. panting; see below). Rockjumpers began panting at T_{air} as low as 20.8 °C when in the sun, which is very low compared to studies on other Southern African passerines, in which birds generally begin panting at temperatures above 25 °C (du Plessis et al. 2012, Smit et al. 2013, Pattinson and Smit 2017). However, the previous studies were all on arid zone birds, and panting may occur at lower temperatures for birds in cooler environments — panting has been demonstrated at similarly low T_{air} in other alpine (albeit non-passerine) birds such as White-tailed Ptarmigan (Johnson 1968). Rockjumpers were rarely recorded panting when in rock-shade, even on hot days (Figure 2.4).

Whereas the probability of an adult panting at any given T_{air} (up to 35.3 °C) was never greater than 33.3 % during my study, concurrently observed juvenile Rockjumpers panted at all instances when T_{air} was above 28.1 °C (N = 4 individuals; unpublished data). Recent studies on physiological responses to heat in Rockjumpers found that despite adults showing no obvious physiological stress at high temperatures (Oswald et al. 2018c), juveniles may face higher overall water and energy demands than adults due to increased rates of both metabolism and evaporative water loss (Oswald et al. 2018b). Additionally, breeding Rockjumpers were significantly more likely to pant than non-breeding birds, even more so in sun than rock-shade, possibly due to changes in metabolism or increased intensity of activity when breeding: breeding can carry high energetic demands resulting in increased metabolic rates and thus increased requirement for evaporative cooling (Weathers and Sullivan 1993, Zhang et al. 2015).

Retreating to shaded microsites is not only useful for thermoregulation, but may also have the advantage of helping with predator avoidance, especially as being under a rock can provide sight-protection from both aerial and ground predators (Visinoni et al. 2015), to which Rockjumpers are vulnerable (Oswald 2016a). However, one would expect breeding birds to be increasingly aware of predation risk as offspring development is directly dependent on adult survival, whereas I in fact found breeding Rockjumpers were more often active in sun.

2.5.2 CONCLUSIONS

My results show that Rockjumpers use cooler microsites at hotter air temperatures, resulting in less need to use evaporative water loss, and providing further evidence that microsite-use may allow endotherms to conserve water and energy at high temperatures (Williams et al. 1995, Williams and Tieleman 2005, Xie et al. 2017). While I was unable to directly link the observed behavioural changes to changes in fitness, other studies showing behavioural changes at high air temperatures document downstream costs of these in terms of reduced provisioning behaviour, chick growth, and adult mass maintenance (du Plessis et al. 2012, Cunningham et al. 2013b). As birds with restricted alpine breeding distributions are likely to be more negatively impacted by climate change than other species (Scridel et al. 2018), the impact of behavioural thermoregulatory responses on overall fitness in range-restricted species with shrinking habitats remains an important avenue for further study.

CHAPTER 3: REDUCED CONDITION FOR OLDER NESTLINGS IS ASSOCIATED WITH INCREASING MAXIMUM TEMPERATURE RESULTS IN A RANGE-RESTRICTED ALPINE BIRD.

3.1 SUMMARY

A number of studies show negative effects of increased temperatures on reproductive success, suggesting a mechanism by which climate change may impact species persistence. For passerines with dependent young, high temperatures can result in reduced parental nest attendance and reduced nestling condition, resulting in lowered fledging success and population recruitment. I examined nest attendance and nestling condition in a South African alpine endemic, the Cape Rockjumper *Chaetops frenatus*, whose population declines correlate to warming habitat. I aimed to determine how reproductive biology was affected by high air temperatures. I placed cameras at 19 nests on 40 days at three nestling age ranges (≤7 days old; 8–12 days old; ≥13 days old), weighing nestlings before and after each film day (N = 65 nestlings, 36 days; from 15/19 nests, 4 nests predated during filming). Full footage was collected from 25 days at 13 nests. Daily maximum temperature correlated to decreasing percent daily body mass change for older nestlings, with no change in provisioning associated with any predictor variable, suggesting older nestling energy demands are not being met on hotter days, possibly as adults are finding smaller prey or nestling demands are elevated by resource requirements for thermoregulation. While any factor resulting in decreased mass gain in nestlings is detrimental toward fledge potential, long-term implications of my results remain unclear, as the only cause of nest failure during this study was directly due to predation.

3.2 INTRODUCTION

Complete life history data can be used to identify demographic responses of individuals and populations to environmental change (McCarty 2001, Walther et al. 2002, Parmesan 2006, Keith et al. 2008, Ozgul et al. 2010, Wilson and Martin 2012), with use of chosen sentinel species allowing for indication of community-level responses (Woolbright et al. 2014, Siddig et al. 2016). Climatic variability can affect avian species' demography by altering reproductive phenology, output, and success (Bradley et al. 1997, Steenhof et al. 1999, Bolger et al. 2005, Borgman and Wolf 2016, Conrey et al. 2016, Martin et al. 2017). In particular, hotter air temperatures ("T_{air}") have resulted in decreased abundance for multiple bird species (Jiguet et al. 2006, Iknayan and Beissinger 2018). Additionally, stochastic weather events (e.g. heat waves, drought) have often resulted in lowered reproductive success (see review: Moreno and Møller 2011), and the chronic sublethal costs of increasing temperatures and heat exposure may lead to further declines in avian populations (Conradie et al. 2019).

Passerine birds produce altricial young (i.e. blind, featherless, and helpless when first hatched), which require parents provide a large amount of care to raise young successfully to independence. In arid-zone passerines, hotter T_{air} has been correlated with decreased provisioning rates to nestlings (Luck 2001, Cunningham et al. 2013b). Such decreases can result in reduced nestling condition (i.e. body mass; "M_b"), leading to reduced fledging success (Cunningham et al. 2013b), and ultimately reduced survival, recruitment, and lifetime fitness (Magrath 1991, Thompson and Flux 1991, Greno et al. 2008, Schwagmeyer and Mock 2008). As avian reproductive success is directly related to the ability to successfully fledge young, increased rates of nest failure under conditions of high T_{air} is a key mechanism by which climate warming may be responsible for decreasing numbers in many avian species

Fledging success in birds not only requires parents adequately provision nestlings, but also that nests be maintained within a consistent temperature range, with incubation temperature directly related to length of incubation and the nestling period (Mueller et al. 2019). This is especially important for altricial birds where nestlings' thermoregulatory abilities are not initially well-developed (Marsh and Wickler 1982, Starck and Ricklefs 1998). While "brooding" to provide warmth is common in birds, some birds have also been recorded "shading" their nests at hotter T_{air} (i.e. maintaining the body above the clutch and/or holding wings askew, to provide protection from solar heat; Clauser and McRae 2017). However, in some instances adult birds reduce their overall time at the nest at hotter T_{air} to reduce their own heat load, potentially with negative consequences for nestling survival (Oswald et al. 2008). Hotter T_{air} may therefore result in a reduction in nestling care at the time when they require it most, with possible negative outcomes for overall breeding success.

I examined reproductive biology in the Cape Rockjumper *Chaetops frenatus* (hereafter "Rockjumper"), an alpine endemic of south-west South Africa. Rockjumpers are facultative cooperative breeders, where territories are maintained by a single breeding pair and up to two additional "helpers" (Holmes et al. 2002). Cooperative breeding can provide benefits to individual adults, as more adults can buffer the effects of environmental stressors through sharing the workload (Ridley and Raihani 2007, Meade et al. 2010, Johnstone 2011, Wiley and Ridley 2016). Rockjumpers are experiencing population declines strongly correlated to habitat warming (Milne et al. 2015), and mountain specialists are most vulnerable to climate due to disproportionate habitat loss and unique ecology within a narrow thermal range (Midgley et al. 2002, Parmesan 2006, Sinervo et al. 2010, Dirnböck et al. 2011, Reif and Flousek 2012, Mahon et al. 2016, Scridel et al. 2018).

My aim was to examine the reproductive biology in a facultative-cooperative breeding bird with limited habitat range and apparent sensitivity to warming weather. I recorded video footage from Rockjumper nests over two breeding seasons to determine if increases in daily maximum temperature affected Rockjumper fledging success. I expected to find daily maximum temperature (1) positively correlated with adult heat dissipation, (2) negatively correlated with Rockjumper nest attendance (time in nest, and provisioning rates), and therefore (3) resulting in reduced nestling daily change in M_b.

3.3 METHODS

3.3.1 STUDY SITE AND ENVIRONMENTAL DATA COLLECTION

This study took place at Blue Hill Nature Reserve ("BHNR"; 33.59 S; 23.41 E; 1000–1530 metres above sea level) in the Western Cape Province, South Africa (see Chapter 1 for further details on study site and species); BHNR consists primarily of Mountain Fynbos, with individual territories in this study consisting of two-three adult Rockjumpers. Data were collected over two breeding seasons (Sept-Nov 2017 and Aug-Dec 2018).

Air temperature (°C) and precipitation (mm) were recorded every 30 min by an on-site weather station at BHNR (Vantage Vue, Davis Instruments Corp., California USA). Daily average T_{air}, average maximum T_{air} and average minimum T_{air} throughout the dates of this study were 13.79 ± 4.64 °C, 21.50 ± 6.53 °C, 6.58 ± 3.57 °C in 2017, and 14.66 ± 5.56 °C, 22.60 ± 7.31 °C, 7.09 ± 4.37 °C in 2018, respectively. Absolute maximum and minimum daily T_{air} were 36.6 °C and −2.1 °C, while total precipitation throughout the dates of this study was 109.8 mm in 2017 and 377.2 mm in 2018. Following Cunningham et al. (2013b), I used maximum daily temperature ("daily T_{max}") as my standard measure of temperature. Extreme temperatures were found to be more useful in describing the thermal environment (Camacho et al. 2015), and daily T_{max} have been used to identify biologically meaningful thresholds for predicting thermal effects on natural population dynamics (Cunningham et al. 2013a, Ma et al. 2015).

3.3.2 STUDY SPECIES AND MONITORING

Nests were located by performing weekly checks at known territories for signs of breeding (e.g. nest material in bill, food in bill, localized area fidelity). Territory designations were based around identifying colour rings on adult birds, caught and ringed with aluminum rings (SAFRING, South Africa), and given a unique colour combination as part of an earlier study (see Chapter 2 for details). After nests were located, they were checked every four to five days to obtain an estimate of hatch date (hatch day = day 1). While more frequent nest visits would have given a clearer indication of lay and hatch days, the distance between nests was prohibitive of more frequent visits while also searching for nests in additional territories.

3.3.3 FILMING SETUP

I filmed individual nests from ~9:00–17:00 SAST (actual start times: 8:35–9:13 SAST; actual finish times: 16:25–17:12 SAST), three days per nest where possible, once from each of three different age ranges (range one: ≤7 days old; range two: 8–12 days old; range three: ≥13 days old). Initially in 2017 nests were recorded with a Panasonic XS-100 video camera (N = 4 cameras), but large amounts of equipment failure (see below) led me to switch in November 2017 to Panasonic HC-V385 (N = 3; Panasonic Corporation, Osaka, Japan). Video cameras were attached via USB to a 12V 7AH rechargeable battery (Securi-Prod, Regal Security Distributors, South Africa) with a Battery Buddy (Lumeno LED, South Africa), to extend recording for ≥8 consecutive hours. Cameras and batteries were wrapped in camouflage duct tape (Sellotape Industrial, Dunstable, UK). The camera setups were placed ~50 cms from nests. A cardboard shade was added to setups on days >25 °C made from strips of cardboard (~20 x 40 cms) wrapped in camouflage duct tape and placed on top of the camera, attached with T Series MIL Spec Ties (HellermannTyton, South Africa). While ~50 cms may seem close enough to alter adult behaviour, personal observation showed birds return to regular feeding within 20 minutes of placing the cameras.

In total I filmed 19 nests on 40 days, collecting full-day film data for 13 nests on 25 days ("full-day"; Table 3.1). Four nests were predated during filming, and I experienced equipment failure on an additional 11 film days ("part-day"; Table 3.1). Nestling M_b data was collected from all full-day nests and from part-day nests regardless of equipment failure (N = 15 nests, N = 36 days), including ΔM_b data on all three age ranges from 9 nestlings at five nests. Direct observations in 2017 showed adults returned to the nest within 20 min of filming start time.

Table 3.1 Sample sizes for nests with only part-day (~9:00–11:00 SAST) and full-day (~9:00–17:00) video data collected from free-living Cape Rockjumper *Chaetops frenatus* nests over two breeding seasons (2017 and 2018). Data were collected from three separate nestlings age ranges (range one: ≤7 days old, "R1"; range two: 8–12 days old, "R2"; range three: ≥13 days old, "R3") between October-November 2017 and August-December 2018 from Blue Hill Nature Reserve, Western Cape, South Africa. Part-day data numbers in parentheses indicate the number of nests where incomplete filming was due to either depredation (dagger) or equipment failure (asterisk). Change in M_b data were collected from all nestlings regardless of equipment failure, barring those depredated during filming.

year	part-day nests			full-day nests				ΔM_b		
	R1	R2	R3	R1	R2	R3	all ranges	number of nestlings	total measures	number of nests
2017	3(2*1†)	4(3*1†)	2(3*1†)	2	1	1	1	8	16	4
2018	0	2(1*1†)	2*	11	6	4	4	22	49	11

3.3.4 NESTLING MASS CHANGE

On film days, I weighed nestlings on a portable electronic scale (AG52-500, Ecotone, Poland) before and after filming at ~9:00 and ~17:00 SAST, to determine percent daily change in M_b (“ΔM_b"). Diurnal ΔM_b was standardised to an 8 hr (480 min) time period, calculated using a modified formula (equation 3.1) from du Plessis et al. (2012):

(Eqn 3.1)

$$\% \Delta M_b = 100 ((M_{b2} - M_{b1})/M_{b1}) / ((t_2 - t_1)/480)$$

where t_2-t_1 is the number of min between morning ($t_1 \cong$ 9:00) and evening ($t_2 \cong$ 17:00), M_{b1} is initial morning M_b, and M_{b2} is evening M_b. At each nest, in 2017 one nestling in each pair was given an identifying black colour ring. When initial video showed parents pecking at identifying black colour-rings placed on one of the two nestlings, I instead clipped a left toenail from the second individual in two-nestling nests. In 2018 when I found nests with three eggs/nestlings, if all three survived until filming (see below), I clipped the left toenail from the second nestling, and the right toenail from the third nestling. Clipped toenails lasted throughout the nestling period until the final evening measurements were taken and nestlings were given an aluminum ring and a unique set of three identifying colour rings. Weighing and ringing nestlings took <2 min after which nestlings were immediately returned to nests.

3.3.5 VIDEO DATA EXTRACTION

In total I analyzed 279 hr of video. I extracted data on each nest visit by an adult bird including: adult heat dissipation behavior (i.e. panting, bill held open ≥2 sec: “0” = absence, “1” = presence), total time in nest ("nest-time"), and occurrence of provisioning (i.e. adult placing food in nestlings bill: “0” = absence, “1” = presence). While initially I recorded time spent brooding or shading, in over 30 % of cases I could not determine the difference between the two, and so this analysis was removed — instead, I examined total adult attendance in the nest ("nest-time") as a proxy for these two behaviours and a general overview of total parental care.

Additional data collected included the territory designation, group size (“adults”), brood size (“nestlings”), length of filming ("total video length"), and age range. Data for both daily T_{max}, and total precipitation for two weeks before filming ("P_{2weeks}"), were calculated for each film day.

3.3.6 ANALYSES

All analyses were performed in the R statistical environment version 3.5.3 (R Core Team 2019) using RStudio version 1.1.463 (RStudio Team 2018). Packages used included *lme4* (Bates et al. 2015), *multcomp* (Hothorn et al. 2013), *glmmADMB* (Fournier et al. 2012), *MuMIn* (Barton 2018), *blme* (Chung et al. 2013), and *segmented* (Muggeo 2017).

For dissipation, provisioning, and thermoregulation I used the full-day dataset (nests with full days of video-recording, N = 25 days at 13 nests; Table 3.1), while for daily Δ M_b I used data from all nests where I collected start and end M_b (N = 65 nestlings from 32 days; Table 3.1). As biological response variables often have non-linear relationships with T_{air} I first ran broken-stick analyses on linear models (LMs) for all response variables with daily T_{max} as predictor, to check for significant inflection points — no significant inflections were identified for any response variable.

To compare the global model with all possible nested models (see below) I used AICc (Akaike information criterion adjusted for small sample size: dissipation and nest-time) or BICc (Bayesian information criterion adjusted for small sample size: provisioning, daily Δ M_b). I discuss all competing models within 2 AICc/BICc of the top model. Parameters are discussed based on the magnitude of their coefficients, and their occurrence in the set of top models. I took $p < 0.05$ as statistically significant in all instances.

Heat dissipation: Due to low hourly occurrence of heat dissipation (N = 3 days with >1 instance per hour), I transformed dissipation into a binomial of daily presence/absence. I fitted heat dissipation to a Generalized Linear Mixed-Effects Model (GLMM) adjusted for zero-inflated models (GLMMADMB; due to issues of singular fit), with potential predictor variables of daily T_{max}, P_{2weeks}, adults, nestlings, and age range, with territory as random effect and a binomial distribution.

Nest-Time: I first used an arcsine transformation to convert proportion of nest-time following Knief and Forstmeier (2018). To explore nest-time, I fitted a Linear Mixed-Effects Model (LMER) with potential predictor variables of daily T_{max}, P_{2weeks}, adults, nestlings, and age range, with territory as random effect and a gaussian distribution.

Provisioning: I first calculated the number of visits with provisioning as an hourly rate (i.e. provisions per hour). My initial LMER for provisioning resulted in issues of singular fit, so I refitted models using a Bayesian LMER (BLMER) as BLMERs resolve issues of singular fit by applying weak priors to fixed parameters (see Quiñones and Wcislo 2015, Franks et al. 2018). To explore provisioning, I fitted a BLMER with potential predictor variables of daily T_{max}, P_{2weeks}, adults, nestlings, and age range with territory as random effect and a gaussian distribution (as data were normally distributed), including an offset for total video length.

Nestling Change in M_b: To explore daily Δ M_b, I fitted a BLMER with potential predictor variables of daily T_{max}, P_{2weeks}, adults, nestlings, and age range with territory as random effect and a gaussian distribution. Further, as initial visualization led me to suspect non-linear relationships between individual age ranges and daily T_{max}, I also created individual models for each age range, fitting each BLMER to potential predictor variables of daily T_{max}, P_{2weeks}, adults, and nestlings, with territory as random effect.

3.4 RESULTS

3.4.1 ADULT HEAT DISSIPATION

Adult heat dissipation was best explained by daily T_{max}, with heat dissipation seen more often on hotter days (top model coefficient estimate = 0.25, 95 % confidence interval −0.05–0.54, Z = 1.63, $p = 0.100$; Figure 3.1); these results were seen across all three of the top competing models, but were only significant in my second top competing model, which included only the predictor variable daily T_{max} (Table 3.2). In two competing models heat dissipation decreased with increasing recent precipitation, and in one competing model heat dissipation was more likely at nests with more nestlings, but these responses were of low amplitude and not significant (Table 3.2). *Post hoc* analysis found no significant interaction between daily T_{max} and P_{2weeks} on adult heat dissipation (coefficient estimate = 0.06, SE = 0.04, $Z_{1,25} = 1.37$, $p = 0.172$).

Table 3.2 Model coefficient summary table for top models (Δ2 AICc; N = 3) explaining adult heat dissipation as a function of maximum daily temperature ("T_{max}"), number of nestlings, total precipitation 2 weeks prior to filming ("P_{2weeks}"), number of adults in the territory ("adults"), and age of nestlings (range one: ≤7 days old; range two: 8–12 days old; range three: ≥13 days old). Data were collected from Cape Rockjumpers (*Chaetops frenatus*) between October-November 2017 and August-December 2018 from Blue Hill Nature Reserve, Western Cape, South Africa. Significant predictor variables and results ($p < 0.05$) are in bold.

model	response variable	estimate	std. error	z-value	Pr(>|z|)
dissipation ~ T_{max} + P_{2weeks} *DF = 3, logLik = −12.543, AICc = 32.2, model weight = 0.441*	Intercept	−4.20	2.79	−1.50	0.130
	T_{max}	0.25	0.15	1.63	0.100
	P_{2weeks}	−0.05	0.05	1.08	0.280
dissipation ~ **T_{max}** *DF = 5, logLik = −9.840, AICc = 32.8, ΔAICc = 0.61, model weight = 0.325*	Intercept	−4.45	1.92	−2.32	**0.020**
	T_{max}	0.21	0.084	2.49	**0.013**
dissipation ~ **T_{max}** + nestlings + precipitation *DF = 6, logLik = −8.418, AICc = 33.5, ΔAICc = 1.27, model weight = 0.233*	Intercept	−8.44	6.56	−1.29	0.200
	T_{max}	0.30	0.21	1.43	0.150
	nestlings	1.67	1.74	0.95	0.340
	P_{2weeks}	−0.06	0.05	−1.18	0.240

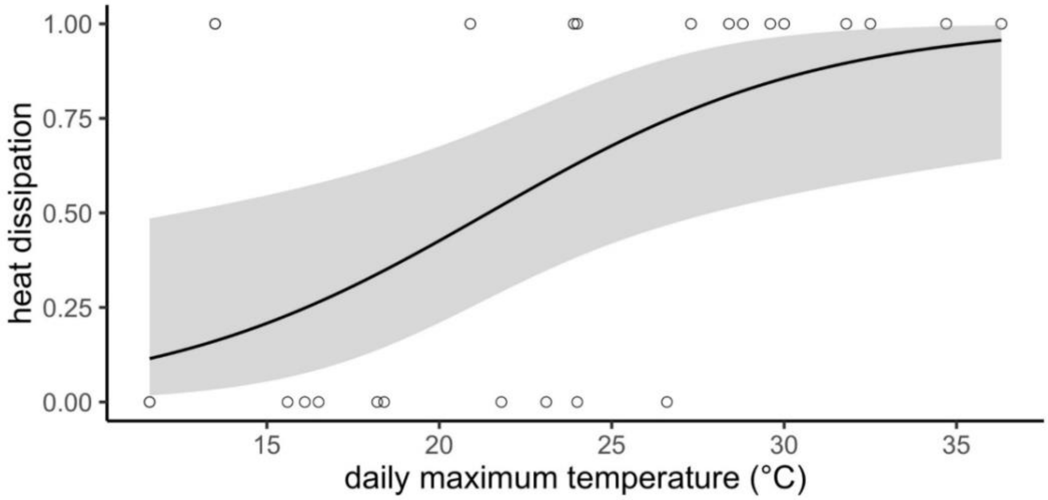

Figure 3.1 Probability of daily occurrence for adult heat dissipation across daily maximum temperature (°C) observed from 9:00–15:00 SAST from 25 days of observations at 13 nests of free-living Cape Rockjumpers *Chaetops frenatus* at Blue Hill Nature Reserve, South Africa, over two breeding seasons (2017-2018). Model fit is GLMM with binomial error structure, logistic regression and shaded 95 % confidence intervals.

3.4.2 NEST-TIME

Total time adults spent in the nest was best explained by the age of nestlings (coefficient estimate = −0.23, 95 % confidence interval = −0.33–−0.14, t = −4.97, $p < 0.001$); this result was the only competing model in my top model set (Table 3.3). Tukey tests found adults spent more time in the nest when nestlings were youngest compared to both older ages (range 2–range 1: $Z_{1,20} = -4.82$, $p < 0.001$; range 3–range 1: $Z_{1,18} = -4.96$, $p < 0.001$; range 3–range 2: $Z_{1,12} = -1.29$, $p = 0.397$; Figure 3.2).

Table 3.3 Model coefficient summary table for top models (Δ2 AICc; N = 1) explaining time adults spent in the nest ("nest-time") as a function of maximum daily temperature ("T_{max}"), number of nestlings, total precipitation 2 weeks prior to filming ("P_{2weeks}"), number of adults in the territory ("adults"), and age of nestlings (range one: ≤7 days old; range two: 8–12 days old; range three: ≥13 days old). Data were collected from Cape Rockjumpers (*Chaetops frenatus*) between October-November 2017 and August-December 2018 from Blue Hill Nature Reserve, Western Cape, South Africa. Significant predictor variable and result ($p < 0.05$) in bold.

model	response variable	estimate	std. error	t-value	Pr(>|t|)
nest-time ~ **age range**	Intercept	0.86	0.10	8.61	**< 0.001**
DF = 4, logLik = −0.385, AICc = 10.8, model weight = 1.000	age range	−0.23	0.05	-4.97	**< 0.001**

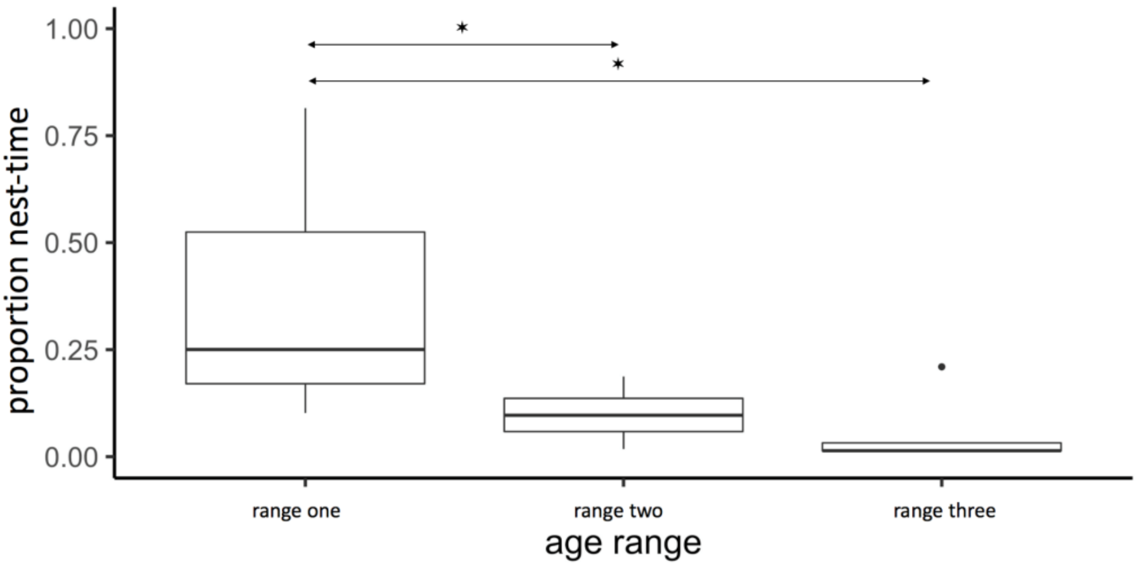

Figure 3.2 Proportion of time adults spent in the nest ("proportion nest-time") at different nestling age ranges (range one: ≤7 days old; range two: 8–12 days old; range three: ≥13 days old) observed from 9:00-15:00 SAST from 25 days of observations at 13 nests of free-living Cape Rockjumpers *Chaetops frenatus* at Blue Hill Nature Reserve, South Africa, over two breeding seasons (2017–2018). Asterisks denote significance at $p < 0.05$.

3.4.3 PROVISIONING

Provisioning rate was not well explained by any predictor variable, as my top competing model included only the offset total time nests were filmed (top model coefficient estimate = −1.48, 95 % confidence interval = −2.00–−0.96, t = −4.822); this result was seen in two of my four top competing models (Table 3.4). In two competing models nests with more nestlings had a greater rate of provisioning (Table 3.4) — while this result was of low amplitude and not significant, Tukey tests found adults provisioned nests with 3 nestlings more than those with one nestling (2 nestlings–1 nestling: $Z_{1,20} = 1.49$, $p = 0.199$; 3 nestlings–1 nestlings: $Z_{1,10} = 2.41$, $p = 0.041$; 3 nestlings–2 nestlings: $Z_{1,20} = 1.35$, $p = 0.365$).

Table 3.4 Model coefficient summary table for top models ($\Delta 2$ BICc; N = 4) explaining provisioning rate as a function of maximum daily temperature ("T_{max}"), number of nestlings, total precipitation 2 weeks prior to filming ("P_{2weeks}"), number of adults in the territory ("adults"), and age of nestlings (range one: ≤7 days old; range two: 8–12 days old; range three: ≥13 days old) with offset log total video time ("video length"). Data were collected from Cape Rockjumpers (*Chaetops frenatus*) between October-November 2017 and August-December 2018 from Blue Hill Nature Reserve, Western Cape, South Africa.

model	response variable	estimate	std. error	t-value	Pr(>Chisq)*
provisioning ~ offset video length *DF = 3, logLike = −42.89, BIC = 95.4, model weight = 0.291*	Intercept	−1.48	0.31	−4.822	
provisioning ~ *DF = 3, logLike = −42.99, BIC = 95.6, ΔBIC = 0.21, model weight = 0.263*	Intercept	4.70	0.31	15.19	
provisioning ~ nestlings + video length *DF = 5, logLike = −39.84, BIC = 95.8, ΔBIC = 0.34, model weight = 0.245*	Intercept	−3.06	0.89	−3.43	
	nestlings	0.79	0.42	1.88	0.061*
provisioning ~ nestlings *DF = 5, logLike = −40.38, BIC = 96.2, ΔBIC = 0.74, model weight = 0.201*	Intercept	3.18	0.90	3.54	
	nestlings	0.76	0.42	1.80	0.072*

* significance for models including "nestlings" derived from Anova.

3.4.4 NESTLING PERCENT DAILY CHANGE IN MASS

Nestling percent daily Δ M_b was best explained by the age of nestlings (top model: $\chi_2 = 7.69$, $p = 0.021$); these results were seen across both of the top competing models (Table 3.5). Tukey tests found the youngest nestlings had higher percent daily Δ M_b compared to both older ages (range 2–range 1: $Z_{1,20} = -2.52$, $p = 0.031$; range 3–range 1: $Z_{1,18} = -2.66$, $p = 0.021$; range 3–range 2: $Z_{1,12} = -0.43$, $p = 0.901$; Figure 3.3). Percent daily Δ M_b was also explained by the number of nestlings in both competing models, but this result was of lower amplitude and not significant (Table 3.5). While number of adults was present in my top competing model, this factor was not significant (Table 3.5).

Table 3.5 Model coefficient summary table for top models (Δ2 BICc; N = 2) explaining nestling daily change in mass ("daily M_b") as a function of maximum daily temperature ("T_{max}"), number of nestlings, total precipitation 2 weeks prior to filming ("P_{2weeks}"), number of adults in the territory ("adults"), and age of nestlings (range one: ≤7 days old; range two: 8–12 days old; range three: ≥13 days old) with offset log total video time. Data were collected from Cape Rockjumpers (*Chaetops frenatus*) between October-November 2017 and August-December 2018 from Blue Hill Nature Reserve, Western Cape, South Africa. Significant predictor variables and results ($p < 0.05$) are in bold.

Model	response variable	Chisq	DF	Pr(>Chisq)
daily M_b ~ adults + **age range** + nestlings *DF = 9, logLik = −216.10, BIC = 469.8, model weight = 0.562*	adults	0.04	2	0.978
	age range	7.69	2	**0.021**
	nestlings	5.39	**2**	0.068
daily M_b ~ **age range** + nestlings *DF = 7, logLik = −220.52, BIC = 470.3, ΔBIC = 0.49, model weight = 0.438*	age range	10.57	2	**< 0.01**
	nestlings	5.87	**2**	0.053

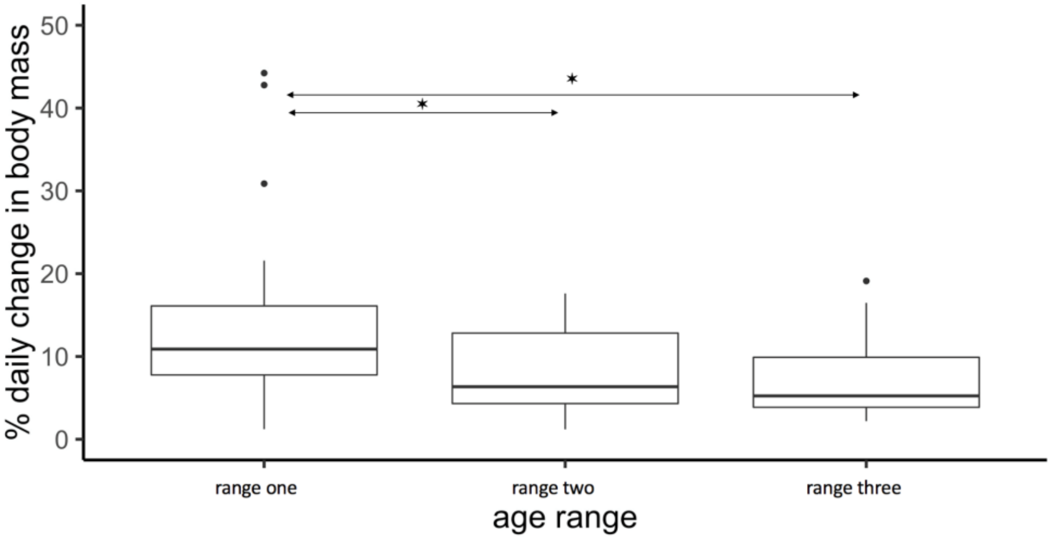

Figure 3.3 Percent daily change in body mass (g) for age ranges (range one: ≤7 days old; range two: 8–12 days old; range three: ≥13 days old) observed from 9:00–15:00 SAST from 25 days of observations at 13 nests of free-living Cape Rockjumpers *Chaetops frenatus* at Blue Hill Nature Reserve, South Africa, over two breeding seasons (2017–2018). Asterisks denote significance at $p < 0.05$.

In absolute terms, daily Δ M_b for each age range was equivalent to 1.43 ± 1.21 g (max = 4.99 g, min = −0.2 g) for range one, 1.80 ± 1.42 g (max = 4.60 g, min = −0.78 g) for range two, and 2.37 ± 2.02 g (max = 5.6 g, min = −2.1 g) for range three nestlings. Absolute daily Δ M_b was not significantly different amongst age ranges (range 2–range 1: $Z_{1,20} = 0.57$, $p = 0.835$; range 3–range 1: $Z_{1,18} = 1.22$, $p = 0.441$; range 3–range 2: $Z_{1,12} = 0.77$, $p = 0.721$). Average initial morning M_b for each age range was 12.49 ± 4.18 g, 25.11 ± 4.20, and 34.54 ± 4.64 g respectively.

Further analysis examining effects of potential predictor variables on individual nestlings from each age range (range 1: N = 30 nestlings; range 2: N = 19 nestlings; range 3: N = 16 nestlings) showed a significant negative correlation between daily T_{max} and percent daily Δ M_b for the oldest nestlings. Older nestlings (range 3) had significantly less daily Δ M_b at increasing daily T_{max} (slope ± SD = −2.48 ± 0.47 g °C^{-1}; $t_{1,16} = -5.24$; $p < 0.001$; Figure 3.4). Neither nestling age range 1 nor range 2 showed a significant relationship between daily Δ M_b and increasing daily T_{max} (range 1: slope ± SD = 0.08 ± 0.34 g °C^{-1}; $t_{1,30} = 0.22$; $p = 0.826$; range 2: slope ± SD = −0.29 ± 0.81 g °C^{-1}; $t_{1,19} = -0.27$; $p = 0.723$). I found no non-linear effects for any of the individual age ranges.

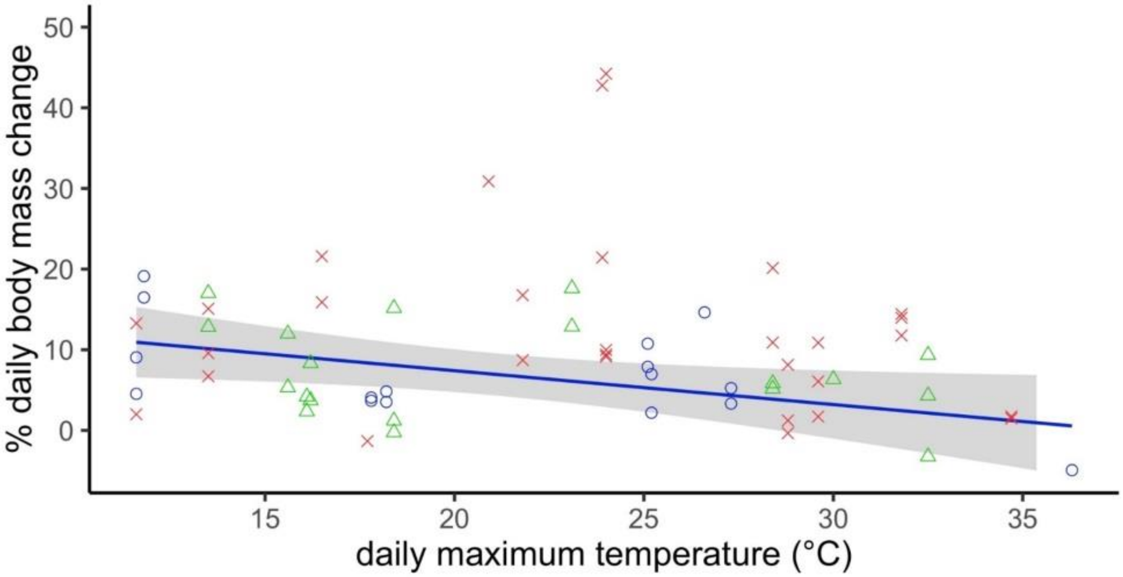

Figure 3.4 The effect of daily maximum temperature (°C) on percent daily change in mass (g) of nestlings. Blue circles and solid line are nestlings ≥13 days old (age range 3), green triangles are nestlings 8-12 days old (age range 2), and red crosses are nestlings ≤7 days old (age range 1). Each data point represents a single nestling (N = 65 nestlings) from 25 days of observations at 15 nests of over two breeding seasons (2017-2018) from free-living Cape Rockjumpers *Chaetops frenatus* at Blue Hill Nature Reserve, South Africa. Line of best fit uses model predictions from a GLMM taking into account variance from random effects.

3.5 DISCUSSION

Overall, I found increased daily T_{max} resulted in increasing probability of observing adult heat dissipation and decreasing daily ΔM_b for older nestlings, while the time adults spent in nests was significantly correlated with the age of the nestlings (decreasing for older nestlings). Provisioning was not significantly affected by any predictor variable. This suggests an interesting possibility that at hotter temperatures, when nestlings have increased water requirements, parents are not able to increase their provisioning rate to compensate — this potentially explains the decrease in daily ΔM_b I saw in older nestlings.

As older nestling mass gain was negatively related to days with hotter temperatures, I thus suggest that either adults are finding smaller prey items on warmer days, nestlings are losing water M_b (i.e. becoming dehydrated) to try and cope physiologically with higher temperatures, or nestlings are putting energy resources into other areas of growth such as feather development (see Murphy 1985). In general, any factor that results in a decrease in daily ΔM_b for nestlings will result in a decrease in the quality of the fledglings and likely have implications for fledging success (Magrath 1991, Thompson and Flux 1991, Greno et al. 2008, Schwagmeyer and Mock 2008). While in general, older nestlings have lower daily ΔM_b compared to younger as they allocate resources to late-stage development (e.g. feathers), any factor which results in decreased daily ΔM_b has the potential to reduce fledge potential. Long-term implications of my results remain unclear, as the only cause of nest failure (i.e. nest not resulting in fledged young) during this study was directly from predation (see Chapter 4).

3.5.1 ADULT HEAT DISSIPATION

Birds panted on all days with daily T_{max} over ~27 °C, with one instance of heat dissipation observed when daily T_{max} was as low as 13.5 °C (Figure 3.1). This supports previous findings showing Rockjumpers have relatively low thermal thresholds for heat dissipation (Milne et al. 2015, Oswald et al. 2019). Along with low thermal thresholds, Rockjumpers were also found to be more likely to pant when breeding versus non-breeding (Oswald et al. 2019); birds increase their overall metabolic functions when breeding, which leads to increased metabolic heat production and an increased requirement to dissipate metabolic heat (Weathers and Sullivan 1993, Williams 2012). In a previous study, while there was no significant difference in basal metabolic rate between breeding and non-breeding Rockjumpers, breeding birds did maintain higher body temperatures (Oswald 2016b), presumably as a method of water conservation (Tieleman and Williams 1999). Interestingly, adults panted on all days at nests with three nestlings. While there was no significant difference in the temperature on film days among nests with different numbers of nestlings (2 vs. 1 nestling: $Z_{1,20} = -1.47$, $p = 0.301$; 3 vs. 1 nestling: $Z_{1,10} = 0.16$, $p = 0.986$; 3 vs. 2 nestlings: $Z_{1,20} = 1.74$, $p = 0.188$), adults did provision nests with three nestlings more than those with one nestling, and so are presumably producing more metabolic heat (from greater activity) at nests with three nestlings with excess heat needing to be dissipated. The lack of significant interaction between temperature and precipitation is surprising because increased precipitation can result in a general increase in humidity resulting in less efficient heat dissipation (Gerson et al. 2014). However, increased precipitation can also lead to an increase in insect numbers (Procheş and Cowling 2006). As insects are likely the main method of water intake for primarily insectivorous birds like the Rockjumper, an increase in insect abundance may mean birds are less at risk from dehydration when dissipating heat (i.e. panting).

3.5.2 NEST-TIME

My only significant finding for amount of time adults spent in the nest was an increase when nestlings were younger and thus likely required increased care. While for this study I was unable to separate brooding and shading, overall time adults spend in the nest can be seen as a proxy for these behaviours, and so more time in nest likely means more time helping nestlings maintain a safe body temperature. Currently, there is no consensus on the precise age that nestlings develop individual thermoregulatory capability. However, it has been shown that altricial birds have limited self-thermoregulatory capabilities in their first few days post-hatch (Ricklefs and Hainsworth 1968b, Dunn 1976, Clark 1982, Pereyra and Morton 2001, Greno et al. 2008, Węgrzyn 2013).

I expected to find groups of three adults spending more time in the nest than groups of two, but found no significant relationship between nest-time and number of adults, suggesting individual adults from groups of three may each have spent less time in the nest. At 3-adult nests the addition of a helper, in all cases male, did not seem to result in equal division of time spent in the nest among all three adults. After removing the single one-adult nest and adding in part-day nests (Table 3.1) to increase the sample size of 3-adult nests, there was no difference in total amount of time spent by males at 3-adult versus 2-adult nests ($t_{1,33} = -0.32$, $p = 0.749$), with the two males in 3-adult territories together spending the same amount of time in nests as one male in 2-adult territories (2-adults: N = 28 days, nest-time by male = 33.78 ± 45.36 min; 3-adults: N = 7 days, nest-time by males: 31.48 ± 53.92; see Appendix 1: Figure S3.1A). This indicates that when there is a male helper, the helper will share reproductive effort with the dominant male, but not the dominant female. To the best of my knowledge, no studies have examined the time adults spend in nests for cooperative breeders where both sexes brood and/or shade (such as is the case for Rockjumpers); although Meade et al. (2010) examined breeding biology for the cooperative breeding Long-tailed Tit *Aegithalos caudatus*, in their case only females brood.

3.5.3 PROVISIONING RATES

While multiple studies have found provisioning rate decreases at increasing T_{air} (Ricklefs and Hainsworth 1968a, Luck 2001, Hoset et al. 2004, Cunningham et al. 2013b; although see Barba et al. 2009), I found no significant relationship between provisioning and daily T_{max}, or any other of my predictor variables. As a previous study found Rockjumper foraging effort did not change between the breeding and non-breeding season (Oswald et al. 2019), it may be foraging efficiency or prey quality is greater during the breeding season when insect productivity in the Fynbos is highest (Lee and Barnard 2015). However, a lack of significant relationship between provisioning and temperature could also occur if provisioning rate is constrained when temperatures are hotter (when nestlings have higher water demands), and not constrained when temperatures are cooler — this would then partially explain my finding of reduced daily Δ M_b at high temperatures for older nestlings. It may also be that Rockjumpers are always provisioning at minimum rate necessary to produce fledglings while decreasing risk of predation (i.e. by minimizing nest activity; see Martin et al. 2000a, Martin et al. 2000b). In general, provisioning rate increases for older nestlings (Grundel 1987, Filliater and Breitwisch 1997, Falconer et al. 2008, Barba et al. 2009), so it seems likely the degree of reduced daily Δ M_b in older Rockjumpers nestlings may be due to a lack of increased provisioning by adults (see below).

As two of the territories used in this study had a helper individual in addition to a dominant breeding pair, I expected to find number of adults would have an effect on provisioning rate, with 3-adult territories having higher provisioning rates than 2-adult, but again number of adults was not a significant predictor variable. Several studies have found helpers share in total care but do not increase the amount of care received by nestlings (Ridley and Raihani 2007, Savage et al. 2015, Wiley and Ridley 2016); Koenig and Walters (2011) refer to this strategy as "compensatory feeding" as opposed to "additive feeding". Additionally, similar to Meade et al. (2010) I again found the presence of a helper male resulted in decreased provisioning by individual males across my full dataset (2-adults: N = 28 days, male proportion provisioning = 0.49 ± 0.17; 3-adults: N = 7 days, male proportion provisioning = 0.61 ± 0.17; Appendix 1: Figure S3.1B). While these results suggest a difference in provisioning rate between sexes, sex was not a significant predictor variable for provisioning — I was only able to distinguish between individual males in one territory, where the helper (offspring from the previous year) provisioned 29.5 % and the dominant male provisioned 24.8 %, while the dominant female provided 45.7 % of all provisions. As with nest-time, it seems that for Rockjumpers the addition of a male helper does result in compensatory nest attendance and provisioning effort (i.e. nest-time and provisioning rate), but only for the dominant male.

3.5.4 DAILY CHANGE IN MASS

Nestlings need to continually gain M_b in order to develop properly and fledge successfully; it seems without exception that heavier nestlings are more likely to fledge and survive to breed themselves (Magrath 1991, Thompson and Flux 1991, Greno et al. 2008, Schwagmeyer and Mock 2008). While in my study absolute daily M_b did not differ amongst age ranges, this resulted in higher daily ΔM_b for younger nestlings. This would follow from other studies where nestling growth follows a logistic growth pattern where younger nestlings gain M_b at a faster rate than older nestling (Murphy 1985, Olson 1992, Pereyra and Morton 2001, Van de Ven 2017). I found older nestlings experienced greater negative affects at increasing daily T_{max}, similar to Murphy (1985), although contrary to Cunningham et al. (2013b).

As adult Rockjumpers maintain provisioning across daily T_{max}, it seems daily ΔM_b decrease in older nestlings is perhaps due to other factors such as the direct physiological costs to nestlings or an increased need for water at high T_{air} (Wolf 2000, Angilletta et al. 2010, du Plessis et al. 2012). Older nestlings may expend extra energy and water as their overall metabolic rates increase as they grow (Olson 1992) or when they are using resources to aid in thermoregulation. A decrease in daily ΔM_b at high T_{air} may also have been due to increased growth rates on warmer days, as high T_{air} has also been associated with stimulated primary growth (i.e. feathers; Murphy 1985). As higher T_{air} has been reported to stimulate feather production in older nestling Eastern Kingbirds *Tyrannus tyrannus* (Murphy 1985), when provisioning rate or quality does not increase to accommodate the increased energy output of feather production, there may be an overall decrease in daily ΔM_b.

As with many other studies on provisioning (e.g. Cunningham et al. 2013b), I was unable to determine biomass for each provision; in many instances the provisioning event was partially covered by either the body of the adult or the nestlings. However, studies have shown adults can maintain daily ΔM_b for older (and thus heavier) nestlings by provisioning greater prey volume (Grundel 1987) or larger prey type (Radford 2008). Overnight M_b loss for similar-sized adult passerines, was found to be 3.82 % (du Plessis et al. 2012). In order to attempt to extrapolate what Rockjumper decreasing M_b gain at increasing temperature may mean for overnight M_b loss, I assumed Rockjumper nestlings must maintain daily ΔM_b of a minimum 5 % based on the overnight M_b loss data available for southern African birds; with this assumption, to avoid losing M_b overnight, older nestlings would begin losing M_b at ~23.5 °C (Figure 3.4).

3.5.5 CONCLUSIONS

For a range-restricted species with a specific habitat niche, such as the Rockjumper, I found adults may be unable to provision at a rate or quality that allowed maintenance of daily change in mass for older nestlings at increasing air temperature. While conjectural as I did not collect overnight mass loss during this study, ~23.5 °C is likely an under-representation of the where older nestlings face potentially unsustainable mass loss; this temperature is far lower than daily maximum temperatures previously recorded as critical thresholds for a southern African passerine Southern Fiscals *Lanius collaris* (33 °C; Cunningham et al. 2013b), although higher than recorded for Mediterranean-climate passerine Spotless Starlings *Sturnus unicolor* (~ 15 °C; Salaberria et al. 2014).

My findings may be complicated by the fact that Rockjumper predation rates were positively correlated with increasing air temperature (see Chapter 4), resulting in few observations on days with daily maximum temperature over 30 °C. However, nestlings experienced mass loss over 8 hrs on the only film day over 35 °C. I suggest the most likely reason for the decrease in daily change in mass for older nestlings at increasing temperature was an increase in nestling physiological demands with no corresponding compensation from adults — for example, no increase in provisioning rate or no increase in prey quality. As with nestling daily change in mass, adult heat dissipation begins at a relatively low temperature compared to other South African passerines (du Plessis et al. 2012, Smit et al. 2013, Smit et al. 2016, Pattinson and Smit 2017), and so adults may themselves face extreme individual risk of heat stress if they attempt to mitigate nestling water costs by spending time shading the nest.

The apparent inability of adult Rockjumpers to mitigate the costs of high air temperature on older nestlings did not manifest as reduced fledging success — the only reason for failed fledging at my study site was nest predation (see Chapter 4). However, reduced nestling condition can result in detriments post-fledge, leading to reduced survival, recruitment, and lifetime fitness (Magrath 1991, Thompson and Flux 1991, Greno et al. 2008, Schwagmeyer and Mock 2008). Any factor which limits daily mass gain could lead to lower quality fledglings, and as Rockjumper fledglings have already shown relatively low thermal thresholds for physiological thermoregulatory responses (i.e. low panting thresholds; Oswald et al. 2018b), high temperatures may lead to overall decreased population recruitment. For the 25 days filmed during this study, half of the film days had a daily maximum temperature of greater than 23.5 °C (N = 13). As global temperatures continue to increase, nestlings may be unable to properly develop if the number of days with daily maximum temperature greater than 23.5 °C later in the nestling phase increases, and we may begin to see decreased fledging success and lifetime fitness.

CHAPTER 4: IMPACTS OF FIRE, PREDATION, AND TEMPERATURE ON NEST FAILURE IN A NEAR THREATENED ALPINE GROUND-NESTING BIRD.

4.1 SUMMARY

Reproductive failure in birds is often due predominantly to nest predation and can be correlated with nest concealment (e.g. lower failure with more vegetative cover). However, predation risk depends on predator type, as predators vary in their ecology and sensory modalities (e.g. visual vs. olfactory). In many habitats, snakes (generally olfactory predators) are a major nest predator for small birds, and in such instances predation is strongly associated with warmer temperatures. Here, I investigated nest failure in a ground-nesting alpine species, the Cape Rockjumper *Chaetops frenatus*. I collected three years of nest data, testing if nest failure was correlated with (1) more open habitat [i.e. “habitat stage”; early post-fire versus late post-fire habitat (≤ 3 years and > 3 years since fire, respectively)], and (2) nest concealment. Forty-six of 54 nests failed due to predation, with temperature my most significant predictor. I also found greater survival slightly correlated with early post-fire habitat and increased snake predation (my main source of predation; N = 19 of 28 identified predation events) at higher temperatures. My findings illustrate that reproductive failure may involve a complex interplay of nest-specific and landscape-level ecological factors.

4.2 INTRODUCTION

For birds, the probability of successfully fledging young is influenced by both intrinsic and extrinsic factors; intrinsic factors may include individual thermoregulatory capabilities, female and nestling body mass, and group size (e.g. Kellett and Alisauskas 2000, Blums et al. 2002, Ridley and Van den Heuvel 2012, Cunningham et al. 2013b), while extrinsic factors may include nest-site selection, weather, food availability, and predation risk (e.g. Martin and Roper 1988, Martin 1992, 2001, Cox et al. 2013b, Carroll et al. 2015b, Carroll et al. 2018). Nest predation has generally been investigated in relation to vegetative concealment in the area directly surrounding the nest (hereafter "nest concealment"); nest failure is often negatively correlated with nest concealment as thicker vegetation decreases the risk of nest-detection by visual predators (Ricketts and Ritchison 2000, Davis 2005, Little et al. 2015; although see Li and Martin 1991). Predation may also be related to concealment within the broader predator landscape (i.e. the openness of the overall breeding habitat landscape, containing multiple potential predators; hereafter "habitat openness"). Less open habitat may decrease adult birds’ ability to detect nest predators, and so reduce their ability to drive off predators before they reach the nest (Dyrcz 1969, Finch 1989, Amat and Masero 2004, Magana et al. 2010).

Avian nest predators include mammals, birds, and snakes, all of which respond differently to nest concealment depending on their hunting strategy (Martin 1987). Although nest concealment may result in decreased predation from visual predators, it is generally unrelated to predation by olfactory predators (Colombelli-Négrel and Kleindorfer 2009, Conover et al. 2010). For example, snake predation (the primary cause of nest failure in New World passerines; Weatherhead and Blouin-Demers 2004) showed no relation to nest concealment (Wray II and Whitmore 1979, Nias 1986, Eichholz and Koenig 1992, Schaub et al. 1992, Stake et al. 2005). Additionally, mammal predation often occurs irrespective of temperature (Cox et al. 2013a), while both snake and avian predation often increase with higher temperatures (Weatherhead and Hoysak 1989, Cox et al. 2013a, DeGregorio et al. 2014). Therefore, understanding the relationship between predation and concealment depends on identifying key predator species (Kleindorfer et al. 2005, Thompson III 2007).

I collected nest data in a ground-nesting alpine bird, the Cape Rockjumper *Chaetops frenatus* (hereafter “Rockjumper”). Rockjumpers are endemic to the alpine Fynbos of South Africa characterised by sparsely vegetated open scree slopes with regularly occurring natural fire (Van Wilgen et al. 2010, Lee and Barnard 2016). Individual Rockjumper territories have progressively denser vegetation (i.e. decreased habitat openness) with increasing numbers of years since fire. Rockjumpers build open-cup nests on the ground under rocky overhangs (Holmes et al. 2002), providing varying amounts of nest concealment. Rockjumpers likely face high predation risk, as low productivity environments such as the Fynbos have higher rates of predation than high productivity environments (Hořák et al. 2011), and open-cup ground-nests have been shown to face the highest rates of nest predation compared to closed-cup ground nests and off-ground nests (Djomo Nana et al. 2014). However, ground-nesters that are also territorial residents, such as Rockjumpers, may retain knowledge of local predator activity (Lloyd 2004), allowing for nest placement in areas that combine the optimal balance of habitat openness and nest concealment.

My study aimed to determine overall patterns of nest success/failure by examining survival probability in order to identify correlations between habitat openeness, nest concealment, temperature, and predation events. I expected to find nest survival correlated with (1) greater habitat openness, and (2) increased nest concealment.

4.3 METHODS

4.3.1 STUDY SITE AND SPECIES

This study was conducted at Blue Hill Nature Reserve (“BHNR”) over two full Rockjumper breeding seasons (Sept–Nov 2017 and Aug–Dec 2018). Rockjumper family groups at BHNR generally consist of two–four individuals at comparatively low densities (1.54 individuals km$_{-2}$; Lee et al. 2015). See Chapter 1 for further details on study site and species.

4.3.2 NEST MONITORING AND GENERAL NEST DATA

Nests were located by spending 4–5 h in territories every 4–5 d, looking for signs of breeding (e.g. nest material in bill, food in bill, localized area fidelity). Birds were observed using binoculars or spotting scopes from 30–100 m distance to minimize observer disturbance. Only nests that reached the egg-laying stage were considered for the purpose of this study. Nests were monitored over two complete breeding seasons (Sept-Nov 2017 and Aug-Dec 2018), with the inclusion of two nests found *ad hoc* in 2016.

Nests were monitored using trail cameras (Bushnell Corporation, Kansas, USA, various models; 2016: N = 2, 2017: N = 7, 2018: N = 9) placed ≤1 m from nests and set to record three photos per low-sensitivity motion sensor trigger. Additionally, between one and four infra-red camera setups (“Handykams”;

Handykam.com, Redruth, UK; 2017: N = 1, 2018: N = 4) were placed ≤0.5 m from nests, set to record 30 sec videos on low-sensitivity motion sensor trigger. Trail cameras were set up at every nest, while Handykams were set up at nests as available. In 2017 and 2018 I performed nest-checks every 4–5 d, for a maximum of 15 min per visit, to check on nests as well as cameras; a meta-analysis of nest failure correlated with researcher presence found researcher visits had no significant effect (Ibáñez-Áalamo et al. 2012) and possibly even reduced the probability of nest failure (MaCivor et al. 1990, Ibáñez-Álamo and Soler 2010).

Exact hatch date could only be determined for five nests. Due to camera placement, I was often unable to determine the purpose of adult visits to determine incubation vs. provision. I thus estimate hatch date with the following procedure using average incubation and nestling time from Holmes et al. (2002; N = ~20 days for both): (1) if a nest was found with nestlings, I estimated the age of the nestlings (using a set of photographs from nestlings with known hatch date) and used average incubation time; and (2) if a nest was found to have hatched between nest checks I assigned a date halfway between the visits. Using these estimates I found similar numbers of nests failed at both stages (N = 24 failed as eggs, N = 22 failed as nestlings; Table 4.1). Due to similarity in failed nests at each nest stage, I decided not to include nesting stage in further analysis.

Table 4.1 Total number of nests, including number of failed nests per nesting stage ("egg stage" or "nestling stage") and month in which they failed (August-December), as well as number and percent of successful nests (i.e. producing at least one fledgling) by month fledged, from Cape Rockjumper *Chaetops frenatus* nests observed August to December 2016–2018 from Blue Hill Nature Reserve, South Africa.

month	total nests	egg stage	nestling stage	fledged*
August	2	1	1	0 (0.0 %)
September	9	6	1	2 (22.2 %)
October	15	10	4	1 (6.7 %)
November	21	5	12	5 (23.8 %)
December	7	2	4	1 (14.3 %)
total	54	24	22	8 (14.8 %)

4.3.3 HABITAT OPENNESS AND NEST CONCEALMENT DATA

For habitat openness, I recorded how recently fire had occurred in each territory, and designated a "habitat stage" for each territory based on the following information: before 2017 all Rockjumper territories were in habitat that last burned in a 2012 wildfire. In April 2017 the northern section of BHNR, which had consisted of old growth stands of Proteaceae, experienced a wildfire (see Chapter 1). While the fire left the landscape denuded of vegetation, and exposed the sandy substrate, primary growth vegetation began to return within a few weeks, with Rockjumpers moving into this area within a few months. I thus referred to territories burned in 2012 as “late post-fire habitat”, and those burned in 2017 as “early post-fire habitat”. For nest concealment I estimated percent vegetative ground cover as viewed from an observer height of ~ 1.75 m, with a one-metre radius (“veg cover”), using the nest as the epicentre. The vegetation of the alpine Fynbos at BHNR is typically ~ 0.5 m tall, and none of the vegetation within the one-metre radius was over one-metre tall.

4.3.5 SUCCESS/FAILURE DATA

For each nest I recorded the territory designation (“territory”; N = 30 unique territories based on unique colour-ring combinations; see Chapter 2), individual nest identification number (“nest ID”), number of adults in the territory (“group size”; N = 1, 2, or 3 per territory), number of eggs and/or nestlings in the nest (“brood size”), and ordinal date (“date”).

In total I collected data on 56 nests over three years (2016: N = 2, 2017: N = 17, 2018: N = 37). Forty-eight nests failed (2016: N = 2; 2017: N = 16; 2018: N = 30), with the remaining eight nests fledging at least one chick (2017: N = 1; 2018: N = 7) — following Borgman and Wolf (2016), nests were considered successful if one or more young fledged. For two instances failure was attributed to an unusual late-season snow cover event that rendered eggs non-viable, and so I removed these nests from my predation analysis, leaving my total number of nests as 54 (2016: N = 2; 2017: N = 17; 2018: N = 35).

Following Shaffer (2004), I calculated daily survival rate with a modified Mayfield method (Mayfield, 1975) by using a logistic exposure model by recording the following data: (1) whether a nest had survived or failed for each exposure period (“survival”; survived = “1”, failed = “0”), and (2) the number of days the nest was exposed between nest checks (“exposure”). For all but four nests (where camera setups experienced equipment failure), I was able to directly record survival on a daily basis using footage and photographs recorded by the camera setups.

At failed nests I scanned trail camera footage (and infra-red camera if applicable) for cause of failure. If I identified a failure event, I recorded the date, time, cause (i.e. “type”: mammal, snake, bird, or other), and species of nest predator (“species”; where possible). Additionally, when collecting cameras at failed nests I examined the area around the nest for signs of predation that would help with identification of cause (i.e. nest disturbance, eggshell presence, etc.).

4.3.6 WEATHER DATA VARIABLES

All weather data were recorded every 30 min by a VantageVue weather station at BHNR (Davis Instruments Corp., USA). I recorded the maximum daily air temperature (T_{maxday}) for each day a nest was active. In instances of predation where I could extract the date and time of failure from camera footage, I also recorded the temperature at time of predation (T_{pred}).

4.3.7 NESTING PERIOD

As the risk of predation increases with longer nesting period, species under high risk of predation should have shorter nesting periods (Perrins 19977; Bosque and Bosque 1995, Martin 1995). To see whether Rockjumpers had an average-length nesting period, I calculated the total time Rockjumper nests are active (i.e. time from egg to fledging) and compared it to data on 26 species of South African passerines (with minimum sample sizes of three; Martin and Lloyd unpublished data; Winterbottom and Wilson 1959, Skead 1960, Winterbottom 1964, Steyn 1966, Tarboton 1971, Piper 1989, Monadjem et al. 1995, Lloyd 1998, Oatley 1998, Holmes et al. 2002, Krüger 2004, Engelbrecht and Lonzer 2009, Maphisa et al. 2009, Dikgale 2012, Engelbrecht and Mathonsi 2012, Ridley and Van den Heuvel 2012). I then extracted the average number of days spent incubating and average number of days spent as nestlings (N = 22 species with incubation data, N = 20 species with nestling data, N = 15 with both incubation and nestling data), and calculated residual mass-specific values for days spent incubating, days as nestlings, and total days in the nest (see Appendix 2: Table S4.1).

4.3.8 ANALYSES

All analyses were performed in the R statistical environment version 3.5.3 (R Core Team 2019) using RStudio version 1.1.463 (RStudio Team 2018). Packages used included *lme4* (Bates et al. 2015), *dplyr* (Wikham et al. 2019), and *blme* (Chung et al. 2013).

Total Survival: I created a Bayesian Generalized Linear Mixed-Effects Model (BGLMM; due to issues of singular fit) fitting survival potential predictor variables habitat stage, veg cover, and T_{maxday}, with random effect of nest ID with a binomial distribution and a modified logit-link function that includes exposure as per Shaffer (2004). Model selection was based on lowest Bayesian information criterion for small sample sizes (BICc), and I present model outputs for top competing models within Δ2 BICc.

Predation: As predation events were primarily due to snakes (see below), I created a BGLMM (again, due to GLMM resulting in singular fit) fitting a binomial of snake predation ("1" = snake predation, "0" = not snake predation) to T_{maxday}, with random effect of nest ID and a binomial distribution.

Nesting Period: I calculated residual mass-specific values for days spent incubating, days as nestlings, and total days in the nest for available species data (N = 22 species with incubation data, N = 20 species with nestling data, N = 15 with both incubation and nestling data).

4.4 RESULTS

4.4.1 CAUSES OF FAILURE

Throughout the three-year study I recorded nest failure at 46 of 54 nests (85.2 %; not including two nests that failed due to snow; see Methods). For failed nests, the cause of failure could not be determined at 19 nests (41.3 %). The majority of failure events from the 28 nests with discernible cause failure were from predation, with Boomslangs *Dispholydus typus* the main predator (N = 18; 64.3 %; Figure 4.1). Other causes of failure included Cape Grey Mongoose *Galerella pulverulenta* (N = 6), Honey Badger *Mellivora capensis* (N = 1), unidentified rat species *Otomys* spp. (N = 1), unidentified egg-eating snake *Dasypeltis* spp. (cause known from egg-shell ejecta, N = 1), and unidentified ants/starvation (N = 1; Figure 4.1).

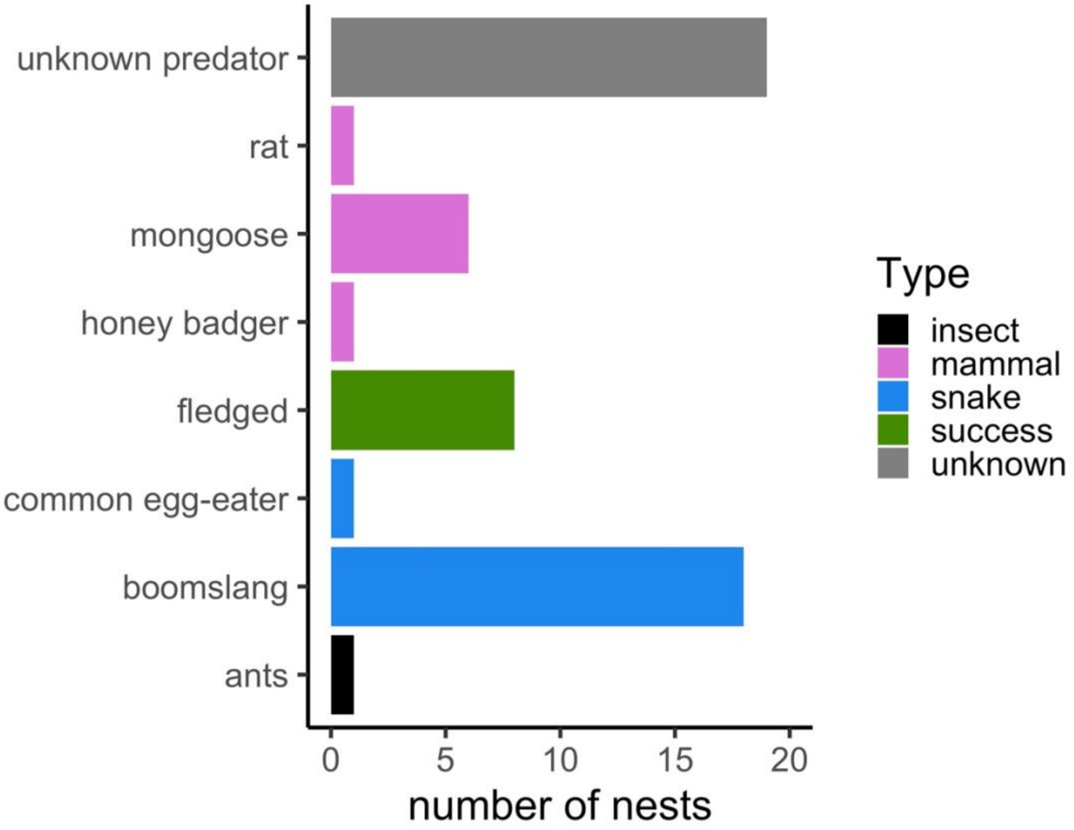

Figure 4.1 Total number of nests from three breeding seasons (2016–2018), of Cape Rockjumpers *Chaetops frenatus* at Blue Hill Nature Reserve, Western Cape, South Africa. Totals include number of successful nests ("fledge") as well as failed nests by cause of failure — failure from predation by Boomslang *Dispholydus typus*, Cape Grey Mongoose *Galerella pulverulenta*, Honey Badger *Mellivora capensis*, unidentified rat species *Otomys spp.*, unidentified egg-eater snake *Dasypeltis spp*, and ants/starvation ("ants").

4.4.2 NEST FAILURE, HABITAT OPENNESS AND NEST CONCEALMENT

My top competing models (Δ2 BICc) explaining nest survival included T_{maxday} and habitat stage as the only predictor variables (see Table 4.2 for model coefficients). In both competing models nest survival was explained predominantly by T_{maxday}, with higher probability of nest survival in days with lower temperatures (coefficient estimate = – 0.09, SE = 0.03, Z = – 3.29, $p < 0.001$; Table 4.2; Figure 4.2). In one competing model habitat stage had a small effect on survivorship with fewer successful nests in territories with less open habitat, although this response was not significant (coefficient estimate = −1.14, SE = 0.59, Z = –1.95, $p = 0.051$; Table 4.2). Although no territories consisted of early post-fire habitat in 2016 or 2017, in 2018, more fledglings resulted from nests in areas with early post-fire habitat [2018 fledge rates: early post-fire habitat = 45.5 % (N = 5/11), late post-fire habitat = 8.3 % (N = 2/24)].

Table 4.2 Model coefficient summary tables for competing models in top model set (Δ2 BICc; N = 2) explaining nest survival as a function of habitat ("habitat stage"; "late post-fire habitat" or "early post fire habitat"), vegetative concealment ("veg cover"), and daily maximum temperature (T_{maxday}). Data were collected from Cape Rockjumpers (*Chaetops frenatus*; N = 54 nests) between October-November 2017 and August-December 2018 from Blue Hill Nature Reserve, Western Cape, South Africa. Significant predictors ($p < 0.05$) are in bold.

model	response variable	estimate	std. error	z-value	Pr(>|z|)
survival ~ $\boldsymbol{T_{maxday}}$	Intercept	4.69	0.71	6.60	**< 0.001**
DF = 2, logLik = −161.4, BICc = 342.3	T_{maxday}	– 0.09	0.03	– 3.29	**< 0.001**
survival ~ habitat stage + $\boldsymbol{T_{maxday}}$	Intercept	5.57	0.87	6.37	**< 0.001**
DF = 3, logLik = −159.1, BICc = 344.2, ΔBICc = 1.9	late post-fire habitat	– 1.14	0.59	– 1.95	0.051
	T_{maxday}	– 0.09	0.03	– 3.17	**< 0.01**

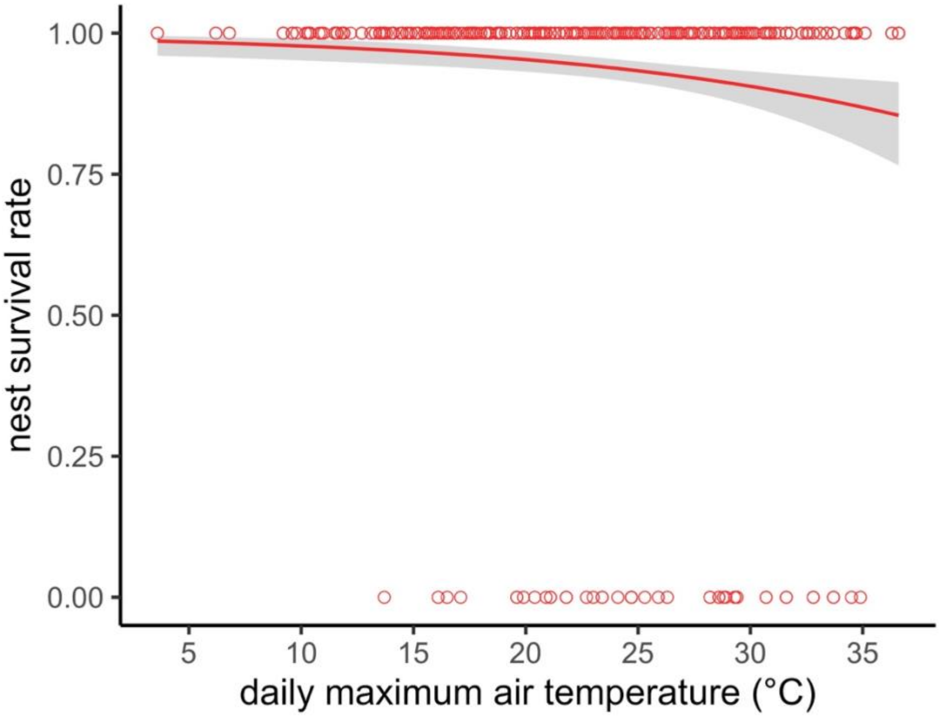

Figure 4.2. The relationship between nest survival ("1" = survived, "0" = failed) and daily maximum temperatures (°C), recorded at all observed nests (*n* = 54) over three breeding season (2016-2018) for Cape Rockjumpers (*Chaetops frenatus*) at Blue Hill Nature Reserve, Western Cape, South Africa. Red lines show the predicted relationship from the GLM (see Table S2) and shaded 95 % confidence intervals.

4.4.3 PREDATION

Predation by snakes had significantly greater probability of occurring at higher temperatures (coefficient estimate = 0.08, SE = 0.04, Z = 2.15, *p* = 0.031; Table 4.3).

Table 4.3 Model coefficient summary table for model explaining snake predation (snake = “1”, not snake = “0”) as a function of daily maximum temperature (T_{maxday}). Data were collected from Cape Rockjumpers (*Chaetops frenatus*; N = 54 nests) over three breeding seasons (2016–2018) at Blue Hill Nature Reserve, Western Cape, South Africa.

model	response variable	estimate	std. error	z-value	Pr(>|z|)
snake predation ~ $\boldsymbol{T_{maxday}}$	Intercept	– 5.77	1.06	– 5.45	**< 0.001**
DF = 1, BICc = 192.8	T_{maxday}	0.08	0.04	0.04	**< 0.05**

4.4.4 NESTING PERIOD

Mass-specific residual data comparing Rockjumpers to other South African passerines showed Rockjumpers have an above average mass-specific length of time as eggs (Fig. 4.3A), slightly above average mass-specific length of time as nestlings (Figure 4.3B), and overall longer total number of days in the nest (Figure 4.3C).

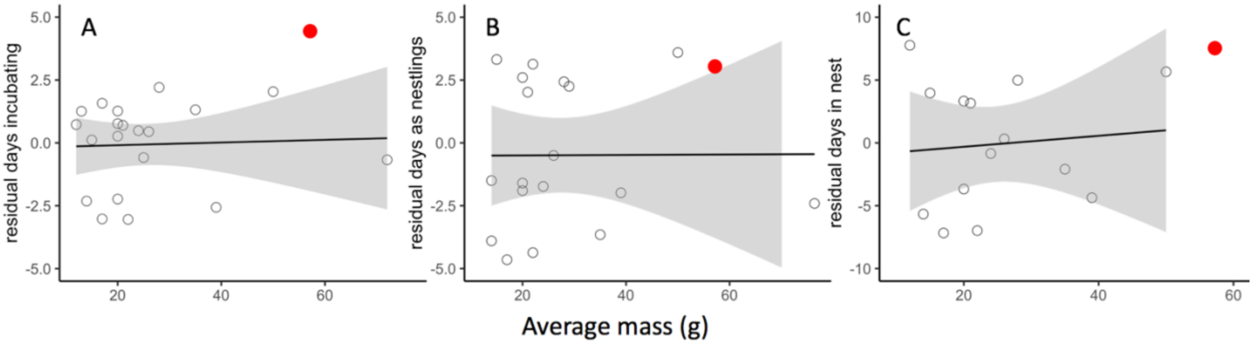

Figure 4.3 Mass-specific average residual number of days spent (A) at egg-stage for 22 species of Southern African passerines ("residual days incubating"), (B) at nestling-stage for 20 species of Southern African passerines ("residual days as nestlings"), and (C) in the nest ("residual days in nest") for 15 species of Southern African passerines, with the Cape Rockjumper *Chaetops frenatus* highlighted as filled circles in red. Model fit is LM with shaded 95 % confidence intervals. Data were collected from Martin and Lloyd (unpublished data), Winterbottom and Wilson (1959), Skead (1960), Winterbottom (1964), Steyn (1966), Tarboton (1971), Piper (1989), Monadjem et al. (1995), Lloyd (1998), Oatley (1998), Holmes et al. (2002), Krüger (2004), Engelbrecht and Lonzer (2009), Maphisa et al. (2009), Dikgale (2012), Engelbrecht and Mathonsi (2012), Ridley and Van den Heuvel (2012).

4.5 DISCUSSION

This study highlights the need to investigate multiple ecological factors such as temperature and concealment for understanding predator-prey interactions in relation to reproductive failure. While I found no relationship between nest concealment and predation, I did find the probability of nest predation by snakes increased with increasing temperatures from the relatively low temperature of ~ 25 °C (Figure 4.2). Since Rockjumpers had lower nest survival on warmer days, likely due to increased snake activity, my study highlights potential vulnerability to increasing temperatures due to climate change in birds whose nests are vulnerable to snake predation. A previous study by Milne et al. (2015) found Rockjumper populations were declining in areas of their habitat experiencing the greatest warming: I suggest it is possible that increased snake predation may be connected to these declines.

4.5.1 NEST FAILURE, HABITAT OPENNESS, AND NEST CONCEALMENT

My main finding that birds had higher probability of nest survival at lower air temperatures indicates birds nesting earlier in the season (i.e. at cooler temperatures) have a higher chance of successfully fledging young. However, my two nests that failed due to snow show nesting early in the breeding season may come with increased risk of failure due to inclement weather.

I found no relationship between nest concealment (i.e. veg cover) and nest survival, suggesting that predators responsible for nest predation of Rockjumpers may not be primarily visual predators. While not significant, birds had lower levels of nest failure associated with greater habitat openness. These results are contrary to previous studies where both increased habitat openness (i.e. overall less vegetated habitat) and decreased nest concealment (i.e. less vegetation around the nest itself) resulted in increased predation (Ricketts and Ritchison 2000, Little et al. 2015). In open grassland systems, nest success is often positively directly correlated with a greater number of years since fire and thus decreased habitat openness (Davis 2005, Grant et al. 2010, Grant et al. 2011). I suggest two possibilities for why there would be less nest failure in a more open predator landscape (i.e. early post-fire habitat): (1) birds may benefit from more recent fire due to increased visibility allowing adults to spot potential predators before the predators are within range to sense the nest, or (2) recently burned areas may have fewer predators.

The relationship of nest success to open landscapes post-fire may be taxa dependent — for a variety of marshland avian taxa Mérő et al. (2015) found success in Passeriformes positively, and Galliformes negatively, correlated to greater time since fire. Multiple species choose nest-sites in open landscapes with large amounts of visibility, presumably to more easily spot potential predators (Dyrcz 1969, Finch 1989, Götmark et al. 1995, Magana et al. 2010). Interestingly, studies from Australia, North America, and the Mediterranean have shown no consensus on the relationship between snake occurrence and fire irrespective of habitat (McDonald et al. 2012, Dovčiak et al. 2013, Santos and Cheylan 2013, Steen et al. 2015). However, recent fire creates open nest surroundings that may allow odours to dissipate more quickly (Shutler 2019), and may also expose snakes to aerial predators of their own.

4.5.2 NEST PREDATION

Throughout my study I identified nest failure attributable to multiple predators, but the greatest number of failed nests were from snakes — almost exclusively by Boomslangs. While Boomslangs have previously been recorded in the Fynbos (Holmes et al. 2002, Jacobsen and Randall 2013), the dominance of Boomslangs as a nest predator of a ground-nesting bird was surprising given their eponymous status as a primarily arboreal hunter (Marais 2011). Boomslang density in the Fynbos may be underreported, partially from the difficulty of properly studying snake ecology due to their often-cryptic behaviour, habitat-use, and activity patterns (Siegel et al. 1987). My finding that Boomslang predation increased in association with higher temperatures corroborate previous work on snakes as nest predators (Weatherhead et al. 2010, Cox et al. 2013a, DeGregorio et al. 2014).

Snakes are generally more active at higher temperatures (Peterson 1987, Nelson and Gregory 2000, Brown and Shine 2002). While this response presumably reaches an upper limit where snakes are then required to seek out shaded microsites (e.g. Huey and Kingsolver 1989, Adolph 1990, Huey 1991), during this study BHNR recorded no temperatures above 36 °C, which is below temperatures at which other snake species have been found to experience physiological stress (Gangloff et al. 2016) and seek out shade (Webb and Shine 1998). Specific temperatures at the time of Boomslang predation during my study were between 14.2 and 31.6 °C (average = 23.4 ± 5.0 °C). While these temperatures fall outside of the average recorded for Boomslang in the Kalahari (19.2 ± 1.7 °C – 31.4 ± 1.3 °C; Alexander, Maritz, Beck & Maritz, unpubl. data), this may partially be due to differences in operative temperatures (the thermal environment experience by the animal) which can be > 10°C above standard measures air temperature (Walsberg & Wolf 1996).

Although I found direct evidence for a single predation by a Common Egg-eater, it is quite possible these small, mostly nocturnal, snakes are responsible for a number of my partial predation events. When doing nest checks, nests were sometimes found containing one egg fewer compared to the previous visit (N = 11 nests). While Egg-eaters generally depredate the entire nest, they have also been recorded partially depredating nests and are likely an underreported cause of predation (Bates & Little 2013). I additionally suggest the lack of recorded Egg-eater predation events (full or partial) may be partially attributed to my lack of recorded nocturnal predation events in general; while my cameras were equipped with infra-red sensors, direct observations indicate nocturnal predation events were underreported. In fact, my Boomslang predation may also have been under-represented, as Alexander, Maritz, Beck & Maritz (unpubl. data) found Boomslang in the Kalahari were sometimes active as early as 2:00 SAST.

As well, I had one nest experience partial predation when two of three nestlings were predated by a Boomslang, and 5-days following the third nestling was also predated by a Boomslang — as per my methods the partial predation was not included in my analysis, but again shows the prevalence of Boomslang as a dominant nest predator. Although I recorded no predation from Chacma Baboons *Papio ursinus* (which are prevalent at BHNR), my camera traps recorded one instance of Baboons exploring a nest which had been depredated by a Boomslang 3 hours previous, and as Baboons are known to opportunistically eat eggs (DeVore & Washburn 1963), it is likely they would have depredated the nest if it had remained active.

4.5.3 IMPLICATIONS FOR POPULATION PERSISTENCE

Past work highlighted potential negative effects of increasing temperatures on Rockjumpers that may explain temperature-related population declines; these include high evaporative water loss rates (Oswald et al. 2018c), foraging trade-offs at high temperatures (Oswald et al. 2019), and insufficient mass gain in older nestlings (see Chapter 3). In this study, I found recent fire may be immediately beneficial to Rockjumper breeding success, and increased temperatures could result in increased predation risk.

Predation is the main cause of nest failure in most birds (Ricklefs and Hainsworth 1968b, Martin 1995, Cox et al. 2013a, Little et al. 2015, Fouzari et al. 2018), and traits that diminish predation risk, such as shorter nesting periods or smaller clutches, are associated with species under high risk of predation (Perrins 1977, Bosque and Bosque 1995, Martin 1995). For my study, the high rate of predation experienced by Rockjumpers makes it surprising they have a proportionally long nesting cycle (Figure 4.3). Although multiple studies have shown nest stage (i.e. egg vs. nestling) has an effect on predation (Lloyd 2004), I found almost identical numbers of nests predated with eggs compared to nestlings (N = 24 and 22 respectively). It is possible Rockjumpers have developed a strategy of infrequent nest visits which reduces overall activity at nests and so may decrease chance of detection and predation (Conway and Martin 2000).

I recorded six territories with more than two adults, all consisting of three adults — for two of these groups the helpers were offspring from the previous breeding season, while the other four groups were discovered already with three adult individuals and so the relationship of the helper was unknown. I expected more cases of cooperative breeding in Rockjumpers, as one of the main benefits of cooperative breeding should be additional individuals to aid in mobbing (Wright et al. 2001, Maklakov 2002). Many birds use "mobbing" behaviour as a strategy for driving off predators, especially snakes, before they discover nests or young (Francis et al. 1989, Forsman et al. 2001, Bell et al. 2009). Indeed, the importance of mobbing as anti-predator defense is such that young birds will join in mobbing behaviour as early as 47-days post-hatch (Francis et al. 1989), often joining together to form multi-species groups (Krams and Krama 2002, Suzuki 2016). For my study, the number of adults in a territory had no significant effect on nest survival (coefficient estimate = 0.12, SE = 0.55, Z = 0.23, $p = 0.822$). However, I did witness nest failure at one nest after the male was no longer recorded by camera or direct observation when nestlings were 8 days old; the female seemed unable to maintain an adequate rate of nest attendance and so failure at this nest was likely due to a combination of ants and starvation.

While throughout this study I witnessed multiple instances of Rockjumpers successfully driving Cape Grey Mongooses away from nests, I witnessed no instances of mobbing successfully deterring Boomslangs. This finding is similar to that of Burton and Yasukawa (2001) who found mobbing did not successfully deter snakes. Based on this I postulate that Rockjumpers may have greater success in areas of early post-fire habitat, not due to increased visibility for predator detection, but rather to: (1) more time for warning calls to chicks and to decrease activity around nests, (2) a decrease in localized nest odour resulting in decreased instances of snakes locating nests, or (3) a decrease in Boomslang numbers as the more open landscape may make Boomslang themselves more vulnerable to predation.

As year-round territorial birds, Rockjumpers are not likely to relocate into recently burned habitat for optimal nest-sites and so may have to use sub-optimal nest-sites within their given territories. While throughout my study I found no evidence that birds will abandon their home territory for one with preferential nest-sites, when fire burned the old-growth stands of Proteaceae in the northern section of BHNR, I witnessed breeding females in adjacent territories shifting their territories slightly to include sections of the newly burned areas. Additionally, unringed birds moved into the newly available habitat within three months of the April 2017 fires, with some breeding by August 2017; these birds were likely helpers opportunistically dispersing from other territories as suitable habitat increased.

4.5.4 CONCLUSIONS

As Rockjumpers have a relatively extended breeding season, especially compared to Northern Hemisphere birds, I was able to examine predation over a large range of weather variables (i.e. from Austral winter to Austral summer). Predicted increases in fire frequency due to climate change for South Africa (Easterling et al. 2000b) may increase habitat openness (i.e. decrease vegetation cover) and allow Rockjumpers to spot predators from further away, with birds then more successful at defending their nests. However, the increasing temperatures also predicted to occur under climate change scenarios may result in increased probability of snake predation. My findings emphasize the need for an integrative approach to assessing species vulnerability. While climate change will have many direct effects on species and individuals (Cunningham et al. 2013b, Martin et al. 2017, Bladon et al. 2019, Van de Ven et al. 2019), these effects may be mediated by indirect species interactions, as well as through direct effects on the focal species. I provide further evidence that examining indirect effects and their ecological interactions are sometimes necessary to inform an accurate framework for determining species vulnerability (Williams et al. 2008).

CHAPTER 5: GENETIC DATA SHOWS EVIDENCE FOR PAST BOTTLENECK AND CURRENT DISPERSAL IN A SKY ISLAND ENDEMIC

5.1 SUMMARY

Mountain habitats physically isolated from one another ("sky islands") represent a unique system for studying dispersal in seemingly isolated populations. The Cape Fold Belt of southwest South Africa forms a sky island archipelago of high-altitude alpine Fynbos of which the Cape Rockjumper *Chaetops frenatus* is an avian-endemic. Continued contraction of habitat due to increasing temperatures may be causing further isolation of *C. frenatus* populations beyond their dispersal capacities. In this study, I sequenced two mitochondrial loci and one nuclear locus of 73 samples from 13 localities representing 8 mountain ranges. I found (1) low overall genetic diversity, (2) no evidence for geographically-based genetic structuring, and (3) no evidence for inbreeding within localities. Haplotype networks suggested that *C. frenatus* may have experienced a bottleneck or founder effect in their recent genetic past — a result supported by a significantly negative *Tajima's D* value. *Chaetops frenatus* may have been isolated in areas of Pleistocene refugia in the Cape Fold Belt. As the first avian genetic study to arise from a range-restricted species of the Cape Fold Belt sky islands, my results show no evidence that *C. frenatus* are unable to disperse across inhospitable lowland habitat, and thus may not experience isolation due to climate change. I thus potentially found further support that selective pressure in species with highly specialized habitat niches may have a stronger effect than dispersal limitations.

5.2 INTRODUCTION

The glacial cycles of the Pleistocene recurrently brought formerly isolated populations into contact with one another during cooler periods that increased low-elevation distributions (Hewitt 1996, Hewitt 2000, Avise 2009). Following the last glaciation period, cooler-adapted species either shifted ranges to higher latitude or else became relicts in mountaintop refugia ("sky islands"; McCormack et al. 2009). Sky islands are analogous to ocean archipelagos, with individual mountain populations isolated due to unsuitable low-elevation habitat that acts as a barrier to dispersal. Predicted increases in temperatures due to climate change will likely result in increased isolation of these high-altitude species as lowland habitat expands and alpine habitat shifts upslope (Kupfer and Cairns 1996, Sekercioglu et al. 2008, Chamberlain et al. 2012, Scridel et al. 2018). Depending on the distance between populations and their ability to disperse, this isolation can lead to a feedback cycle of increased inbreeding depression among populations and ultimately descending into an "extinction vortex" (Frankham 2015).

The inhibited gene flow and localized genetic drift resulting from decreased dispersal in sky islands means alpine species often develop genetic differentiation among isolated populations (McCormack et al. 2009). This isolation can be seen genetically in geographically-based genetic structuring (e.g. Bech et al. 2009, Jackson et al. 2015, Lonsinger et al. 2015). By examining genetic structure in isolated populations within species, areas of low connectivity may be identified (Allendorf et al. 2013). Especially for species at risk, understanding the genetic diversity underlying the spatial structure of populations is important for establishing the appropriate scale and subunits for conservation management (Laikre 2010). While it has been suggested that species in isolated populations should evolve more efficient dispersal ability (Travis et al. 2013), studies have shown that effective dispersal distance (i.e. that which results in the disperser contributing to the gene pool) is constrained by population growth rate and distance between habitat patches (Van Dyck and Baguette 2005, Baguette and Schtickzelle 2006). However, even if populations are separated by geographic barriers, they may have low genetic diversity due to strong selective pressure if they occupy highly specialized habitat niches (Orsini et al. 2013). In instances of highly specialized niches, a general analysis of genetic variation may not accurately identify the underlying processes driving this variation, and may require analysis of both neutral (i.e. genes under no selective pressure) and non-neutral (i.e. genes under selective pressure) genetic variation (Orsini et al. 2013).

As would be expected, genetic structuring in sky island endemics has been seen across nearly all taxa, including plants (e.g. Gizaw et al. 2013, Lexer et al. 2013), arthropods (e.g. Masta 2000, Knowles and Richards 2005), amphibians (e.g. Vörös et al. 2017), birds (e.g. Bech et al. 2009, Jackson et al. 2015), and mammals (e.g. Browne and Ferree 2007, Lonsinger et al. 2015). The sky islands of South Africa's Cape Fold Belt have as yet been overlooked for such studies among birds, despite the possibility of elevation-based species diversification (Verboom et al. 2015), and presence of high levels of endemism (proportional to geographic size) within the Fynbos across taxa (Cowling and Holmes 1992, Picker and Samways 1996, Sharratt et al. 2000, Wishart and Day 2002). Here, I focused on the Cape Rockjumper *Chaetops frenatus*, an avian sky endemic restricted to the Mountain Fynbos of southern African sky islands. The most recent expansion of Mountain Fynbos results from recent historical shifts in precipitation regimes; it expanded ~96–37 KYA ("KYA": thousand years ago) and then contracted resulting in the current isolated patches of Mountain Fynbos across the Cape Fold Belt (Quick et al. 2016). Population declines correlated with warming habitat (Milne et al. 2015), as well as a small population size, led to *C. frenatus* being placed as Near Threatened on the IUCN Red List of Endangered Species in 2017 (IUCN 2017). The possible continued contraction of Mountain Fynbos habitat due to the expansion of warmer lowland habitat from climate change may be one reason for the decline and isolation of *C. frenatus* populations in warmer areas of their habitat.

In this study, I aimed to determine genetic structuring among sky island populations of *C. frenatus* using a combination of mitochondrial DNA (mtDNA) and nuclear DNA (nDNA) to test if *C. frenatus* are experiencing geographically-based genetic isolation. I hypothesized that unsuitable lowland habitat between the geographically distinct mountain ranges would act as a barrier to effective dispersal between populations, resulting in genetic structuring aligned with the topography of the Cape Fold Belt. If I find geographic genetic structuring, suggesting some populations of *C. frenatus* are genetically isolated from one another, this may indicate key areas in need of conservation. Alternatively, if selective pressure is at work due to the highly specialized habitat occupied by *C. frenatus*, I may find low overall genetic diversity and no genetic structuring, as suggested by Orsini et al. (2013). As both sister-species within family Chaetopidae represent small relict groups at the far end of early radiation of passerines into Africa of high taxonomic interest (Fjeldså and Bowie 2008), I chose the Drakensberg Rockjumper *C. aurantius* as my outgroup. I also chose *Picathartes gymnocephalus* as an additional outgroup as the next nearest relation (Oliveros et al. 2019) the relationship within Chaetopidae has yet to be fully determined.

5.3 METHODS

5.3.1 STUDY AREA AND SAMPLE COLLECTION

The study area encompassed much of the Western and Eastern Cape provinces of South Africa, spanning the species distribution range for the *C. frenatus*. During 2016 and 2017, I collected blood samples of 73 *C. frenatus* from 13 localities representing eight mountain ranges of the Cape Fold Belt (Figure 1). For two additional localities I attempted to sample *C. frenatus* based on records from the South African Bird Atlas Project ("SABAP") 1 & SABAP 2 (sabap2.adu.org.za), but were unable to locate birds at these localities (e.g. Tsitsikamma; Figure 1). Although generally contiguous, many of these mountain ranges are interspersed by >20 km of lowland habitat (Lee and Barnard 2016). This lowland habitat is generally warmer than habitat occupied by *C. frenatus*, and is often also either drier (e.g. Karoo) or densely vegetated (e.g. Albany thicket), thus representing a potential dispersal barrier for the *C. frenatus*. Localities ranged from 32° and 34° S latitude and 18° to 25° E longitude, spanning from ~100 metres above sea level ("masl") near the southwest tip of South Africa to ~1,800 masl in the northern Cederberg mountains (Figure 5.1). Despite the low elevation occurrence of *C. frenatus* near the southwestern tip of South Africa, this area does in fact consist of the short Ericaceae-dominated Mountain Fynbos (Figure 5.2). I additionally collected 15 blood samples of *C. aurantius* from two localities at 30° S latitude and 27° to 28° E longitude in the Lesotho Highlands, spanning from ~2,600 masl to ~2,800 masl (Figure 5.1). Localities were selected through field surveys and from occurrence data on the South African Bird Atlas Project ("SABAP") 2 (sabap2.adu.org.za).

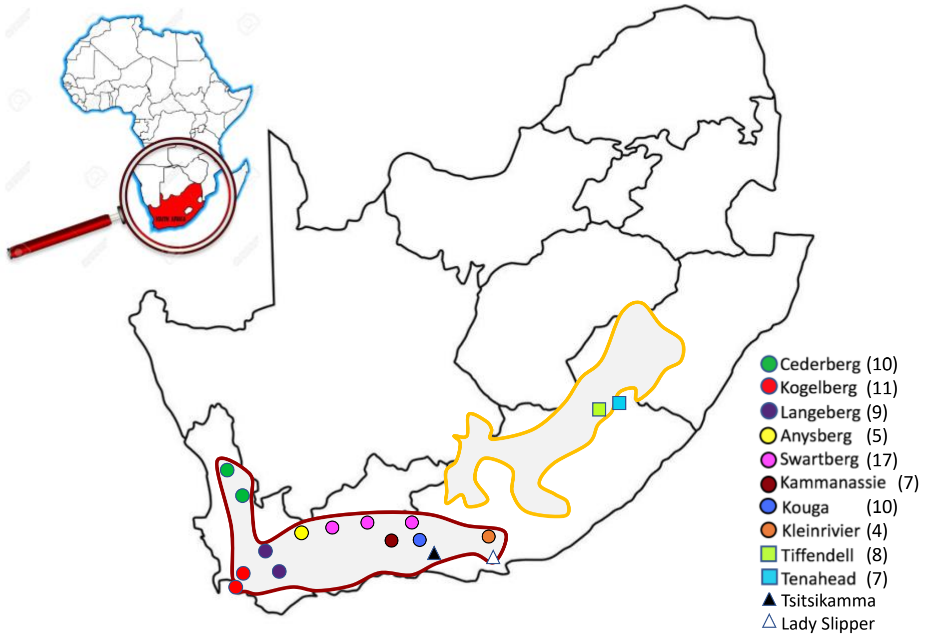

Figure 5.1 Map of South Africa showing locations of successful (circles; N = 8) and unsuccessful (triangles; N = 2) sample collection from 10 mountain ranges across the distribution of *Chaetops frenatus* (shaded grey area outlined in dark red), and from two sites (squares; N = 2) within the distribution of *C.* aurantius (shaded grey area outlined in orange). Samples were collected from Oct 2016 to Oct 2017 in the Western and Eastern Cape provinces of South Africa. Numbers in parentheses indicate sample size collected per mountain range.

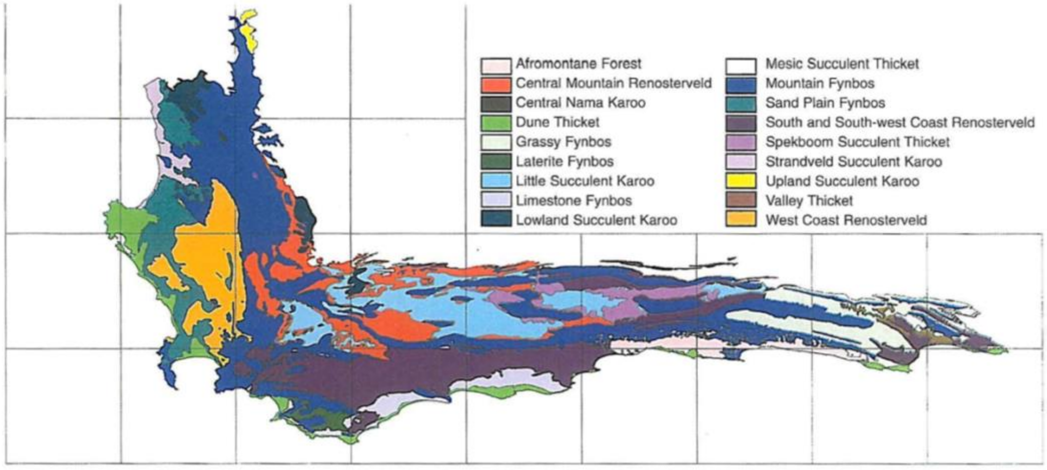

Figure 5.2 Cape Floristic Region showing major delineations of vegetation types from Cowling and Heijnis (2001), with Mountain Fynbos (i.e. alpine Fynbos, habitat suitable for *Chaetops frenatus*) shown in dark blue.

I caught wild-living individual *C. frenatus* and *C. aurantius* using snap traps baited with tenebrionoid spp. Upon capture, I recorded a GPS point, and fitted birds with unique numbered aluminium rings (SAFRING). Blood samples (~50 µL) were collected by brachial vein puncture, whereby a small pin-prick was made with a 26-gauge needle and the resulting blood droplet collected into a capillary tube and preserved in ~90 % alcohol. The entire sampling process took <5 min of handling time and occurred adjacent to, or within, birds' territories for release immediately after sampling. Blood samples were stored at 4 °C until further use for DNA extraction.

5.3.2 DNA EXTRACTION AND PRIMER SELECTION

Genomic DNA was extracted from blood samples in a dedicated lab following standard salt extraction techniques (Bruford et al. 1992) using Proteinase K (QIAGEN, Germany; 10 mg mL^{-1}), modified by use of lysis and elution buffers (buffers ATL and AE respectively; QIAGEN, Germany). To have the first grasp of population structure of a South African sky island endemic, I chose to analyse two mtDNA markers and one nDNA marker.

Primers were prepared by Integrated DNA Technologies, USA. Two primer sets were selected from Zuccon and Ericson (2012) for mtDNA markers: "ND2" which encodes the NADH dehydrogenase subunit 2 and "cytb" that encodes the cytochrome b. For the selected nDNA marker, the recombination activating gene 1 — "RAG1", I designed the primer online (www.ncbi.nlm.nih.gov/tools/primer-blast/) using sequences of *C. frenatus* and my additional outgroup *P. gymnocephalus* (representing the sister family Picathartidae) available from GenBank® (www.ncbi.nlm.nih.gov/genbank/; Date: 04-03-2019; Table 5.1).

Table 5.1 Overview of forward and reverse primers used to amplify segments of three genetic markers (NADH dehydrogenase subunit 2 — “ND2”, cytochrome b — “cytb”, and recombination activating gene 1 — "RAG 1") from families Chaetopidae and Picathartidae.

gene	Primer name	direction	sequence 5’–3’	source
ND2	ND2-F241	forward	ACCGGRCAATGRGAYATYACYCA	Zuccon and Ericson (2012)
ND2	ND2-R811	reverse	CWRCTGGRGCTATBTCYTGTTT	Zuccon and Ericson (2012)
cytb	cytb-bird-F179	forward	GCATCTACCTACACATYGGCCGAG	Zuccon and Ericson (2012)
cytb	cytb-bird-R655	reverse	TTGGCTGGTGTGAAYTTTTCTGGGTC	Zuccon and Ericson (2012)
RAG1	pica_RAG1F	forward	TGAACTGGAGGCTATAATGC	This study
RAG1	pica_RAG1R	reverse	TTTCATTCCCATGTGCTACA	This study

5.3.3 DNA AMPLIFICATION AND SEQUENCING

For amplification of mtDNA, PCR reaction occurred in a final volume of 27 μL containing approximately 100 ng of genomic DNA, 0.4 μM of each primer, and 12.5 μL of a mixture dNTPs, $MgCl_2$, Taq polymerase and stabilizers (cytb: iTaq™ Universal SYBR Green Supermix® by Bio-Rad Laboratories Inc.; ND2: TopTaq PCR MasterMix ©QIAGEN). For amplification of the nDNA the PCR final volume was 33 μL and contained approximately 200 ng of genomic DNA, 0.6 μM of each primer, and 12.5 μL of a mixture of dNTPs, $MgCl_2$, Taq polymerase and stabilizers (iTaq™ Universal SYBR Green Supermix® by Bio-Rad Laboratories Inc.).

Mitochondrial DNA PCR protocol was as follows: initial denaturing step of 94 °C for 5 min, 40 cycles of denaturing at 94 °C (30 s), annealing at 58 °C (ND2) or 60 °C (cytb; 30 s), and extension at 72°C (40 s), final extension at 72 °C (5 min). Nuclear DNA PCR protocol was as follows: initial denaturing at 94 °C (5 min), 40 cycles of denaturing at 94 °C (30 s), annealing at 51.5 °C (40 s), and extension at 72 °C (40 s), final extension at 72 °C (5 min). Sequence data for *P. gymnocephalus* were retrieved from GenBank for ND2 (Fuchs et al. 2006), cytb (Ericson and Johansson 2003), and RAG1 (Barker et al. 2002; see Table S1 for accession numbers). Before sequencing, PCR efficiency and correct fragment size were checked by electrophoresis in 1.0 % agarose gel stained with CoralLoad Gel loading dye (©QIAGEN). Sequencing of the three loci was outsourced to Macrogen Europe (Amsterdam, the Netherlands); sequences were only produced in the forward direction. I visually checked each sequence individually for base-calling of individual nucleotides.

Sequences have been deposited in GenBank (accession numbers LR723324-LR723539; see Appendix 3 Table S5.1 for individual accession numbers).

5.3.3 PHYLOGENETIC ANALYSIS

Sequences were aligned in MEGA (v 7.0.62; Kumar et al. 2016) with the ClustalW method. I tested for saturation in each codon of each marker using DAMBE v. 7 (Xia 2018), and found no evidence of saturation in any of the codon positions. I estimated uncorrected p-distances both among groups/species (*C. frenatus*, *C. aurantius*, and *P. gymnocephalus*) and within groups/species (*C. frenatus* and *C. aurantius*) in MEGA to investigate the degree of divergence and examine overall genetic variation. Population structure was examined using minimum-spanning networks (Bandelt et al. 1999) for both cytb and ND2 in PopART (Leigh and Bryant 2015; http://popart.otago.ac.nz).

Genetic differentiation between populations was examined using an Analysis of Molecular Variance (AMOVA; Excoffier et al. 1992) in ARLEQUIN v. 3.5 (Excoffier and Lischer 2010). *Chaetops frenatus* and *C. aurantius* sequences were split into eight and two groups respectively based on localities where samples were obtained (see Figure 1). Fixation indices were used to estimate the proportion of genetic variability found within populations (F_{ST}; i.e. within each mountain range), among populations within groups (F_{SC}; i.e. among mountain ranges) and between groups (F_{CT}; i.e. between *C. frenatus* and *C. aurantius*). Due to the lack of nucleotide differences between individuals and populations of *C. frenatus* and *C. aurantius* at the RAG1 locus, I did not perform an AMOVA on RAG1.

Sequence data were also used to detect signal of population expansion, within each species (*C. frenatus* and *C. aurantius*) as estimated with *Tajima's D* (ARLEQUIN v3.5). When $D = 0$ indicates no evidence of selection, $D > 1$ indicates population contraction, and $D < 0$ indicates a post-bottleneck expansion (Tajima 1989).

I then determined whether polymorphisms for both mtDNA loci showed evidence of selective pressure using a McDonald-Kreitman Test (MKT) with divergence corrected by Jukes&Cantor (http://mkt.uab.es/mkt/; Egea et al. 2008). The MKT compares neutral and non-neutral codons between closely related species to determine whether replacement differences within the sequence (i.e.

polymorphisms) are adaptive (McDonald and Kreitman 1991). The results of an MKT give a Neutrality Index (NI) and a proportion of adaptive substitutions (α) which can be used to determine what proportion of amino-acid substitutions are driven by natural selection (Smith and Eyre-Walker 2002).

To determine the evolutionary model that best fit the dataset using Bayesian Information Criterion adjusted for low sample size I first used jModelTest v. 2.1.10 (Darriba et al. 2012) for each marker. Results of jModelTest suggested best fits were two rate categories for each locus, with cytb using uniformly distributed proportions of invariable sites (HKY + I; Hasegawa et al. 1985), ND2 using four-category gamma distributed invariable sites (HKY + Γ + I; Hasegawa et al. 1985), and RAG1 using equal rates (K80; Kimura 1980). Phylogenetic inference trees were created online in CIPRES Science Gateway v. 3.3 (Miller et al. 2011) with data partitions based on each genetic marker (cytb, ND2, and RAG1) and priors set according to results of jModelTest. As I did not have sequences for the same individuals of *P*. *gymnocephalus* across all three markers, I used available sequences for RAG1 in my consensus trees.

For Bayesian inference of phylogeny I used the program MrBayes v. 3.2.6 on XSEDE with BEAGLE (Miller et al. 2010) to obtain Markov Chain Monte Carlo (MCMC) approximations of posterior trees; MCMC was run for 20,000,000 generations, sampling trees every 1,000 generations, with the first 2,500,000 generations (2,500 trees) discarded as burn-in. For maximum likelihood (ML) inference, I used Garli v. 2.0.1 on XSEDE (Bazinet et al. 2014) to obtain approximations of posterior trees based on 100 bootstraps; I ran this analysis twice to ensure the independent ML searches produced the same tree topology. I determined best fit phylogeny of Bayesian vs. ML trees based on greater number of node posterior probabilities of >95 % or >70 % (Bayesian and ML respectively; Bates et al. 2013).

5.4 RESULTS

5.4.1 SEQUENCE VARIATION

In total I produced 75 cytb sequences (380 bp), 78 ND2 sequences (505 bp), and 68 RAG1 sequences (455 bp). For the cytb marker I found more genetic variation within *C. aurantius* (N = 5 haplotypes) compared to *C. frenatus* (N = 4 haplotypes). For the ND2 marker I found five haplotypes in *C. aurantius*, and 15 haplotypes for *C. frenatus* (see below for details). Uncorrected p-distances within *C. frenatus* varied from 0.0–0.002, within *C. aurantius* varied from 0.0–0.003, and between *C. frenatus* and *C. aurantius* varied from 0.0–0.043 (Table 5.2).

Table 5.2 Uncorrected *p*-distances based on data of *Chaetops frenatus* and *C. aurantius*, for two mtDNA markers (Cytochrome b "cytb", and NADH dehydrogenase subunit 2 "ND2") and one nDNA marker (recombination activation gene 1 "RAG1").

	cytb	ND2	RAG1
within species			
C. frenatus	0.001 ± 0.001	0.002 ± 0.001	0.0 ± 0.0
C. aurantius	0.003 ± 0.002	0.003 ± 0.001	0.0 ± 0.0
between species			
C. frenatus - C. aurantius	0.015 ± 0.006	0.043 ± 0.008	0.0 ± 0.0

Tajima's D for both the mitochondrial loci in *C. frenatus* were significantly negative (cytb: *Tajima's D* = −1.70, *p* = 0.020; ND2: *Tajima's D* = −1.77, *p* = 0.023), while significantly negative for cytb but not significant for ND2 in *C. aurantius* (cytb: *Tajima's D* = −0.78, *p* = 0.028; ND2: *Tajima's D* = 1.08, *p* = 0.893).

5.4.2 POPULATION GENETIC STRUCTURE

I found no evidence for genetic differentiation among *C. frenatus* localities, with low fixation indices showing strong evidence for interbreeding among the various populations (cytb: F_{ST} = 0.035, DF = 6; ND2: F_{ST} = 0.057, DF = 6). Despite the proximity of *C. aurantius* sample populations to one another, I found little evidence for interbreeding among them, with higher fixation indices than those for *C. frenatus* (cytb: F_{ST} = 0.277, DF = 1; ND2: F_{ST} = 0.470, DF = 1). The phylogenetic networks did not show any clear pattern of genetic structure separating the sky islands (Figure 5.3)

The haplotype network for cytb showed little variation or pattern, while I found a "starburst" pattern for *C. frenatus* in the ND2 network (Figure 5.3). When visualized by frequency per locality, ND2 showed little evidence for spatial genetic structure (see inset Figure 5.4 below). The low number of haplotypes within *C. frenatus* at the cytb locus (N = 4) resulted in a haplotype network which did not have the variability to visualize frequency by locality. Results of the MKT showed that while there was little evidence the polymorphisms for cytb were under selective pressure (NI = NULL, α = NULL, χ_2 = 0.325, *p* = 0.568), there was evidence the polymorphisms for ND2 were under negative selective pressure (NI = 1.559, α = – 0.559, χ_2 = 0.309, *p* = 0.578).

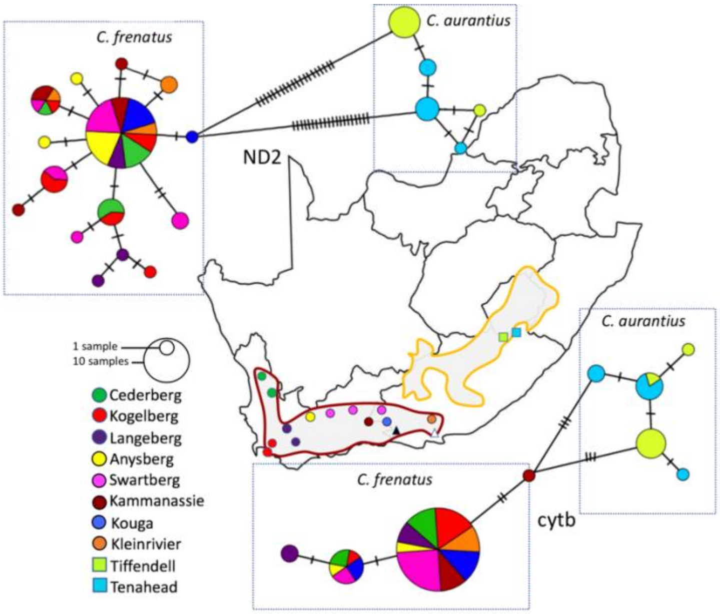

Figure 5.3 Minimum-spanning haplotype networks for mitochondrial loci cytb and ND2. Each circle represents a haplotype with its size proportional to haplotype frequency, each branch illustrated one nucleotide change and each hash-mark indicates an additional nucleotide difference. Circles are colour-coded according to sampling locality. Distributions of *Chaetops frenatus* and *C. aurantius* are depicted by outlined shaded areas in red and orange respectively.

Overall, most of genetic variation was within populations of *C. frenatus* (cytb: 96.48 %, ND2: 94.26 %; see Table 5.3 for summary of AMOVA), with similar variation partitioned between species *C. frenatus* and *C. aurantius* (cytb: 93.86 %; ND2: 93.77 %). I also found that while some variation existed within individual populations of both *C. frenatus* and *C. aurantius* (cytb: 5.59 %; ND2: 5.35 %), there was little variation among populations (cytb: 0.55 %; ND2: 0.88 %). High fixation indices for both cytb and ND2 showed there was little evidence for interbreeding between *C. frenatus* and *C. aurantius* (cytb: F_{CT} = 0.939, DF = 1; ND2: F_{CT} = 0.938, DF = 1).

Table 5.3 Analysis of molecular variance (AMOVA) based on data for 8 localities of *Chaetops frenatus*, and 2 localities of *C. aurantius*, for two mtDNA markers (Cytochrome b "cytb", and NADH dehydrogenase subunit 2 "ND2"). F-statistics are provided for genetic differentiation between groups (F_{CT}), among populations within groups (F_{SC}), and among populations (F_{ST}). All values significant at $p < 0.001$.

source of variation	locus	DF	variance components	% variation	*F*-statistic
between two genetic groups (*C. frenatus* and *C. aurantius*)					
between groups	cytb	1	5.75	93.86	F_{CT} 0.939
	ND2	1	10.29	93.77	F_{CT} 0.938
among populations	cytb	7	0.03	0.55	F_{ST} 0.944
	ND2	7	0.10	0.88	F_{ST} 0.946
within populations	cytb	62	0.34	5.59	F_{SC} 0.090
	ND2	66	0.59	5.35	F_{SC} 0.141
within *C. frenatus* genetic group					
among populations	cytb	6	0.01	3.52	F_{ST} 0.035
	ND2	6	0.04	5.74	F_{ST} 0.057
within populations	cytb	49	0.30	96.48	
	ND2	53	0.59	94.26	
within *C. aurantius* genetic group					
among populations	cytb	1	0.19	27.68	F_{ST} 0.277
	ND2	1	0.50	47.03	F_{ST} 0.470
within populations	cytb	13	0.49	72.32	
	ND2	13	0.56	52.97	

My consensus tree based on ML inference resulted in stronger predictive weight of node probabilities compared to my Bayesian tree (see Appendix 3 Figure S5.1 for Bayesian inference tree), and while I found no obvious structuring within *C. frenatus*, I did find strong support for two clear clades within family Chaetopidae being *C. frenatus* and *C. aurantius* (Figure 5.4).

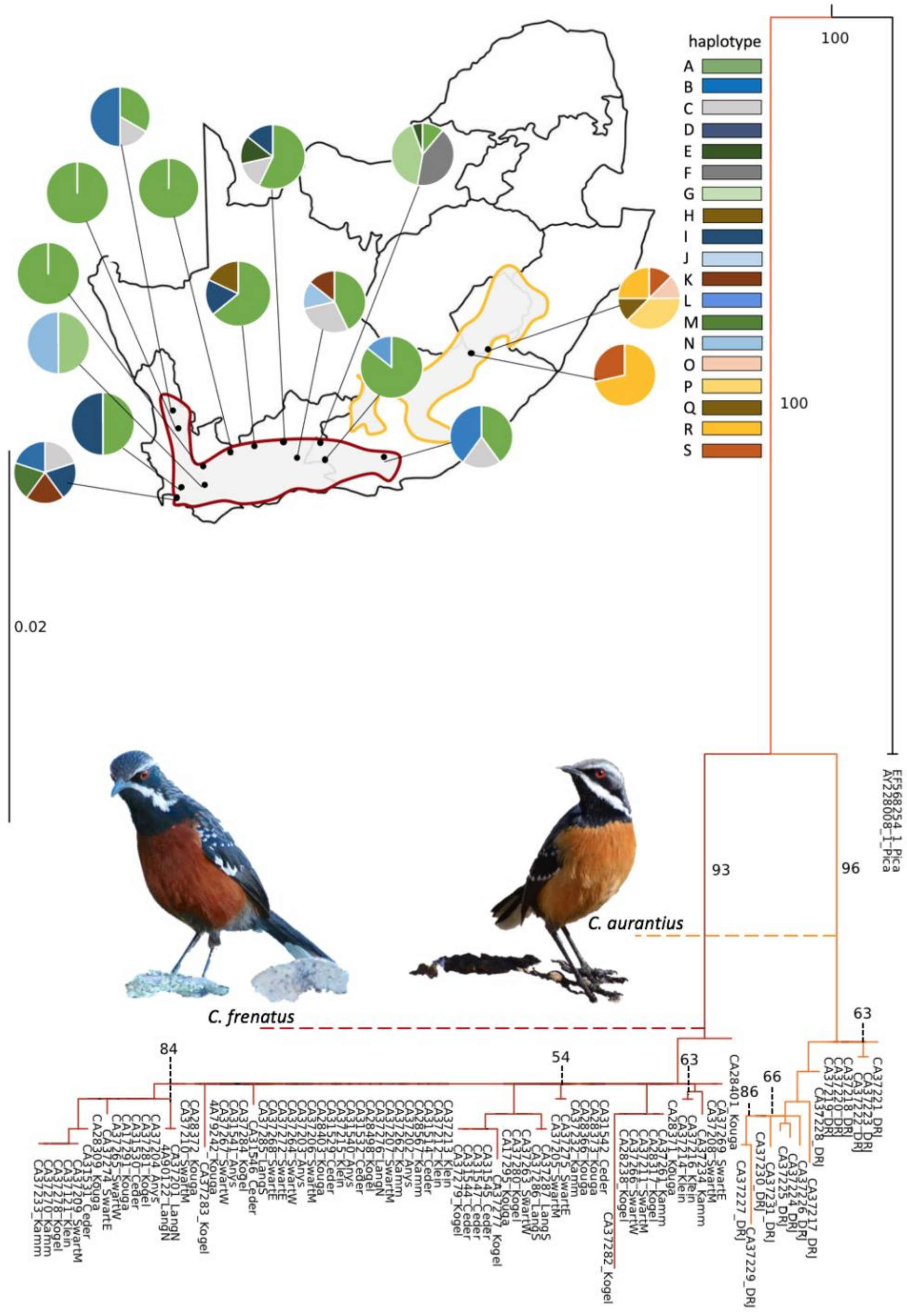

Figure 5.4 Consensus tree based on maximum likelihood inference for three genetic markers (two mtDNA: cytb and ND2; one nDNA: RAG1), from *Chaetops frenatus* (N = 71), with outgroups *C. aurantius* (N = 15) and *Picathartes gymnocephalus* (N = 2). Bootstrap scores of >50 are indicated on each branch. Inset: ND2 haplotype frequencies showing relative frequency per locality of each haplotype (*C. frenatus* haplotypes N = 15, "A" through "N"; *C. frenatus* haplotypes N = 5, "O" through "S"). Localities are indicated on inset map of South Africa with species distributions shaded in grey and outlined in red (*C. frenatus*) or orange (*C. aurantius*).

5.5 DISCUSSION

I found no evidence for genetic structure among populations of *C. frenatus*. The resulting population substructure among populations ($F_{ST} < 0.05$) indicated only a slight to moderate genetic differentiation among the populations, similar to two other studies on genetic structuring in sky island endemic birds (Bech et al. 2009, Sittenthaler et al. 2018). Instead, it is possible my study provides further support for the hypothesis that species with specialized niche requirements may experience selective pressure which limits their overall genetic diversity [see Orsini et al. (2013)]. I also found evidence for interbreeding among individuals from different mountain ranges, suggesting that birds may be able to effectively disperse between mountain ranges. This suggests *C. frenatus* is not currently experiencing inbreeding. However, the lack of structure may also indicate the chosen loci are under selective pressure and so are similar due to mutations relevant for alpine species. The shape of my mtDNA haplotype networks suggest *C. frenatus* experienced a bottleneck or founder effect in their recent genetic past. *Tajima's D* also showed support for a past bottleneck event in *C. frenatus* at both mtDNA markers. In addition, overall low genetic diversity within *C. frenatus* indicates the potential for negative effects from a reduced effective population size.

5.5.1 POPULATION VARIATION, STRUCTURE, AND DISPERSAL

My finding that most of the genetic differentiation within *C. frenatus* was from within populations, as opposed to among populations, suggests some genetic structuring while my haplotype frequency network implies this is not geographically based (Figure 5.4). The genetic composition of *C. frenatus*, along with the lack of geographic distribution of genetic populations, suggest that although mountain populations of *C. frenatus* are separated from one another by unsuitable lowland habitat, the actual degree of isolation does not hamper gene flow. The question then remains as to how *C. frenatus* are managing to effectively disperse across large tracts of unsuitable habitat, presenting an interesting avenue for future research. While in some sky islands (e.g. Mexican Jays *Aphelocoma ultramarine*; McCormack et al. 2008), low occurrence rates in lowland habitat implied dispersal through these habitats, according to SABAPs 1 and 2 (1987–1991, and 2007–present, respectively) there is currently a complete lack of observations for *C. frenatus* in the lowland habitat separating the mountain ranges of the Cape Fold Belt (sabap2.adu.org.za; Harrison et al. 1997).

I also found evidence that while populations may be interbreeding, *C. frenatus* have low overall genetic diversity among populations for both cytb and ND2 markers (i.e. genetic variation <5 %). Low genetic variation among populations may be from low diversity within the species, or close inbreeding within an otherwise diverse population (Ceballos et al. 2018); since the results of the AMOVA suggest *C. frenatus* populations are interbreeding, there may be low diversity within the species itself. Low diversity can arise from a recent demographic expansion (e.g. bottleneck), here possibly tracking the Mountain Fynbos expansion ~37 KYA. A bottleneck may have extirpated many individuals, reducing overall genetic variability, but because such a population expansion would be recent in evolutionary terms there may not yet be measurable mutations. Alternatively, as the loci analysed are protein-coding, natural selection may be purging all but a few advantageous alleles (e.g. strong stabilising selection due to habitat specialisation; Orsini et al. 2013), as *Tajima's D*'s for the mtDNA loci were negative, indicating a higher frequency of rare alleles than would be expected under neutrality.

Although *C. frenatus* had a greater number of ND2 haplotypes than *C. aurantius* (N = 15 and 5, respectively), the number is not proportionally greater considering the difference in distribution coverage (~750 km and ~20 km respectively). The results of my MKT suggest the polymorphisms present between *C. frenatus* and *C. aurantius* at the ND2 loci are indicative that negative selection may be preventing the fixation of harmful mutations, as would be expected if species were under selective pressure from habitat specialization (Orsini et al. 2013).

5.5.2 BOTTLENECK OR FOUNDER EFFECT

The haplotype network for ND2 showed the predicted mtDNA starburst pattern for a population that had experienced a bottleneck or founder effect, i.e. a star-like shape where core haplotype is shared by most populations and then many less-common peripheral haplotypes (Ferreri et al. 2011; Figure 5.4). This result was corroborated by *Tajima's D*, wherein a negative result indicated a population expansion after a bottleneck event (Ramakrishnan et al. 2005); for this study I was unable to determine whether this pattern was due to a bottleneck versus a founder effect. Either instance may be due to changes in habitat distribution during the last Pleistocene glacial period — a possible extrapolation of the Pleistocene refugia hypothesis (Grubb 1982). The Pleistocene refugia hypothesis (sometimes referred to as Holocene Refugia) suggests that repeatedly expanding glaciers toward the end of the Pleistocene epoch resulted in a large proportion of speciation events, especially among sister taxa (Avise and Walker 1998, Avise 2009). While the Pleistocene refugia hypothesis has previously undergone criticism stating many of these divergence events preceded the Pleistocene (Whitten 1979, Knapp and Mallet 2003), there remains a large number of studies across taxa where speciation or isolation events correlated with major changes in climate ~37 KYA (e.g. Johnson and Cicero 2004, Ribera and Vogler 2004, Foltz et al. 2008, Quick et al. 2016, Vörös et al. 2017).

However, Africa did not have glaciers in the Pleistocene, and so changes in distribution of *C. frenatus* were likely due not to glaciers specifically, but to shifts in vegetation structure from changing weather patterns during the last glacial period. As the Fynbos experienced a major shift wherein ericaceous Fynbos contracted >96 KYA, expanded ~96–37 KYA, and again retreated ~37 KYA (Quick et al. 2016), I suggest two possibilities in relation to this hypothesis: (1) *C. frenatus* may have been confined to one mountain range when Fynbos retreated >96 KYA, then radiated out from this bottleneck population when Fynbos expanded ~96–37 KYA; or (2) *C. frenatus* was extirpated (or not initially present) in the Cape Fold Belt, but the expansion of ericaceous Fynbos ~96–37 KYA, along with shrinking surrounding Afro-montane forests, led to colonisation by a founder population of the sister *C. aurantius* lineage. In the second scenario, speciation may have been promoted by geographic isolation that occurred after the initial colonization, then resulting in the current differences between the two species. However, the bottleneck or founder population of *C. frenatus* may also have originated much earlier during the Miocene, as Cape Fold uplift during this time period has been suggested as the main source of speciation among Fynbos plant communities (Cowling et al. 2009, Pirie et al. 2016)

From a purely genetic perspective, my results suggest *C. frenatus* and *C. aurantius* have low species-level diversity based on uncorrected *p*-distance values. My recorded cytb *p*-distance result for *C. frenatus*-*C. aurantius* (1.5 %) was below most *p*-distance values for species-level distances of 3.3–12.8 % in passerines (Martens et al. 2005, Luo et al. 2014, Liu et al. 2016), although Martens et al. (2011) suggested sister-species can be <3 %. Similarly, my recorded ND2 *p*-distance results for *C. frenatus*-*C. aurantius* (4.3 %) were at the lower range of *p*-distance values for previous species-level distances of 2.0–13.7 % of passerines (Aliabadian et al. 2012, Zuccon and Ericson 2012, Luo et al. 2014). However, this is not entirely surprising, as Martens et al. (2011) indicate one should use caution in applying previous species *p*-distance values to apparent sister species.

These species are superficially similar in appearance and vocalization, their main difference being breast colouration and distribution, with *C. aurantius* inhabiting high-altitude grassland of the Drakensberg Mountains and Lesotho Highlands as opposed to high-altitude Fynbos (Hockey et al. 2005). I thus recommend further investigation into their taxonomic status using a holistic approach examining their morphology (e.g. source of colour variation), likely ability to interbreed (e.g. difference in vocalizations and breeding system), and timing of genetic differentiation (e.g. molecular clock dating).

5.5.2 *C. FRENATUS* AND EDGE EXTINCTION

Mountain Fynbos in South Africa extends from the coast of the Cape Peninsula (in the very southwest corner of South Africa), to ~300 km north into the Cederberg mountains, and ~600 km east ending near Port Elizabeth. Thus, while the Cape Peninsula consists of habitat which is suitable for *C. frenatus*, there have been no records of birds on these mountains in recorded history (Cohen and Frauenecht 1993); indeed, there are also no records from the eastern coastal edges of Mountain Fynbos habitat (Lee and Barnard 201). Species extinction is often preceded by initial habitat fragmentation and increasing distance between suitable patches, resulting in local population extinction on the edges of a species distribution (Woodroffe and Ginsberg 1998, Ceballos and Ehrlich 2002). Conceivably *C. frenatus* were once located in this area but have since been extirpated. This may have been due to human encroachment (or human-associated species such as domestic cats and dogs, or invasive rats) or the area became unsuitable due to too many years between fires. In the first instance, it may be that *C. frenatus* do occasionally recolonize the mountains only to be again driven off by anthropogenic disturbance, and in both instances it may be that once *C. frenatus* edge territory populations become extinct they are unlikely to recolonize [as suggested by Ceballos and Ehrlich (2002)]. Such edge extinction may have occurred as recently as the last three decades; despite seemingly suitable habitat on the Lady Slipper mountain range near Port Elizabeth, Eastern Cape, where birds were recorded by SABAP1 (1987–1991), there are no records from the more recent SABAP2 (2007–present).

In addition, while *C. frenatus* samples were collected from the furthest east known occurrence of *C. frenatus* in 2017 (i.e. Kleinrivier), on return to the area in 2019 I recorded no occurrence of *C. frenatus*. As in Black Grouse *Tetrao tetrix* (Sittenthaler et al. 2018), the greatest genetic variation for *C. frenatus* was found in edge populations, areas such as Kogelberg where the habitat ends abruptly with the Southern Ocean (inset Figure 5.4). Increased variation at the edge of species' distributions has been attributed to reduced dispersal and gene flow (Sittenthaler et al. 2018), fragmentation, isolation, genetic drift, and small population size (Arnaud-Haond et al. 2006, Böhme et al. 2007), or human conflict (Woodroffe and Ginsberg 1998). In all cases, these edge populations are placed at increased risk of extinction (Woodroffe and Ginsberg 1998, Ceballos and Ehrlich 2002). In fact, the edge population of *C. frenatus* at Kogelberg seemed to contain a larger population density to those elsewhere (personal observations), although this was possibly due to lower elevation at sea-level resulting in more productive habitat.

5.5.3 CONCLUSIONS

While I did not detect any geographical genetic structure in *C. frenatus* populations, their overall low genetic diversity suggests further research is needed to conserve remaining populations and dispersal avenues. As well, while my mtDNA did show differences among and between populations, these findings would be significantly strengthened by the addition of an alternate DNA sequence or longer mtDNA sequences. Although the cause of low genetic diversity in *C. frenatus* has yet to be determined, its potential negative effects seem clear — genetic theory predicts reduced effective population size will result in a substantial loss of genetic variation, corresponding to a reduction in allele number and heterozygosity at polymorphic loci (Nei 1978, Varvio et al. 1986). It thus seems possible that declining populations are resulting in an overall loss of genetic diversity, although low diversity may also be due to selective pressure. Moreover, as *C. frenatus* habitat continues to warm, and suitable alpine Fynbos retreats upslope, it seems likely climate change will impact gene flow in the future. However, my finding of low genetic variation and no genetic structuring may be complicated by the specialized niche inhabited by *C. frenatus*; that being said, a lack of genetic diversity nevertheless may indicate an inability to adapt to changing environments. The signature of a bottleneck/founder effect within *C. frenatus* suggests an interesting link between paleoclimate, the potential for climate refugia, and current species distributions in the Fynbos. While this is the first genetic structuring study on an avian endemic of the Cape Fold Belt sky islands, my study provides insights into processes that may have impacted speciation and evolution within this unique study system.

CHAPTER 6: FINAL CONCLUSIONS

6.1 BENEFITS OF A DIRECT MECHANISTIC APPROACH

For the last few decades, studies examining how climate change may affect species' distributions have predominantly used ecological niche modelling to predict baseline organismal responses to changing weather patterns (e.g. Biggs et al. 2008, Bellard et al. 2012, Bonebrake et al. 2017, Freeman et al. 2019). While these are by no means uninformative, and have been the prevailing methodology for their ability to provide species responses on a large scale, these studies often do not have the fine-scale ecological information necessary to completely understand how individual species are likely to respond to changing climate (Carignan and Villard 2002, Heikkenen et al. 2006, Scridel et al. 2018, Freeman et al. 2019). In particular, these studies do not also consider changes in population persistence, which may or may not be associated with contracting distributions. Here I show the importance of collecting fine-scale ecological data on a sentinel species, and how such data collection can unearth vulnerability to climate change, by examining potential negative effects on population persistence in the Cape Rockjumper (*Chaetops frenatus*).

Previous research on Cape Rockjumpers and the other Fynbos endemic-passerines collected basic physiological data on heat tolerance and correlated this with changing habitat characteristics and species distributions (Milne et al. 2015); the results of this study suggested there may exist a direct link between physiological heat thresholds and declining reporting rates of Cape Rockjumpers in warming areas. However, a follow-up study specifically on Cape Rockjumpers found little evidence that declining populations were a direct result of a low capacity to cope physiologically with high temperatures birds are likely to experience (Oswald et al. 2018). It thus seemed the direct interactions of increasing temperatures (e.g. physiological capacity) are not as straightforward as was expected, but required more data on other aspects of Rockjumper biology to understand why their populations are declining in warmer areas.

In this thesis I have gathered data which may help explain why Cape Rockjumper populations are declining in those areas of their habitat that are experiencing the greatest degree of warming [as seen in Milne et al. (2015)]. My previous work on Cape Rockjumpers found possibly unsustainable water requirements at high temperatures for birds in respirometry chambers (Oswald et al. 2018b, c). The behavioural changes at high temperatures I found in Chapter 2 have the potential for as yet undemonstrated negative knock-on effects, and the low heterozygosity and genetic diversity found in Chapter 5 may be indicative of a potential inability to evolve to changing environments. While the aforementioned results from physiology, behaviour, and genetics, all suggest possible explanations for declining populations, the most compelling evidence for a mechanism underlying population declines in warming regions came in Chapters 3 and 4 (a potential decrease in daily mass for older nestlings beginning at ~23.5 °C, and increased probability of snake predation beginning at ~25 °C). Given my two main findings of negative effects due to increasing temperature were found in respect to the Cape Rockjumpers' reproductive success, it seems Cape Rockjumper population declines are likely occurring due to compromised fledgling quality and fledging success limiting an inability to reproduce and have effective population recruitment in warming habitat. I thus have provided a case study representing how in some cases focusing on collecting a large amount of broad ecological data on a specific sentinel species is necessary to truly grasp where a species shows vulnerability to climate change. By doing so, I have found potential points of Cape Rockjumper vulnerability to climate change, and have provided a few key areas of future work which could help determine limits on their population persistence.

6.2 IMPLICATIONS FOR FUTURE POPULATION PERSISTENCE

To extrapolate what these low temperature thresholds may mean for the future of Cape Rockjumper breeding success, I produced predictive maps showing future temperature scenarios within the current Cape Rockjumper habitat distribution and breeding season (August 15-December15). These maps compare data from 2014 and to 2074 climate change projections, and show the change in the consecutive number of days over 23.5 °C, and the change in total number of days over 25 °C. While snake predation would not have cumulative effects, and therefore total days are more informative than consecutive days over 25 °C, I chose to examine consecutive days over 23.5 °C for predicting negative effects of climate change on nestling daily mass gain, as the effects of reduced mass loss are likely additive over successive days (see Gardner et al. 2017). While the value of 23.5 °C was extrapolated from a very small set of studies on overnight mass loss in southern African birds (du Plessis et al. 2012; Van de Ven 2017), it is nonetheless useful for gaining an estimate of potential negative effects.

Predictive maps were created using future climate change projections (2076–2100 CE) obtained from the National Center for Atmospheric Research (Boulder, CO; https://esgf-node.ipsl.upmc.fr/search/cmip5-ipsl/). Models were created using experiment *r6i1p1* RCP 8.5 scenario of the CCSM4 projection from CMIP V (https://cmip.llnl.gov/cmip5/). Species distribution data were obtained from BirdLife International and NatureServe (2013; http://datazone.birdlife.org/species/search). Figures were created in the R statistical environment version 3.5.3 (RCoreTeam 2019) using the R Studio version 1.1.463 (RStudio Team 2018; see Conradie et al. 2019 for further details on methodology; Figure 6.1).

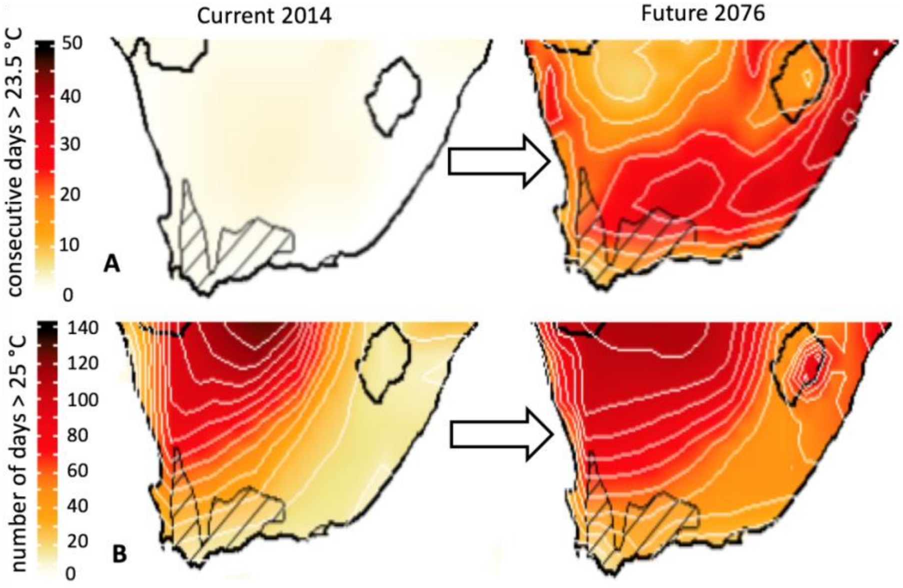

Figure 6.1 A — Consecutive number of days per breeding season (Aug 15-Dec 15) on which older Cape Rockjumers *Chaetops frenatus* nestlings may acquire insufficient mass gain to offset overnight mass loss (i.e. days >23.5 °C), and B — Average number of days per breeding season (Aug 15-Dec 15) on which Cape Rockjumpers are exposed to increased probability of Boomslang *Dispholydus typus* predation (i.e. days >25 °C), in recent years ("Current 2014") as well as a future scenario ("Future 2076").

Not surprisingly, predictive models indicate the potential for negative effects on Cape Rockjumper population persistence. Firstly, while climate data shows the number of consecutive days over 23.5 °C in 2014 was less than five, predictive modelling suggests there may be 20–30 consecutive days over 23.5 °C by 2076 (Figure 6.1A). Given that at temperatures over 23.5 °C older nestlings may not be able to maintain growth rates due to unsustainable overnight mass loss and it seems likely Cape Rockjumper nestlings will not properly develop and successfully fledge. Secondly, while the total number of days over 25 °C in 2014 was ~25, predictive modelling suggests this number will increase to between 40 and 60 by 2076; a simple extrapolation then suggests there will be twice as many days where nests have increased probability of predation due to snakes (specifically Boomslangs *Dispholydus typus*; Figure 6.1B).

As far as management strategies are concerned, I suggest an interesting possibility for conserving this near-threatened species. Under climate predictions it seems the furthest southwest corner of South Africa will remain relatively cool, and so I suggest the possibility of translocating Rockjumpers to the mountains surrounding Cape Town (e.g. the mountains of the Cape peninsula) which currently consist of appropriate habitat. However, this would require effective management in regard to controlling anthropogenic expansion and use of these mountains, as well as effectively excluding human-related potential predators (e.g. feral cats, dogs, and rats) from the area.

6.3 AVENUES FOR FUTURE RESEARCH

My thesis presents novel research showing how interconnected and complex species responses may be to climate change, and how for some species, ecological changes may occur at surprisingly mild temperatures. I suggest a follow-up study on post-fledge survival in order to examine whether decreased mass gain at high temperatures in older nestlings has negative effects on their long-term survival, recruitment, and breeding success (e.g. Magrath 1991, Thomson and Flux 1991, Greno et al. 2008, Schwagmeyer and Mock 2008).

Second, I suggest further study into the implications of foraging in the sun and the possibility of missed opportunity costs when birds are using shaded microsites at high temperatures. A supplementary study for Cape Rockjumper behaviour, examining foraging success, and energy acquisition from different prey types, would allow for a better understanding of whether there are negative costs associated with birds using shade to try and cope with high temperature.

Third, I suggest a study examining the success of individual Rockjumpers post-fledging in relation to temperature, provisioning, mass gain while nestlings, and habitat openness, combining results from Chapters 3 &4. In general, a study on how fitness varies with different fledgling weights would help determine potential consequences of data collected in this study.

Fourth, I suggest an in-depth study on the biology and abundance of Boomslangs in the Fynbos. Given their prevalence as nest predators for Cape Rockjumpers during this study, it is likely they are a major nest predator of all avian species in the Fynbos, and so increasing temperature may also place the other endemics and near-endemics at risk. However, their distribution and population abundance throughout the Fynbos is as yet unknown.

Fifth, I also recommend similar studies be performed on other populations of Cape Rockjumpers, and perhaps their sister-species the Drakensberg Rockjumper, as the current thesis was not only species-specific, but in most cases population-specific. Current distribution maps for Boomslangs show no overlap with Drakensberg Rockjumpers (Marais 2011; SABAP2), and so it would be especially interesting to examine their nest success and predation in the absence of what is, for the Cape Rockjumper, a major nest predator.

Sixth, I suggest further work on genomics for family Chaetopidae, involving multiple loci including possibly genomics and molecular dating.

Lastly, I suggest that ecological studies should be performed on multiple populations when possible, as throughout this study I found slightly different life history traits than the previous study by Holmes et al. (2002; i.e. multiple re-nesting attempts, and larger clutches).

6.4 CAPE ROCKJUMPERS AS SENTINEL FOR A CHANGING WORLD: *REDUX*

South Africa is experiencing increases in overall temperatures, extreme heat waves, instances of drought, and fires (Easterling et al. 2000a, Easterling et al. 2000b). While the Fynbos of South Africa may not expect to see such dramatic environmental changes as other South Africa biomes such as the Kalahari (Moise and Hudson 2008), small changes may have greater effects on its ecological framework due to the Fynbos' historically stable climate (Cowling et al. 2015). It thus seems shrewd to develop a framework for determining how these predicted environmental changes may alter the ecological makeup of particularly vulnerable areas.

Within this thesis I have identified areas of vulnerability to increasing temperature in the ecology of the Cape Rockjumper through a novel multi-faceted ecological data approach that can be used for assessing vulnerability in other species with similar niches or life histories. Specifically, Fynbos endemics as well as other alpine specialists and range-restricted species, as they likely have similar niche requirements and sensitivity for coping with climate change (e.g. through an inability to move to cooler/wetter habitat). In addition, the moderate air temperatures at which I found potential negative effects both in Cape Rockjumper nestling mass gain in Chapter 3, and potential nest failure from predation in Chapter 4, are indicative of the particular sensitivity to changes in environmental conditions that may occur in the Mountain Fynbos.

Cape Rockjumpers are an ideal sentinel for examining climate responses since they occupy sky islands (McCormack et al. 2009), are candidate climate relicts (Woolbright et al. 2014), show high habitat specialization (Scridel et al. 2018), and are incapable of moving to cooler habitat (Kupfer et al. 2005). I argue that examining Cape Rockjumper vulnerability to climate change may even be useful for determining vulnerability of the Fynbos itself, as species strongly associated with a particular habitat type can be useful indicators for the habitat itself (Carignan and Villard 2002). The results of this study can be used as an example of how collecting information on a single species can help identify areas of vulnerability that are often overlooked — specifically for Cape Rockjumpers, how the interacting effects of temperature and the broader ecological community suggest population declines are possibly due to increased nest predation from snakes at higher temperatures.

APPENDICES

APPENDIX 1: SUPPORTING MATERIALS FOR CHAPTER 3

FIGURES

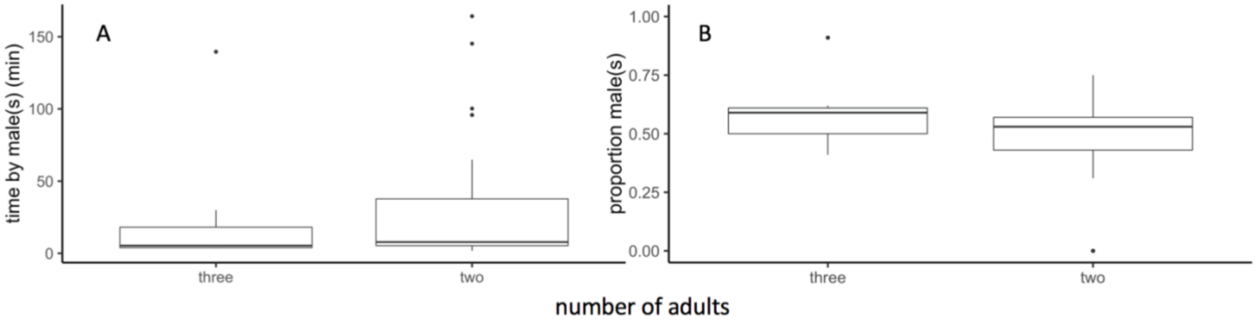

Figure S3.1 Data from 40 days filming 16 nests of wild-living Cape Rockjumpers *Chaetops frenatus* at Blue Hill Nature Reserve, South Africa, over two breeding seasons (2017-2018) showing (A) overall time in nest spent by male(s), and (B) proportion of provisioning events by male(s), in territories with either three or two adults (two or one male, N = 7 days or N = 25 days respectively, from 12 territories).

APPENDIX 2: SUPPORTING MATERIALS FOR CHAPTER 4

TABLES

Table S4.1 Data for time spent in the nest from 26 species of South African passerines, including: average number of days spent incubating ("days incubating"), average number of days spent as nestlings ("days nestling"), average mass of species ("average mass"; g), total number of days spent in the nest ("total days"), mass-specific average number of days spent incubating ("mass-specific incubating"), mass-specific average number of days spent as nestlings ("mass-specific nestling"), mass-specific total number of days spent in the nest ("mass-specific total"), residual number of days incubating ("incubating residual"), residual number of days as nestlings ("nestling residual"), residual total number of days in nest ("total residual"). Data were collected only for species where the number of nests in the sample size was greater than three (Martin and Lloyd unpublished data; Winterbottom and Wilson 1959, Skead 1960, Winterbottom 1964, Steyn 1966, Tarboton 1971, Piper 1989, Monadjem et al. 1995, Lloyd 1998, Oatley 1998, Holmes et al. 2002, Krüger 2004, Engelbrecht and Lonzer 2009, Maphisa et al. 2009, Dikgale 2012, Engelbrecht and Mathonsi 2012, Ridley and Van den Heuvel 2012).

species	days incubating	days nestling	average mass (g)	total days	mass-specific incubating	incubating residual	mass-specific nestling	nestling residual	mass-specific total	total residual
Chersomanes albofasciata	13		25		13.58	-0.58				
Emberiza capensis	14.5		20		13.23	1.27				
Cercotrichas coryphaeus	14		20		13.23	0.77				
Turdoides jardineii	16.2		72		16.87	-0.67				
Crithagra atrogularis	14		13		12.74	1.26				
Crithagra flaviventris	14.6		17		13.02	1.58				
Chaetops frenatus	20.3	19.6	57	39.9	15.82	4.48	16.49	3.11	32.39	7.51
Certhilauda chuana	15.6	11	35	26.6	14.28	1.32	14.65	-3.65	28.69	-2.09
Motacilla clara	13.5	16	20	29.5	13.23	0.27	13.4	2.60	26.17	3.33
Eremopterix leucotis	10.3	9.2	22	19.5	13.37	-3.04	13.57	-4.37	26.51	-6.98
Spizocorys sclateri	11	11.5	20	22.5	13.23	-2.23	13.40	-1.90	26.17	-3.67
Heteromirafa ruddi	14.1	13.4	26	27.5	13.65	0.45	13.90	-0.50	27.18	0.32
Eremopterix australis	10.5	9	14	19.5	12.81	-2.31	12.90	-3.90	25.17	-5.67

Eremopterix verticalis	10	8.5	17	18.5	13.02	-3.02	13.15	-4.65	25.67	-7.17
Motacilla capensis	14	15.5	21	29.5	13.30	0.70	13.48	2.02	26.34	3.16
Calandrella cinerea	14	12	24	26	13.51	0.49	13.73	-1.73	26.84	-0.84
Cossypha caffra	16	16.5	28	32.5	13.79	2.21	14.07	2.43	27.52	4.98
Laniarius atrococcineus	17.4	19.5	50	36.9	15.33	2.04	15.91	3.60	31.21	5.66
Pycnonotus capensis	12	13	39	25	14.56	-2.56	14.99	-2.00	29.36	-4.36
Serinus canicollis	13	16.3	15	29.3	12.88	0.12	12.98	3.32	25.33	3.97
Crithagra mozambica	13.4	19.2	12	32.6	12.67	0.73	12.73	6.47	24.83	7.77
Turdoides bicolor	14	15.7	76.4	29.7	17.18		18.11	-2.41		
Oenanthe familiaris	14	16.7	22	30.7	13.37		13.57	3.13		
Crithagra sulphuratus		16.4	29				14.15	2.25		
Spizocorys conirostris		11.4	14				12.90	-1.50		
Cercotrichas leucophrys		11.8	20				13.40	-1.60		

APPENDIX 3: SUPPORTING MATERIALS FOR CHAPTER 5

TABLES

Table S5.1 Genbank accession numbers of individual sequences included in the phylogenetic analysis. Sequences are of three genetic markers (NADH dehydrogenase 2 — "ND2", cytochrome b — "cytb", and recombination activating gene 1 — "RAG1") from *Chaetops frenatus* and *C. aurantius*. References for *Picathartes gymnocephalus*: Fuchs et al. 2006; Harbaugh and Baldwin 2007; Fjeldsa et al. 2010; Zuccon and Ericson 2012.

sample ID	species	genetic marker		
		ND2	cytb	RAG1
4A79242_Kouga	*Chaetops frenatus*	LR723405		
4A90122_LangN	*Chaetops frenatus*			LR723527
4A90122_LangN	*Chaetops frenatus*		LR723376	
4A90122_LangN	*Chaetops frenatus*	LR723457		
CA17291_Kouga	*Chaetops frenatus*	LR723402	LR723328	LR723487
CA17295_Kouga	*Chaetops frenatus*		LR723329	
CA28238_Kogel	*Chaetops frenatus*	LR723480		LR723537
CA28309_Kouga	*Chaetops frenatus*	LR723401	LR723327	LR723486
CA28317_Kogel	*Chaetops frenatus*	LR723483	LR723397	LR723539
CA28366_Kouga	*Chaetops frenatus*	LR723398	LR723324	LR723484
CA28371_Kouga	*Chaetops frenatus*	LR723399	LR723325	
CA28372_Kouga	*Chaetops frenatus*	LR723404		
CA28373_Kouga	*Chaetops frenatus*	LR723403	LR723330	LR723488
CA28401_Kouga	*Chaetops frenatus*	LR723406	LR723331	LR723489
CA28403_Kouga	*Chaetops frenatus*	LR723400	LR723326	LR723485
CA28498_Kogel	*Chaetops frenatus*	LR723482		LR723538
CA28567_Kamm	*Chaetops frenatus*	LR723433	LR723358	LR723507
CA31514_Ceder	*Chaetops frenatus*	LR723476	LR723393	
CA31529_Ceder	*Chaetops frenatus*	LR723477	LR723394	
CA31530_Ceder	*Chaetops frenatus*	LR723478	LR723395	LR723536
CA31531_Ceder	*Chaetops frenatus*	LR723479	LR723396	
CA31532_Ceder	*Chaetops frenatus*	LR723481		
CA31540_Anys	*Chaetops frenatus*	LR723451		LR723522
CA31541_Anys	*Chaetops frenatus*	LR723450	LR723371	LR723521
CA31542_Ceder	*Chaetops frenatus*	LR723475	LR723392	
CA31544_Ceder	*Chaetops frenatus*	LR723474	LR723391	
CA31545_Ceder	*Chaetops frenatus*	LR723473		
CA31546_Ceder	*Chaetops frenatus*	LR723472	LR723390	
CA31547_Ceder	*Chaetops frenatus*	LR723471	LR723389	LR723535

CA37121_Klein	*Chaetops frenatus*	LR723422	LR723347	
CA37201_LangN	*Chaetops frenatus*	LR723456	LR723375	LR723526
CA37202_Anys	*Chaetops frenatus*	LR723452	LR723372	LR723523
CA37203_Anys	*Chaetops frenatus*	LR723453		LR723524
CA37204_Anys	*Chaetops frenatus*	LR723454	LR723373	
CA37205_SwartM	*Chaetops frenatus*	LR723438		LR723510
CA37206_SwartM	*Chaetops frenatus*	LR723439	LR723362	LR723511
CA37207_SwartM	*Chaetops frenatus*	LR723440	LR723363	LR723512
CA37208_SwartM	*Chaetops frenatus*	LR723441	LR723364	LR723513
CA37209_SwartM	*Chaetops frenatus*	LR723442		LR723514
CA37210_SwartM	*Chaetops frenatus*	LR723443	LR723365	LR723515
CA37211_SwartM	*Chaetops frenatus*	LR723444	LR723366	LR723516
CA37213_Klein	*Chaetops frenatus*	LR723423	LR723348	LR723500
CA37214_Klein	*Chaetops frenatus*	LR723424	LR723349	LR723501
CA37215_Klein	*Chaetops frenatus*	LR723425	LR723350	
CA37216_Klein	*Chaetops frenatus*	LR723426	LR723351	
CA37217_DRJ	*Chaetops aurantius*	LR723407	LR723332	
CA37218_DRJ	*Chaetops aurantius*	LR723408	LR723333	LR723490
CA37219_DRJ	*Chaetops aurantius*	LR723409	LR723334	LR723491
CA37220_DRJ	*Chaetops aurantius*	LR723410	LR723335	LR723492
CA37221_DRJ	*Chaetops aurantius*	LR723411	LR723336	
CA37222_DRJ	*Chaetops aurantius*	LR723412	LR723337	
CA37223_DRJ	*Chaetops aurantius*	LR723413	LR723338	LR723493
CA37224_DRJ	*Chaetops aurantius*	LR723414	LR723339	LR723494
CA37225_DRJ	*Chaetops aurantius*	LR723415	LR723340	LR723495
CA37226_DRJ	*Chaetops aurantius*	LR723416	LR723341	LR723496
CA37227_DRJ	*Chaetops aurantius*	LR723417	LR723342	LR723497
CA37228_DRJ	*Chaetops aurantius*	LR723418	LR723343	LR723498
CA37229_DRJ	*Chaetops aurantius*	LR723419	LR723344	
CA37230_DRJ	*Chaetops aurantius*	LR723420	LR723345	
CA37231_DRJ	*Chaetops aurantius*	LR723421	LR723346	LR723499
CA37232_Kamm	*Chaetops frenatus*	LR723431	LR723356	LR723505
CA37233_Kamm	*Chaetops frenatus*	LR723432	LR723357	LR723506
CA37234_Kamm	*Chaetops frenatus*	LR723434		LR723508
CA37261_Kamm	*Chaetops frenatus*	LR723435	LR723359	LR723509
CA37262_Kamm	*Chaetops frenatus*	LR723436	LR723360	
CA37263_SwartW	*Chaetops frenatus*	LR723445	LR723367	LR723517
CA37264_SwartW	*Chaetops frenatus*	LR723446	LR723368	LR723518

CA37265_SwartW	*Chaetops frenatus*	LR723447	LR723369	LR723519
CA37266_SwartW	*Chaetops frenatus*	LR723448	LR723370	LR723520
CA37267_SwartW	*Chaetops frenatus*	LR723449		
CA37268_SwartE	*Chaetops frenatus*	LR723428	LR723353	LR723503
CA37269_SwartE	*Chaetops frenatus*	LR723427	LR723352	LR723502
CA37270_Kamm	*Chaetops frenatus*	LR723437	LR723361	
CA37272_SwartE	*Chaetops frenatus*	LR723429	LR723354	
CA37274_SwartE	*Chaetops frenatus*	LR723430	LR723355	LR723504
CA37275_SwartE	*Chaetops frenatus*	LR723455	LR723374	LR723525
CA37276_LangN	*Chaetops frenatus*	LR723458	LR723377	LR723528
CA37276_LangN	*Chaetops frenatus*	LR723462		
CA37277_Kogel	*Chaetops frenatus*	LR723463	LR723381	LR723531
CA37278_Kogel	*Chaetops frenatus*	LR723464	LR723382	
CA37279_Kogel	*Chaetops frenatus*	LR723465	LR723383	LR723532
CA37280_Kogel	*Chaetops frenatus*	LR723466	LR723384	
CA37281_Kogel	*Chaetops frenatus*	LR723467	LR723385	LR723533
CA37282_Kogel	*Chaetops frenatus*	LR723468	LR723386	
CA37283_Kogel	*Chaetops frenatus*	LR723469	LR723387	
CA37284_Kogel	*Chaetops frenatus*	LR723470	LR723388	LR723534
CA37285_LangS	*Chaetops frenatus*	LR723459	LR723378	LR723529
CA37286_LangS	*Chaetops frenatus*	LR723460	LR723379	
CA37287_LangS	*Chaetops frenatus*	LR723461	LR723380	LR723530
DQ125989.1	*Picathartes gymnocephalus*	DQ125989		
EF569254.1	*Picathartes gymnocephalus*			EF569254
GU816831.1	*Picathartes gymnocephalus*	GU816831		
AY228008.1	*Picathartes gymnocephalus*			AY228008
AY228076.1	*Picathartes gymnocephalus*		AY228076	
JN614899.1	*Picathartes gymnocephalus*		JN614899	

FIGURES

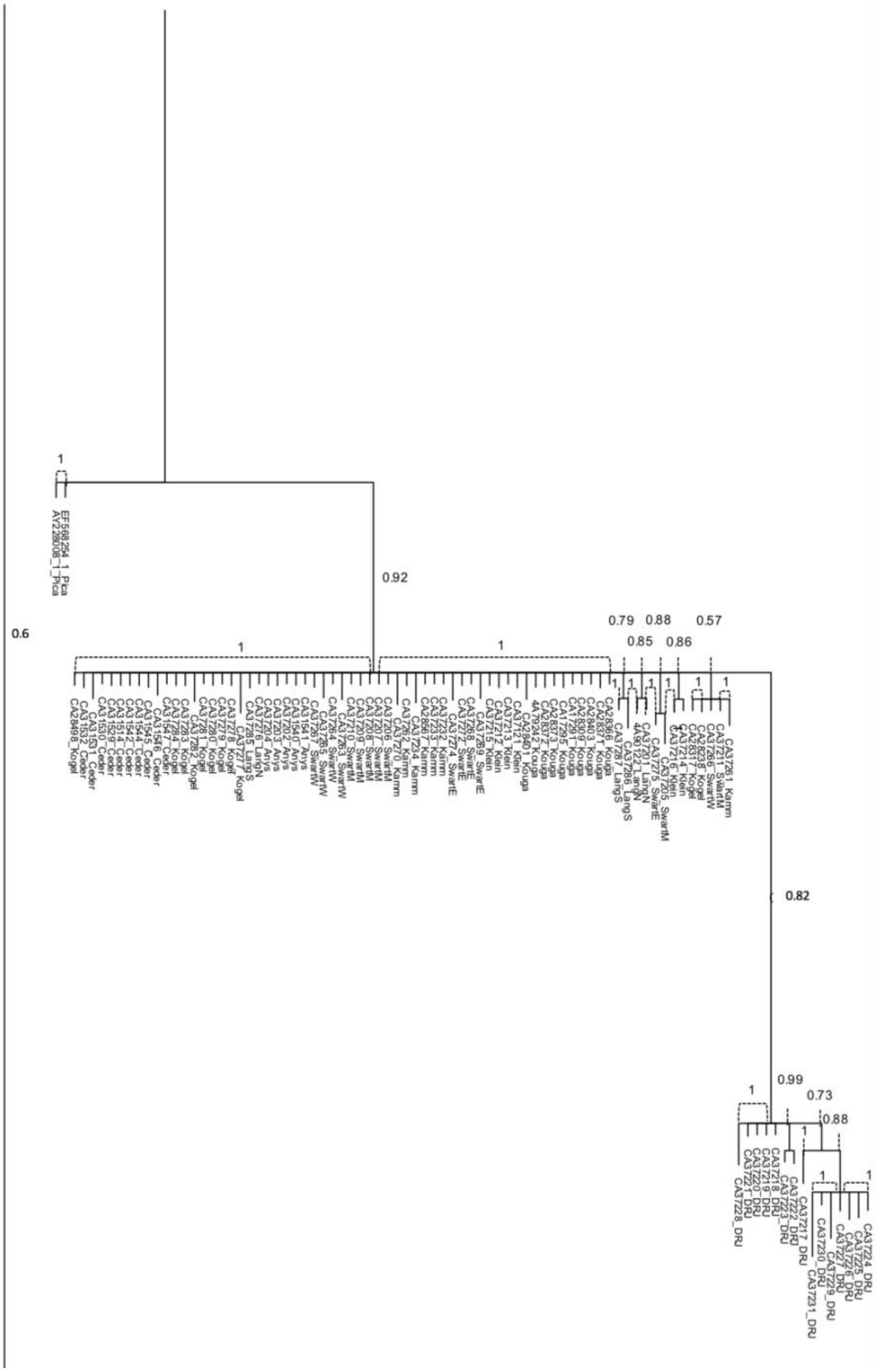

Figure S5.1 Consensus tree based on Bayesian inference for three genetic markers (two mtDNA: Cytochrome b and NADH dehydrogenase subunit 2; one nDNA: recombination activating gene 1), from *Chaetops frenatus* (N = 71), with outgroups *C. aurantius* (N = 15) and *Picathartes gymnocephalus* (N = 2).

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