The use of ringing data in the study of climatic influences on common passerines

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SEEC - Statistics in Ecology, Environment and Conservation

Declaration

I hereby declare that all the work presented in this thesis, titled "The use of ringing data in the study of climatic influences on common passerines", is my own, except where otherwise stated in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

Signed in Ruurlo (Netherlands) in February 2016

Signed by candidate

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Dorine Yvette Manon Jansen

Dedication

This thesis is dedicated to my father (1922-2013)
without whose listening ear I would never have made it this far
and
to Max and Charlie, forever in my heart.

Table of Contents

Abstract

Title: The use of ringing data in the study of climatic influences on common passerines

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To understand the potential impact of forecasted increases in climatic variability we need to determine the impact of climatic stochasticity on demographic rates. This thesis used available long-term ringing data collected by volunteers, augmented by data from research projects, to investigate the influence of climatic variation on survival of 10 common passerines in southern Africa. Through sheer numbers common species are fundamental to ecosystem functioning.

Migratory species are subject to climatic stochasticity in breeding and wintering grounds, and during migration. In a population of African Reed Warblers *Acrocephalus baeticatus* (an azonal wetland specialist) a capture-mark-recapture model correlated higher temperature in the breeding grounds with higher adult survival (1998-2010), but - contrary to expectations - not wetter winters. A spatial analysis using a multi-state model in a Bayesian framework did not link survival in populations across southern Africa to environmental seasonality. However, as hypothesised, migratory populations appeared to survive better than sedentary populations.

Increased climatic variation could synchronize survival of species assemblages and colonies in meta-populations. I investigated a 3-species assemblage in climatically stable fynbos (2000-2007) and a 4-species assemblage in more seasonal wetland (1999-2013) with a hierarchical model, run in WinBUGS, with a temporal, synchronous (common) and asynchronous (species-specific) component. Comparison of models with and without climatic covariates quantified the impact of climatic stochasticity as a synchronizing and desynchronizing agent. As expected, the wetland assemblage exhibited more synchronous and asynchronous variation in survival than the fynbos assemblage, but the analysis did not find evidence of climatic forcing. Demographic rates of a population of 25 colonies of a Sociable Weaver *Philetairus socius* meta-population in savanna near Kimberley did not correlate with climatic indices during 1993-2014. Age-specific survival and fecundity of the largest colony were influenced by climatic variation reinforcing earlier inference that colonies respond differently to environmental stochasticity. The integrated population model using count, ringing, and productivity data enabled the first estimation of annual fecundity, juvenile survival and recruitment.

The volunteer data yielded the first estimates of adult survival of two African endemics and estimates of a second population for three other species. A review of volunteer ringing resulted in recommendations to improve its use from a demographic perspective.

Layout and contributions

This thesis consists of four main chapters. The first two main chapters have already been published and were included with permission from the Chair of the Doctoral Degrees Board Professor Visser and support from the Dean of the Faculty of Science Professor Le Roex. Author contribution statements detailing the contribution of all authors and signed by all authors can be found at the end of the contribution section below. These chapters have been included in this thesis as published, therefore, the page numbers are as in the publication journals. As publications both chapters include an Acknowledgements section. The last two main chapters were written as submissions for publication: tables and figures follow the references, followed by the appendices. A certain overlap in the climatic context between the introduction of this thesis (Chapter 1) and the four main chapters could not be avoided. Similarly, there is a small overlap in the Data analysis sections between the four main chapters. Associate Professor Res Altwegg commented on all drafts and contributed to the study design of all main chapters.

Chapters 2 & 3

Data were collected by volunteer ringers, at Paarl mainly by the late Gordon Schultz. The South African Ringing Unit (SAFRING) curated the data and Dieter Oschadleus extracted the subsets from the SAFRING database. Weather data for Chapter 2 were provided by Lisa Coop of UCT's Climate Systems Analysis Group. René Navarro extracted the vegetation units of the study locations of Chapter 3 with ArcView GIS.

Chapter 4

Dieter Oschadleus suggested long-term ringing sites to explore for species assemblages and extracted the data subsets from the SAFRING database. The data were collected by volunteer ringers and curated by SAFRING. The ringing at Darvill was coordinated and encouraged by Dr D. Johnson, Dr B. Taylor and Dr M. Brown over the last 35 years, and UKZN funded the program for many years. Dieter shared his knowledge and field experience of the Darvill study subjects and the study site. Mark shared his knowledge of the Darvill study site and the ringing there. Weather data were provided by Chris Jack and Chris Jennings of UCT's Climate Systems Analysis Group. The ringing data of Koeberg were collected as part of a research project and provided by Penn Lloyd. Penn shared his knowledge of the Koeberg study site and the study subjects. Weather data were provided by Eskom's Koeberg Nuclear Power Station's weather station.

Chapter 5

The ringing, fecundity, and census data were collected as part of a long-term research project and provided by Rita Covas. Rafael Mares prepared the productivity data. Rita, Rafael, and Claire Doutrelant shared their first-hand knowledge of the study species and the study site. Rita and Claire provided funding that enabled me to spend three months at the Centre d’Ecologie Fonctionnelle et Evolutive (CEFE), Montpellier. Roger Pradel (CEFE) contributed to the data selection and the definition of the integrated population model. Weather data were provided by the South African Weather Service.

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SANBI

Author contribution statement - Chapter 2

Manuscript

Jansen, D.Y.M., Wilson, A.M. & Altwegg, R. 2015. Climatic influences on survival of migratory African Reed Warblers *Acrocephalus baeticatus* in South Africa. Ardea 103:163-174.

Author contributions

I (Dorine Y.M. Jansen) designed the study, carried out the analysis, interpreted the results, and wrote the manuscript.

Adam M. Wilson downloaded the NDVI data (MODIS MOD13C2, monthly values per 0.05 degree grid cells) from the Land Processes Distributed Active Archive Centre (LP DAAC), located at the U.S. Geological Survey (USGS) Earth Resources and Science (EROS) Centre (lpdaac.usgs.gov), carried out the initial subsetting, processing and validation of the large volume of data with custom scripts, and contributed to manuscript revisions.

Res Altwegg contributed to the study design and manuscript revisions.

Date: 1/18/2016

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D.Y.M. Jansen A.M. Wilson R. Altwegg

Author contribution statement - Chapter 3

Manuscript

Jansen, D.Y.M., Abadi, F., Harebottle, D. & Altwegg, R. 2014. Does seasonality drive spatial patterns in demography? Variation in survival in African reed warblers *Acrocephalus baeticatus* across southern Africa does not reflect global patterns. Ecology and Evolution 4:889-898.

Author contributions

I (Dorine Y.M. Jansen) designed the study, carried out the analysis, interpreted the results, and wrote the manuscript.

Fitsum Abadi (current affiliation: School of Statistics and Actuarial Science, University of Witwatersrand, Johannesburg) helped with data analysis and contributed to manuscript revisions.

Doug Harebottle (current affiliation: Sol Plaatje University, Kimberley) introduced me to 'Mucina, L. & Rutherford M.C. (eds) (2006) The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria', which was instrumental to the study design.

Res Altwegg contributed to the study design and manuscript revisions.

Date: 22 January 2016

Signed

D.Y.M. Jansen F. Abadi D. Harebottle R. Altwegg

Acknowledgements

First and foremost I have to thank Res Altwegg and Les Underhill for taking a chance on me, when I came to them in August 2010 to discuss a PhD. Les made me feel welcome and told me that at the ADU the most important thing was to have fun, the science would follow automatically. Both helped me through the awkward period of changing supervisors. Les invited me to the Barberspan Ringing Conference in March 2011, which introduced me to the world of bird ringing, new friends and more of the beautiful natural diversity of South Africa. And we had fun! Les enabled me to go the PAOC 2013 conference in Oct 2012 to learn about bird conservation in Africa, which was an eye-opener that started a thread that ultimately led to this thesis. Les was a rock when I needed to go home to spent time with my father in 2013; he took care of all the registration paperwork that year.

Res, still at SANBI, became my direct supervisor and found a place for me there. In the initial months until the beginning of 2011 he never stopped believing I had the skills to master the statistics, which I frequently did. All these years he encouraged me, kept believing in me, and guided me with positive criticism that was clear and severe between the lines when I needed it. Without him I would not have come to this point, enjoyed my analyses as much, had the opportunity to attend many workshops, courses and conferences, or had the courage to present my work at the EURING 2013 and ISEC 2014 conferences. Both conferences introduced me to the makers and shakers of the statistical ecology world, besides the two gentlemen I'd already had the privilege to meet! Just being near these statistical ecologists/ecological statisticians made me more statistically savvy.

Secondly, I could not have carried out any of the studies presented in this thesis were it not for the tireless efforts of southern Africa's volunteer ringers. Without their data we would not be able to determine, and subsequently understand, many aspects of the life histories of southern Africa's avifauna. I salute you.

The 'stats lectures' of Fitsum Abadi and Res were instrumental to the analyses presented in this thesis. The first lecture was painful: I recognized three words but was hazy on their meaning. After each passing lecture my understanding and appreciation of the power of statistics to tease information from ringing data increased. Fitsum, thank you for making statistical ecology seem within my grasp and for being such a joy and a gentleman to work with.

Roger Pradel was another such joy and gentleman to work with. His formidable knowledge of ecological modelling and his kindness and patience were instrumental in my being able to make the leap from ringing models to integrated population modelling.

Dieter Oschadleus is the driving force - and during most of my years at UCT the only force - behind the South African Ringing Unit (SAFRING) and the curator of the SAFRING database. Despite his many commitments he always found the time to help me understand species and ringing, and never tired of discussing life histories and ringing in general. His belief in the value of ringing birds and passion to improve and expand it gave me the impetus to think about ways to accomplish that, resulting in the recommendations presented in this thesis.

In this context I also want to thank Stephen Baillie (British Trust for Ornithology) and Michael Schaub, Marc Kéry and Jacques Laesser (Swiss Vogelwarte) for their thoughtful input and advise when we discussed ringing in their respective countries.

Many people were always willing to discuss my study subjects and sites. For Chapter 3 one such discussion with Doug Harebottle led to a new and much improved study design. This led me to René Navarro, who kindly took the time to help me with ArcView GIS. For chapter 4 Mark Brown and Penn Lloyd never tired of my questions and always took the time to answer them thoughtfully. For Chapter 5 Rita Covas and Claire Doutrelant first of all saw potential in my proposal of an integrated population model for their sociable weaver data. Secondly, they arranged funding for me to spend time with Roger Pradel at CEFE. And during all the time that particular analysis took they always tried to find time between their field research travels to answer my questions. Rafael Mares not only prepared data for me, but also thought along with me. Thank you, all of you! For chapter 2 I also want to thank Adam Wilson for explaining the downloading and handling of satellite-derived data from a US source and, when the internet connection proved to be too slow for the huge amount of data, for freeing considerable time to do it for me. Brilliant!

At UCT I could not have navigated the required administration or arranged conference attendance without three very accomplished women: Hilary Buchanan at the Fitz, Sue Kuyper at the ADU, and Celene Jansen-Fielies at the Department of Statistical Sciences. You made me feel welcome in Cape Town.

As did another formidable woman, and my friend, Margaret Koopman, the former librarian of the Niven Library at the Fitz. The Niven is the best ornithological library in the Southern Hemisphere, not in small measure thanks to her. She also made it a warm and inviting place and was never stumped when I asked for obscure research publications. I loved our cultural discussions and your generous hospitality.

While 'at UCT' I want express my gratitude to the Postgraduate Research Office and the Department of Statistical Sciences for the funding I received for conference and workshop attendance. As I am to the South African National Biodiversity Institute. I am also thankful for the Marie Curie grant (318994-Cooperation) I received through the International Research Staff Exchange Scheme for working with Roger Pradel at CEFE, and the National Research Foundation of South Africa grant (85802) that supported Res.

At the ADU I need to thank Michael Brooks and René Navarro for keeping Elvis in the air and accessible from, often, very far away. I must have driven you mad during the 'loadshedding' seasons in Cape Town. Forgive me. Fellow researchers Greg Duckworth, Chris Oosterhuizen, and Silvia Kirkman were grace personified when it came to sharing Elvis. Thank you!

Last, but certainly not least, I want to thank my family - my mother, my sister San, my nephew Lasse, and my brother Tef and his husband Wal. It has been a long journey, this start of a second life, and I could not have done it without you. You never failed to offer me encouragement and help when I needed it. You made me feel safe during this journey. Mam, San, and my friends Frances and Ton and Paul, offered me places to stay when I did not know where to go. I can never thank you enough. Hetty, your faith in my being able to accomplish this seemed, at times, misplaced but you were right! I can't wait to go birding with you again. My father shared my journey in more ways than one. I am sad that he could not see the end of this journey but grateful for the time we shared it.

Chapter 1

Introduction

"Ongoing ringing is like having money in the bank,

ready when needed"

I. Newton 2014

This introduction describes the background and methodological context of the studies of the influence of climate on common passerines presented in the following chapters. I first provide an overview of recent and future climate change with examples of observed and predicted impacts on birds. I then give a review of the history and scope of bird ringing - the people and organisations, the rings, and the research areas - and the statistical methods and software developments that together have created the potential to carry out this type of research. The first provides the background for the recommendations in Chapter 6. The latter eliminated the need to explain the advantages of the methods and software used in the analyses chapters themselves. Thus, the analyses chapters could be written as for publication. As independent studies a certain overlap with the climatic context of this introduction could not be avoided. Subsequently, I describe the aims and structure of the thesis.

Climate change and birds

Since the latter part of the 20th century, the global climate has shown a warming trend and increases in climatic variability and extreme events. Recently released climatic data show that 2015 was the warmest year on record, surpassing 2014 and continuing the unprecedented warming observed over the past thirty years (IPCC 2014; Tollefson 2016). New models have revealed that the recent warming has been substantially stronger than previously estimated (Ji *et al.* 2014). Rainfall in the mid-latitudes of the Northern Hemisphere has decreased significantly since the start of the 20th century, but long-term trends elsewhere are unclear (IPCC 2013). The variability of the El Niño Southern Oscillation (ENSO) - the climatic pattern responsible for rainfall variability and extreme weather across the globe - has increased in response to the warming trend resulting in an increase of extreme events (McGregor *et al.* 2013; Power *et al.* 2013). At the beginning of the 21st century heatwaves used to occur twice a century in Europe (Christidis *et al.* 2015). That probability has now increased to twice a decade.

In South Africa recent warming has exceeded global warming: mean annual temperatures were 1.5 times higher than the global average (DEA 2013). The warming trend started in the 1950s and accelerated in the 1960s (Kruger & Shongwe 2004; DEA 2011; Kruger & Sekele 2013). Rainfall has not shown a clear trend but appears to have decreased in some summer rainfall areas and increased in some winter rainfall areas (DEA 2011). Extreme events have increased in both duration and intensity (Mason *et al.* 1999; New *et al.* 2006; DEA 2011; Kusangaya *et al.* 2014).

The recent changes in climate have had discernible influences on birds. In response to warmer springs many species have advanced their breeding seasons (meta-analyses in Parmesan & Yohe 2003 and Chambers *et al.* 2013). Warmer springs have caused phenological mismatches between food supply and demand during the breeding season, particularly for long-distance migrants (Both *et* *al.* 2010). Species breeding at lower, and thus warmer, latitudes have been able to expand their ranges northward (Thomas & Lennon 1999; Hitch & Leberg 2007). In the temperate regions warming has had a positive impact on survival and fecundity of woodland specialists (Leech & Crick 2007). However, extreme climatic events like heatwaves and hurricanes have resulted in significant population declines of many bird species (review in Moreno & Møller 2011). For example, heatwaves have been responsible for mass mortality of desert birds (examples in McKechnie & Wolf 2010). In a meta-analysis Ockendon *et al.* (2014) examined the mechanisms underlying the observed impact of climatic change on population dynamics. In most studies changes in population abundance were driven by the indirect effects of changes in species interactions, e.g. with prey or predators.

In South Africa, the common swift *Apus apus* has substantially increased its range since the 1960s in response to the warming trend (Guo *et al.* 2016). The pied crow *Corvus albus* has increased its abundance by expanding its range into the warmer shrublands of the Karoo and Fynbos biome, while its numbers decreased in the cooler north-eastern parts of the country (Cunningham *et al.* 2016). The range expansion of this tree-breeder was assisted by an increase in electricity poles in the mainly treeless shrublands. This corvid is a fierce predator that could have a negative impact on the abundance of its new neighbours. Altwegg *et al.* (2012) found that migratory Palearctic barn swallows *Hirundo rustica* that spend their non-breeding season in South Africa have advanced their departure from the most northern parts of the country by eight days, while those in the most southern area have delayed their departure by six days. Earlier departure was correlated with increases in rainfall (approximated by the Southern Oscillation Index). Two of the six passerines endemic to the Fynbos biome, the Cape rock-jumper *Chaetops frenatus* and the Protea canary *Serinus leucopterus*, have shown a decrease in range and abundance of over 30% in response to the warming trend (Lee & Barnard 2015). Milne *et al.* (2015) could not correlate this decline to their physiological thermal threshold, but the Cape rock-jumper had the lowest thermal threshold of the six species and the decline occurred in the parts of its range where the warming trend was significant.

The latest climate change forecasts indicate that the global warming trend will increase, as will climatic variability and climatic extremes (IPCC 2014). Climate change forecasts for the coming two decades predict a likely global increase in mean surface air temperature of 0.3-0.7 ^{o}C (depending on emission scenarios) compared to the end of the 20th century (Kirtman *et al.* 2013). This warming will transpire faster than any climate change the world has experienced in the past 1000 years (Smith *et al.* 2015). Long-term forecasts predict an increase of 1.5-2.0 ^{o}C (Collins *et al.* 2013). Using the standard deviation (SD) of temperature over 1951-1980 as baseline Hansen *et al.* (2012) predicted that heatwaves of +3SD will become the norm, while heatwaves of +5SD will become regular.

For Africa, the climate forecasts predict that warming will very likely exceed global mean warming with the largest increases in sub-tropical Africa (IPCC 2007). In South Africa the warming trend will very likely be greatest in the interior and least along the coast (DEA 2011; Christensen *et al.* 2013). In the near-future more than +2SD (standard deviation) of the 1961-1990 mean temperature baseline are predicted for Fynbos, a global biodiversity hotspot endemic to South Africa (Beaumont *et al.* 2011). Predictions of less rainfall and changes in the timing of rainfall have less confidence. Less rainfall is predicted for the winter rainfall areas and more rainfall for the summer rainfall areas (DEA 2011). Annual runoff will likely decrease through higher evaporation in the long-term (Collins *et al.* 2013). Less rainfall and decreasing soil moisture will significantly increase drought conditions.

Predicted climate change could have a considerable negative impact on bird populations in South Africa. Population simulations under the predicted decrease in rainfall and increase in rainfall variation suggested that the population persistence of the tawny eagle *Aquila rapax* will decline substantially in the arid savanna of the southern Kalahari (Wichmann *et al.* 2003). Huntley *et al.* (2012) predicted that 74% of 78, mainly endemic, bird species will experience abundance and range decreases - by more than 80% for 19 species. Species richness of bird assemblages in the Fynbos and grassland biomes of South Africa could decrease by as much as by 30-40% by 2085 (Huntley & Barnard 2012). The already fast declining Rudd's lark *Heteromirafra ruddi* and Botha's lark *Spizocorys fringillaris* could disappear altogether by 2055, when climatic conditions are predicted to become unsuitable for these species. The Important Bird Area (IBA) network in southern Africa could become less important for the conservation of endemic birds by the end of the 21st century. Coetzee *et al.* (2009) investigated bioclimatic niches of 50 endemic species in IBA's under climate change. Almost two-thirds of the species could lose suitable climatic space, five species more than 85%. Coetzee *et al.* also identified crucial climatically suitable areas under the changed climatic conditions and had to conclude that most were currently not included in the IBA network. In a similar study of 72 species in the Fynbos, grassland, savanna, and thicket biomes of South Africa, Walther & van Niekerk (2015) predicted a species turnover of around 33% for the four biomes, with the greatest uncertainty for thicket, by 2050.

Adequate conservation measures - to protect those species that will experience negative impacts of future climate change - can best be developed if we know how species will respond to predicted climate change. To predict the impact of future climate change on bird species we need to determine the influence of recent climate (change) on population dynamics. As illustrated by the aforementioned studies, and many others (a review including bird studies in Moritz & Agudo 2013), species responses to recent climate change have been varied. However, there is growing evidence that recent climate change impacts on avian populations show a latitudinal gradient: populations respond differently in the northern, temperate region and the southern, temperate region (Pearce-Higgins *et al.* 2015b). Birds have different life histories in the southern, temperate regions and the northern, temperate regions due to the differences in climatic seasonality, which is less pronounced in the south (Lack 1947; Skutch 1949; Ashmole 1963). In general, they have smaller clutch sizes - probably in response to higher predation rates, and higher adult and juvenile survival rates - the former is attributed to the trade-off of fecundity for adult survival, the latter through longer development and parental care periods (Martin 1996; Ghalambor & Martin 2001; Martin *et al.* 2007; McNamara *et al.* 2008). In the northern, temperate region temperature appears to have a greater impact on bird populations than rainfall (Pearce-Higgins *et al.* 2015a). In a country like South Africa - with its semi-arid climate (in general), and thus limited water supply, and its highly variable rainfall pattern - rainfall is more likely to be a greater driver of avian population dynamics than temperature (Allan *et al.* 1997; DEA 2011; Williams & Kniveton 2012; Kusangaya *et al.* 2014). Relative to its size South Africa is one of the most geographically and environmentally diverse countries in the world (Allan *et al.* 1997; Mucina & Rutherford 2006). The populations of species that inhabit various biomes, e.g. habitat generalists and the habitat specialists of azonal habitats like wetlands, experience different seasonalities and climates, which prohibits the extrapolation of inference regarding the influence of climate on population dynamics pertaining to one population to the species level.

To determine the influence of climate on avian population dynamics we need to determine its influence on the vital rates that drive those dynamics, i.e. survival, fecundity, and dispersal (Begon *et al.* 2006). For which we need suitably long-term datasets (Frederiksen *et al.* 2014). In southern Africa long-term data of common birds (see Aims of the thesis for the focus on common birds) are collected by research projects, e.g. the sociable weaver *Philetairus socius* (Chapter 5 in this thesis), and by volunteer ringers. The latter data are curated by the South African Bird Ringing Unit (SAFRING) and readily available for analysis. The collection of the SAFRING data is not geographically coordinated nor are they methodologically standardized. This lends them statistically most suitable for survival analyses (see Constant effort ringing in Chapter 6 of this thesis). Therefore, three chapters pertain to investigations of the influence of climate on survival. Chapter 5 was based on the ringing data, productivity data, and population counts collected by a long-running research project, which enabled a full investigation of the influence of climate on population dynamics. In the four main chapters the hypotheses regarding the influence of climatic conditions on avian vital rates investigated one population of a migrant passerine in both its breeding and wintering area (Chapter 2), populations of the same passerine - both migratory and sedentary - across southern Africa (Chapter 3), two species assemblages in habitat of differing seasonality (Chapter 4), and a meta-population regarded as one population (Chapter 5; see Aims of the thesis for more details).

Bird ringing

History of bird ringing

In 1899 Danish schoolteacher H. C. C. Mortensen initiated the systematic marking of birds with individually numbered rings, engraved with an address to facilitate the reporting of ring-numbers when dead birds were recovered by the public (Preuss 2001). By 1930 ringing schemes were operational in most countries in Europe, North America, India, Australia, New-Zealand and a few countries in Africa and South America (Preuss 2001). The ornithologist and founding editor of British Birds magazine H. F. Witherby followed Mortensen's endeavours closely and instigated the British Birds Ringing Scheme in 1909 (Tucker 1944). In 1937 the British Trust for Ornithology (BTO) took over the scheme and its headquarters moved to the British Museum - the address is still used on the rings to this day (Greenwood 2009). In the mid-1950s a ringing permit system was launched and measurements of a species' tarsi instead of experience were used to establish the correct ring size. The BTO still runs the Ringing Scheme, now from their offices at Thetford. In the first 100 years of marking birds (1909-2009) more than 37 million birds were ringed, more than 2 million recaptured and almost 700,000 recovered in the British Isles; in the centennial year more than 2,500 licensed ringers - most volunteers - were active (Clark *et al.* 2010).

In North America, Dr P. Bartsch of the Smithsonian Institute first marked birds with individually numbered rings in 1902 (Tautin 2005). In 1909 L. Cole of the University of Wisconsin formed the American Bird Banding Association to oversee all systematic ringing, which was taken over by the government in 1920. In the first 100 years (1902-2002) more than 63 million birds were ringed and 3.5 million recovered in North America and Canada; currently, there are 6,100 licensed ringers - many volunteers - active (Tautin 2005).

The North American Bird Banding Programme joined its administration with its Canadian counterpart in 1923 (Tautin 2005). Because of language barriers it took much longer before ringing was coordinated at a similar spatial scale in Europe (Preuss 2001). The European Union for Bird Ringing (EURING) was founded in 1963 to facilitate the exchange of data. Today, 32 ringing schemes in 28 European countries - mainly run by private organisations - cooperate under its banner and share their ringing data in the EURING Data Bank (Preus 2001; Nikolov 2015). In contrast, in the whole of South Asia there are two ringing stations, operated by scientists of the Bombay Natural History Society (BNHS) in India (Buner *et al.* 2015). The BNHS, which issues all rings, has been collecting ringing data since 1929, but without volunteer ringers a 'mere' 500,000 birds have been ringed (no passerines). In 2013, with aid from English experts, the BNHS and the government have initiated the first ringing courses - National Park staff only - as a start to remedy this situation.

It was not long before the first birds ringed by the European ringing schemes were recovered in South Africa. The earliest recorded recovery was a European stork in 1908. In 1912 a farmer called J. Mayer found a barn swallow in Natal (BTO 2015, 11 Nov). Details of the recovery were sent in a letter by C. H. Ruddock, an amateur ornithologist and local hotel owner, to H. F. Witherby, who recorded this first recovery of a British bird (McCarthy 2010). The bird was ringed as a nestling by a licensed volunteer ringer named J. Masefield with ring-number B830 in Cheadle, Staffordshire, in 1911. It was not until 1946 that systematic large-scale ringing was first discussed by two members of the Southern African Ornithological Society, Dr. A. Roberts and C.J. Skead (McLachlan 1966). In 1948 the ringing scheme was initiated, organized by Dr Ashton, and its records kept by the Transvaal Provincial Administration. The first bird ringed in South Africa was a Cape vulture *Gyps coprotheres* nestling in the Magalies Berg with the aid of the local mountaineering club (D. Oschadleus pers. comm.). In the first year 148 rings were used by ringers from bird clubs and museums from the Cape to Uganda (Ashton 1950). In 1970 the National Union for Bird Ringing Administration was created to take over the administration of the ringing scheme (Underhill *et al.* 1991). Renamed the South African Bird Ringing Unit (SAFRING) the unit moved to the Department of Statistical Sciences of the University of Cape Town in 1977. In half a century more than 2.2 million birds were ringed, almost 169,000 recaptured, and almost 25,000 were recovered (SAFRING 2016, 27 Jan). In the ringing scheme's 50th year 127 ringers were active across southern Africa (Oschadleus 1998). This year also saw the creation of a computerized database (Oschadleus & Best 1998).

The coordination of ringing at the scale of the African continent was first discussed at the 3rd Pan-African Ornithological Conference held in South Africa in 1969 (AFRING 2016, 28 Jan). It took until 2004 before the intra-African ringing coordination scheme AFRING was actually established, with funding from the Dutch government, run by the Animal Demography Unit at the University of Cape Town. AFRING aims to train local ringers in an effort to establish long-term systematic ringing, focussing on European waterbirds at their stop-over and wintering areas on the continent. AFRING coordinates African and European ringing within this context. Another goal is to establish a central database for African ringing data, incorporating historical records. Currently, there are four ringing schemes on the continent: SAFRING, the East African Ringing Scheme, and schemes in Ghana and Morocco (AFRING 2016, 29 Jan).

Rings, and other marks

Mortensen ringed his first birds with zinc rings of different sizes in 1890 (Preuss 2001). The rings proved too heavy and it took him until 1899 to create an aluminium ring that was suitable for systematic ringing. In 1950 rings of coloured celluloid, in a unique combination of two colours, were first used in a study on the breeding biology of fulmars *Fulmaris glacialis* by zoologists of the

University of Aberdeen on a small island in the Orkney archipelago in Scotland (Dunnet *et al.* 1963; Cormack 1964).

Since the 1990s technological advances have provided tracking devices that are small enough to be inserted under the skin or attached to a ring like Passive Integrated Transponders (PIT tags; also called Platform Transmitter Terminal tags), light-weight geolocators (also called data-loggers), and satellite transmitters combined with a Geographic Positioning System (GPS) device (Elbin & Burger 1994; an example of PIT tags in Becker & Wendeln 1996; reviews in Calvo & Furness 1992, Gauthier-Clerc & le Maho 2001, Fiedler 2009, and Robinson *et al.* 2010). The International Cooperation for Animal Research Using Space, the ICARUS Initiative, has developed a tiny satellite transmitter that can be attached to animals as small as large insects (Wikelski *et al.* 2007). This will enable tracking across the globe from space. The experimental system will be installed on the International Space Station in 2016 (ICARUS 2016, 25 Jan). From a 'passerine study' perspective the disadvantage of PIT tags is the required reader, which has a short detection range (a few metres). Geolocators cannot determine location with high precision (errors of a few kilometres) and need to be retrieved to collect the data, i.e. the bird needs to be recaptured. Current GPS devices are still too heavy to be useful for birds less than 200 g (most passerines). Therefore, the conventional markers, i.e. metal and colour rings, are still the most useful, and cost-effective, devices to study passerines.

Ringing research areas

Mortensen started ringing birds to determine natal dispersal and breeding-site fidelity (Preuss 2001). He was also interested in migration routes. Ringing has been and still is used to determine movement, moult, morphology, behaviour, phenology, sustainable harvest levels, control of pest species, longevity, productivity and survival (reviews in Baillie 2001, Anderson & Green 2009, and Brown & Oschadleus 2009 - also the source of the following unless stated otherwise).

Movement is studied locally - resident movement between years, daily movement for foraging and roosting, and to determine home ranges and territories; at the scale of populations - the temporal and geographic separation and mixing of populations of the same species, and natal dispersal patterns; at the scale of countries and continents pertaining to migration - routes (flyways), stop-over sites, and wintering areas. In 1926 L. Thomson published the first movement maps, and inferences, based on recoveries reported by the public (Greenwood 2009). To this day migration has still not been unravelled for many species (Sanderson *et al.* 2006; Greenwood 2009; Vickery *et al.* 2014; review from a spatial-analysis perspective in Thorup *et al.* 2014).

Behavioural studies of ringed individuals cover many different aspects of behaviour (review in Sharp 2009): feeding behaviour - food selection and procurement strategies; parental care and mating systems - for example, Griffith *et al.* (2002) dispelled the long-held belief that most passerines are monogamous in a meta-analysis of molecular genetic studies based on samples of ringed birds; social behaviour - the forms, the direct benefits like increased safety from predators and greater chances of finding food, and the indirect benefits, i.e. altruism, of safe-guarding your kin; vocal communication - in a recent colour ringing study York *et al.* (2016) proved experimentally that the song of male white-browed sparrow-weavers *Plocepasser mahali* contains information regarding their health.

The red-billed quelea *Quelea quela* is one of the most abundant bird species globally and its eruptions cause huge damage to small-grained seed crops in sub-Saharan Africa (Elliott 2006). Ring recoveries are used to infer, among others, movement decisions and the effect of control operations (Oschadleus 1999). Longevity of wild birds is based on recoveries and, less often, on recaptures. A recent recapture in a long-term study of sociable weavers near Kimberley set a new longevity record of over 16 years for this small passerine, extending its recorded longevity by five years (Spottiswood 2005; Covas 2012).

Avian influenza and climate change are more current fields of ringing research (Brown & Oschadleus 2009; Greenwood 2009). Research into the effects of recent climate change encompasses all study areas mentioned above. For example, Kruuk *et al.* (2015) investigated the effect of recent climate change on the body size of juvenile superb fairy-wrens *Malurus cyaneus* in Australia, where over the past 26 years temperatures and the frequency of heatwaves have shown an increasing trend and rainfall a decreasing trend. Due to the contrasting effects of short-term and long-term associations - prior and during the nestling period heatwaves were negatively associated with body mass, but maximum temperature and more rainfall had a positive effect, as did long-term mean maximum temperature - mean body size did not change over the study period. Another study on the effects of climate change on morphology found that the substantial increase in wing length of citril finches *Carduelis citrinella* of two populations near Barcelona over 1986-2010 were positively correlated with increasingly warmer winters (Björklund *et al.* 2015). Björklund *et al.* inferred that the large increase in wing length was an adaptive response to recent climate change. Cole *et al.* (2015) studied breeding phenology changes associated with climate change using ringed individuals and breeding data from a long-running study in Wytham Woods, Oxfordshire. During 2001-2013 great tit *Parus major* and blue tit *Cyanistes caeruleus* egg laying phenology and the peak abundance of their main prey winter moth larvae *Operophtera brumata* were related to the greening phenology of oak trees *Quercus robur* on which the moths lay their eggs. The budding of oak trees is initiated when temperatures rise in spring. In North America, an analysis of ringing data of two populations of barn swallows and climatic indices in the breeding and wintering areas showed that climatic conditions in both breeding and wintering area influences survival of adult barn swallows of the western population, but did not affect survival of the eastern population (García-Pérez *et al.* 2014). Either the selected climatic indices were not representative of local climate in the breeding and/or wintering areas of the eastern population or the western population wintered in a smaller area, which would facilitate finding a climatic correlation with adult survival.

Statistical methods

Survival analysis - the basics

Ringing data in the form of captures, i.e. initial captures, recaptures and resightings, and dead recoveries are part of a larger collection of capture-mark-recapture (CMR) data. Since I did not use recoveries in this thesis and the statistical methods differ for this type of ringing data, recoveries are not reviewed here. For the sake of brevity and because the methodology 'sees' them as the same entity recaptures and resightings are referred to as recaptures. These data of marked individuals are analysed in the form of encounter histories (Lebreton *et al.* 1992; also the source of the following unless stated otherwise). A capture during a capture occasion is signified by '1' and when the individual is not captured by '0'. Thus, 10110 is an encounter history of an individual that was alive and captured in occasions 1, 3 and 4 - at time t_1, t_3 and t_4 - and not captured at time t_2 and t_5. The encounter history indicates that the individual was alive up to and including its recapture at t_4. Since the animal was not captured in the last occasion, we do not know whether the animal was alive after t_4. The animal could have been not recaptured, it could have died, or it could have emigrated from the study area. Fig. 1 shows the encounter history with the survival probability ϕ_t, i.e. the probability that the animal survived from t to $t + 1$, and recapture probability p_t, i.e. the probability that if alive and in the study area the animal will be recaptured at time t. There is no p_1, because an encounter history is conditional on initial capture in a CJS model (see below). The probability of this encounter history is then:

$$\phi_1(1 - p_2)\ \phi_2 p_3\ \phi_3 p_4\ (1 - \phi_4 p_5)$$

The survival and recapture probabilities only pertain to the marked individuals, i.e. the sampled segment of the study population, and the assumption is that the marking itself has no effect on the animals (Lebreton *et al.* 1992; Nichols 1992).

The Cormack-Jolly-Seber (CJS) model for open populations - with time-dependent survival and recapture $\phi(t)p(t)$ - is the most general population model used in survival analyses (Cormack 1964; Jolly 1965; Seber 1965; Lebreton 2001). Open population models allow births, deaths, and dispersal (immigration and emigration). Mortality cannot be separated from permanent emigration (Lebreton *et al.* 1992). Therefore, the estimated survival probability pertains only to local individuals. The CJS model assumes homogeneity in survival and recapture, i.e. that all individuals have the same probability of surviving and of being recaptured. The latter also precludes a behavioural response to recapture - so-called trap-dependence, i.e. an individual caught at time *t* - 1 has a different recapture probability at time *t* than an individual not caught at *t* - 1, conditional on the latter individual being present at time *t* - 1. Individuals can become trap-happy or trap-shy, which needs to be accounted for in the analysis (Pradel 1993). Passerine data often contain transients; transients are individuals that are only captured once and, thus, have zero survival probability after initial capture, which, if not accounted for, produces a negative bias in survival (Buckland & Baillie 1987; Pradel *et al.* 1997). The homogeneity assumptions generate another assumption: recaptures should take place instantaneously or in an interval much shorter than the period between the capture occasions. Smith & Anderson (1987) and Hargrove & Borland (1994) tested this assumption and found that its violation does not result in large bias or a large reduction in parameter precision as long as the recapture probability is not low and recaptures are not spread too unevenly over the longer capture occasion. Which is one of the reasons why ringing effort should be standardized (a review of CMR study designs in context of population models and their analysis in Lindberg 2012). Chapter 5 in this thesis illustrates how the absence of a well-defined study protocol from the start of a long-term study complicated the modelling of the data.

CMR analyses - methodological developments

Demographic analyses encompass the estimation of survival, recruitment and dispersal in the form of immigration and emigration, which are the demographic parameters that govern population dynamics (Baillie & Schaub 2009). The earliest avian demographic analysis was a survival analysis by Lack in 1943, based on recoveries (Lack 1943; Lebreton 2001). The analysis of CMR data started with the abundance estimation of fish in 1913 (Buckland *et al.* 2000), survival merely being a nuisance parameter (Lebreton *et al.* 1992). Before the development of the Jolly-Seber model, which is not conditional on first capture, and the CJS model models were deterministic, i.e. estimates were based on a fixed sample (Buckland *et al.* 2000). With the advent of stochastic models survival was allowed to vary individually independent of the other animals in the occasion sample.

Given that ringing data constitute the largest body of CMR data, EURING instigated interdisciplinary teamwork between statisticians, biologists, and ecologists to discuss the way forward in CMR analysis, from the 1970s onwards in triennial EURING Analytical Meetings (Thomson *et al.* 2009; de Bernardinis 2012). This accelerated methodological developments.

In the 1980s survival became the parameter of primary interest with detection probability of already marked animals having to be estimated as nuisance parameter (Lebreton *et al.* 1992; Nichols 1992). Advances in statistical methods, together with improvements in computational power and specialized software (see below), allowed model generalization, specialization like the combination of (features of) the existing population models (e.g. recovery and recapture in one model), and the accounting for assumption violations, e.g. transience - two different methods are described in Chapters 2 and 3 in this thesis (reviews in Seber 1986, Lebreton *et al.* 1992, Nichols 1992, Schwartz & Seber 1999, and Buckland *et al.* 2000). Survival and recapture parameters could be constrained to be constant over the study period, which meant fewer parameters. A more parsimonious model that explains the variation in the data reduces the sampling variance and, thus, increases parameter precision. The parameters could also be constrained to groups (sex, age, sites) and covariates pertaining to, for instance, climate (a review of the use of covariates in Pollock 2002). The emphasis of CMR analysis changed from fitting to building and selecting models (Lebreton *et al.* 1992).

Hierarchical models

The statistical models used to analyse CJS population models advanced from fixed-effects ultra-structural models to mixed-effects hierarchical models. Aside from noise, ultra-structural models assume that all variation is explained by the model parameters, e.g. temporal variation in survival is explained by variation in a climatic covariate, and that individual covariates like body weight remain constant after measuring (Grosbois *et al.* 2008). Mixed-effects (incorporating both fixed and random effects) hierarchical models can model the complexity of nature more effectively (Clark 2005; a comparison of the different methods in Francis & Saurola 2009). Using a temporal random effect enables sharing of available information, which improves the precision of survival estimates, particularly in years with sparse data (Gelman 2005; Gimenez *et al.* 2009). Adding a climatic fixed effect to a temporal random effect, instead of replacing it, avoids overestimation of the climatic effect, because this assumes that there is unexplained environmental variation in addition to that explained by climatic stochasticity (Barry *et al.* 2003; Gimenez & Choquet 2010).

Models are hierarchical when one process is conditional on another, so they contain more than one level, i.e. a data model incorporating a process model, which might incorporate a parameter model, and, at least, one level contains a random effect (Cressie *et al.* 2009; Schaub & Kéry 2012). The scope of hierarchical models continues to expand. Hierarchical models can now incorporate time-varying individual covariates (Bonner *et al.* 2010); separate (biological) process variation from sampling variation (Link & Barker 2004); investigate spatial variation in parameters (Péron *et al.* 2011); investigate non-linearity of effects (Bonner *et al.* 2009; Gimenez *et al.* 2009); account for unexplained environmental stochasticity or other, unknown, sources of variation (Burnham & White 2002; Francis & Saurola 2009; Schmutz 2009; White *et al.* 2009); model individual heterogeneity such as frailty in survival, i.e. some individuals are more likely to die than others (Gimenez *et al.* 2007; Gimenez & Choquet 2010).

The use of hierarchical models in ecology has increased exponentially. Because it is, at present, easier to fit complex hierarchical models in a Bayesian framework - for which there exist appropriate enumeration methods and software, a paradigm shift from Frequentist to Bayesian statistics has occurred simultaneously (Clark 2005; de Valpine 2009; Lele & Dennis 2009; Kéry & Schaub 2012; Yuan & Johnson 2012, but see de Valpine (2012) for a Frequentist analysis of a hierarchical model).

Bayesian versus Frequentist statistics

In ecology Bayesian statistics were first applied in a genetic study in 1917 (Ellison 2004) and formally established in 1939 (Wade 2000). The 1990s saw a growing trend in the ecological application of the Bayesian approach to hierarchical modelling (Dennis 1996; Clark 2005), including in the analysis of avian CMR data (Brooks *et al.* 2000). Particularly after an entire issue of Ecological Applications was devoted to the topic (Dixon & Ellison 1996). The Bayesian approach is not without its serious detractors (Dennis 1996; Gelman 2008; Lele & Dennis 2009), but as a different route to inference it provides another source of information in a broad approach to complex ecological systems and problems (Brooks *et al.* 2000; de Valpine 2009).

The so-called philosophical difference between Frequentist and Bayesian statistics lies in their definition of probability: Frequentist probability refers to the frequency of trials in which the data would have been observed given a particular fixed parameter value or hypothesis, whereas Bayesian probability is a degree of belief in the estimated parameter value given the observed data (Wade 2000; de Valpine 2009). The parameters themselves are viewed as random with a certain distribution. Frequentist statistics were founded by R.A. Fisher in 1922 (Cox 2005). Bayesian statistics date back to the 18th century, when Bayes (1763) formulated his theorem and Laplace asserted a similar principle and used it for statistical inference (Stigler 1986). Bayes theorem states:

$$p(\mathrm{A}|\mathrm{B}) = \frac{p(\mathrm{B}|\mathrm{A})p(\mathrm{A})}{p(\mathrm{B})}$$

where p is the probability, A and B are events, and | stands for 'conditional on'. When applied to statistical inference, this translates into: the probability of the parameter (A) given the data (B - the posterior distribution) approximates the probability of observing the data given the parameter (the Frequentist likelihood) times the probability of the parameter (the prior distribution), divided by the probability of the data. The probability of the data is a constant for a given data set and only scales the equation (Ellison 2004).

The most obvious advantage of Bayesian statistics is the formal and transparent use of prior information, which can only be used 'after the fact' in Frequentist statistics (maximum likelihood estimation), when prior knowledge indicates that the estimate makes no biological sense (Kéry & Schaub 2012). Priors can be subjective when they reflect expert opinion (Wolfson *et al.* 1996) or when data is used of comparative populations or species (Wade 2000). Priors can be objective when they are non-informative, i.e. the posterior is based on the data alone (Link *et al.* 2002; Ellison 2004; Clark 2005). However, the choice of the parameter, such as precision or variance, used as a uniform prior will influence the posterior (de Valpine 2009). Priors can be data-based, when they include estimates of the parameter from other studies (Brooks *et al.* 2000; Gelman 2006), or in sequential studies, where the previous study's results become the prior in the subsequent study (Dennis 1996; Ellison 2004; Cox 2005). Priors can reduce model complexity and the effective number of estimated parameters (increasing precision) and can, therefore, represent years of (costly) sampling data in a Frequentist approach (McCarthy & Masters 2005). Sensitivity analysis of priors is of paramount importance, especially in complex hierarchical models in which their influence only slowly abates with increased sample size (Brooks *et al.* 2000; Royle 2008; de Valpine 2009; Lele & Dennis 2009).

Frequentist statistics depend on asymptotic approximation, whereas Bayesian statistics only infers based on the collected data, which makes them more realistic (Brooks *et al.* 2002; Cox 2005). This is also an advantage in the case of sparse data, which is fairly common in CMR studies, since it enables estimation of uncertainty in such datasets (Wade 2000; Clark 2005). Continuous, time-varying, individual covariates with missing values pose an insurmountable problem to Frequentist enumeration, but can be adequately handled by the Bayesian approach, which functions well when survival and recapture rates are low (Bonner *et al.* 2010). Another advantage of Bayesian statistics is that, because the posterior distribution represents the exact probability of different parameter values given the observed data, the results including the uncertainty can be clearly visualized and are, thus, easier to communicate to stakeholders (Wade 2000; de Valpine 2009; Kéry & Schaub 2012).

State-space formulation

State-space formulation of CMR hierarchical models - as opposed to multinomial formulation - separates the state process, i.e. the biological process or the true state, from the observational process or observed state (Fig. 2; de Valpine & Hastings 2002; Buckland *et al.* 2004; Dennis *et al.* 2006). The observed state is conditional on the true state. It was first used in CMR survival analysis in 2007 by Gimenez *et al.* It facilitates the incorporation of random effects, both intrinsic (individual) and extrinsic (environmental), individual fixed and random effects, and spatial effects (Gimenez *et al.* 2007; Brooks *et al.* 2008; Royle 2008; Ballie & Schaub 2009; Péron *et al.* 2011). Fig. 3 shows a state-space formulation of a multi-state model. Observed individuals can often be accorded a state like being in location A or B, or breeding or not-breeding. Multi-state models allow for these different states, which permits the estimation of state-specific survival and recapture (Lebreton *et al.* 2009). The transition from one state to another is modelled as a transition probability.

Integrated Population Models

Until recently, the study of population dynamics - changes in population size governed by the demographic parameters survival, fecundity, and dispersal - used population projection matrices, in which separately estimated demographic parameters were incorporated to estimate abundance and, thus, population growth rate (Caswell 2001; Caswell & Fujiwara 2004; Schaub & Abadi 2011). If count data were available, then the separately estimated population growth rate could be compared to that of the projection matrix for inference about the validity of the population model. In this context a population model describes the relationship between abundance and the demographic rates (Caswell 2001). This type of modelling was severely hampered by scarce or missing data of one or more of the demographic rates (Doak *et al.* 2005). For instance, the collection of demographic data, particularly fecundity, of cooperatively breeding bird species with their complex population structure and multiple broods during long breeding seasons demands intensive CMR studies (Rowley & Russell 1991). To illustrate: a pair of sociable weavers (the study species of Chapter 5 in this thesis) produced 14 clutches in a six month period during the breeding season of 2013, yielding no fledglings.

The count data alone do not contain enough information to estimate all parameters in a population model separately (Besbeas *et al.* 2005; Schaub & Abadi 2011). Even if data were available of different age classes, juvenile/adult survival and fecundity would still be confounded. An integrated population model (IPM) incorporates count data, CMR data, and, if available, productivity data, and their separate models. By integrating the respective likelihoods and analysing their joint likelihood - which is estimated as a product of the separate likelihoods - via the parameters the three models share (Fig. 4) the uncertainty of the estimated demographic parameters and the population growth rate, and correlation between the datasets can be fully accounted for (Besbeas *et al.* 2002; Schaub & Abadi 2011). This method also provides more coherent demographic parameter estimates than separate models - in relation to the data and to each other - and improves precision and accuracy (Besbeas *et al.* 2003; Abadi *et al.* 2010; Cave *et al.* 2010). IPM's allow for the full use of the available data, i.e. census data include information on fecundity and survival, which enables the estimation of demographic parameters pertaining to the entire study period despite temporal gaps in the data (Besbeas *et al.* 2002; Brooks *et al.* 2004; Schaub *et al.* 2007).

Software

More powerful computers enabled the building of generally accessible specialized software, which facilitated and extended the use of advances in statistical methods in the analysis of ecological data (Schwartz & Seber 1999; Baillie *et al.* 2009; Gimenez *et al.* 2009). An example is program MARK for the analysis of CMR data (White & Burnham 1999), which first enabled modelling with individual covariates (Pollock 2002). Program U-CARE tests the goodness-of-fit of CJS models, i.e. whether the data does not violate any of the assumptions underlying the model (Choquet *et al.* 2009).

Software like WinBUGS (Lunn *et al.* 2000), and updated MARK (White *et al.* 2009), allowed easy, efficient and dependable application of Bayesian Monte Carlo-based (sampling-based) methods implemented by Markov Chain Monte Carlo (MCMC) algorithms - such as the rediscovered Metropolis-Hastings algorithm from the 1950s (McCarthy 2007) and the Gibbs sampler developed in 1970 (Gelfand & Smith 1990) - to sample the posterior distribution (Brooks *et al.* 2000). MCMC can fit complex hierarchical models to analyse large, multivariate datasets (Link *et al.* 2002), which non-sampling-based methods cannot (Clark 2005). The new and improved MCMC methods avoid the complex integration needed to determine the exact posterior distribution: they merely sample it (Schwartz & Seber 1999). Individual effects in state-space models, including multi-state models, are easily fitted in WinBUGS and their likelihood estimation simplified with MCMC making the Bayesian approach a natural framework (Gimenez *et al.* 2007; Royle 2008). Gimenez & Choquet (2010), though, found numerical integration with the Gauss-Hermite quadrature (Frequentist statistics) to be faster.

The package R2WinBUGS facilitated the use of WinBUGS, particularly in the case of complex and numerous datasets and when one needs to run many similar models, as these are loaded and defined in R and then 'uploaded' to WinBUGS (Sturtz *et al.* 2005; Gimenez *et al.* 2009). The posterior distributions can be saved easily, which enables further analysis and manipulation (e.g. graphics) of the output (Kéry & Schaub 2012).

Toolbox papers and books tailored to answer specific ecological questions, and often written to standardize and/or enhance studies in particular fields of research, have also greatly improved the accessibility of complex modelling. Papers pertaining to this thesis' research area are, for example, Schaub & Abadi (2011) - IPM's; Lindberg (2012) - CMR study design and corresponding analysis; Grosbois *et al.* (2008) - the use of climatic covariates in survival analyses; Jenouvrier (2013) - avian populations and climate change; Frederiksen *et al.* (2014) - linking vital rates to the environment; Kéry (2010) - an introduction to ecological modelling using WinBUGS; Kéry & Schaub (2012) - a WinBUGS book that provides scripts that can be adapted and combined to suit the study in hand. Recently, publications have started to provide scripts of the study's models, for example Lahoz-Monfort *et al.* (2011) used in Chapter 4 in this thesis. No two datasets are alike, no two field protocols are alike, and no two research questions are alike, therefore, scripts always need to be customised and the user needs to understand the statistical methods and the underlying assumptions, but the availability of 'toolboxes' and scripts brings complex modelling within reach of the ecological community.

Aims of the thesis

Most studies on the impacts of recent climate change have been conducted in the northern, temperate region (Gordo 2007; Collen *et al.* 2009; Felton *et al.* 2009; Chambers *et al.* 2013; IPCC 2014). We know little of the influence of climate on avian population dynamics in southern Africa. The principal aim of this thesis is to investigate the influence of climate on the vital rates that govern population dynamics of bird populations in South(ern) Africa.

Birds act, among others, as seed dispersers and pollinators, regulate the populations of plant pests and rodent populations, and as scavengers prevent the spread of diseases like anthrax - as such they are an integral part of the functioning of ecosystems (Sekercioğlu *et al.* 2004). Many species of plants depend on these ecosystem services, i.e. the evolution of mutualism between plants and birds (Whelan *et al.* 2008). These ecosystem services are also of great value to humans (Wenny *et al.* 2011). By definition common species are numerous and widespread and, thus, pivotal to ecosystem functioning (Gaston & Fuller 2008; Gaston 2010). Generally, common bird species have not received a large amount of scientific attention (Lindenmayer *et al.* 2011). Unfortunately. The much-cited examples of the decline of the house sparrow *Passer domesticus* and the starling *Sturnus vulgaris* illustrated how quickly, and unnoticed, the populations of common species can decline (Crick *et al.* 2002; Summers-Smith 2003; Shaw *et al.* 2008). The findings of, among others, Inger *et al.* (2015) - a dramatic loss of farmland birds across Europe, most common species - led to the establishment of the 'Keeping common birds common' initiative by Birdlife International (BLI 2016, 31 Jan). In southern Africa, where funding for research is scarcer than in the affluent West, we know little of the population dynamics of most common species. Therefore, common birds are the focus of the studies of climatic influences on bird populations presented in this thesis. The 'secondary' aim of this thesis is to improve our knowledge of the population dynamics of southern Africa's common birds and to provide baseline estimates for future studies.

Structure of the thesis

Chapter 2 investigates the influence of climatic conditions in the breeding and wintering area of a migratory population of the African reed warbler *Acrocephalus baeticatus* in Paarl (Western Cape) - modelled in program MARK.

As a habitat specialist of azonal wetlands this species can be studied across southern Africa in climatically diverse environments. **Chapter 3** explores the influence of climate in the form of the seasonality of the different wetland environments on survival of African reed warbler populations in 16 locations across the subcontinent - modelled in a hierarchical, multi-state, state-space CMR model in WinBUGS via R2WinBUGS. This analysis is carried out in the context of Life History Theory, which predicts a latitudinal gradient in survival depending on the seasonality of the habitat.

Chapter 4 focusses on the synchronizing potential of climate in two passerine assemblages in wetland (KwaZulu-Natal) and in fynbos (Western Cape) - modelled in a hierarchical model with a synchronous and an asynchronous random effect.

Chapter 5 investigates the effects of climatic extremes on the population dynamics of a population of sociable weavers near Kimberley (Northern Cape). A separate analysis of the largest colony during the study period elaborates on the synchronizing potential of climate.

Chapter 6 synthesises the results. Collectively, the four demographic analyses generated another finding that is described and further explored in an analysis of current volunteer ringing in South Africa, followed by recommendations to improve volunteer ringing and the use of the data collected by volunteers.

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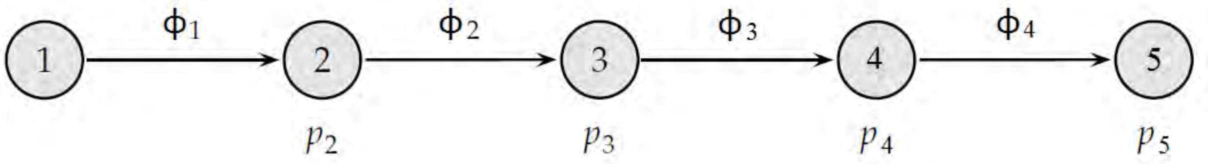

Figure 1. Diagram of an encounter history of five capture occasions (circles) and the survival probability ϕ_t from time t to t + 1 and the recapture probability p_t at time t.

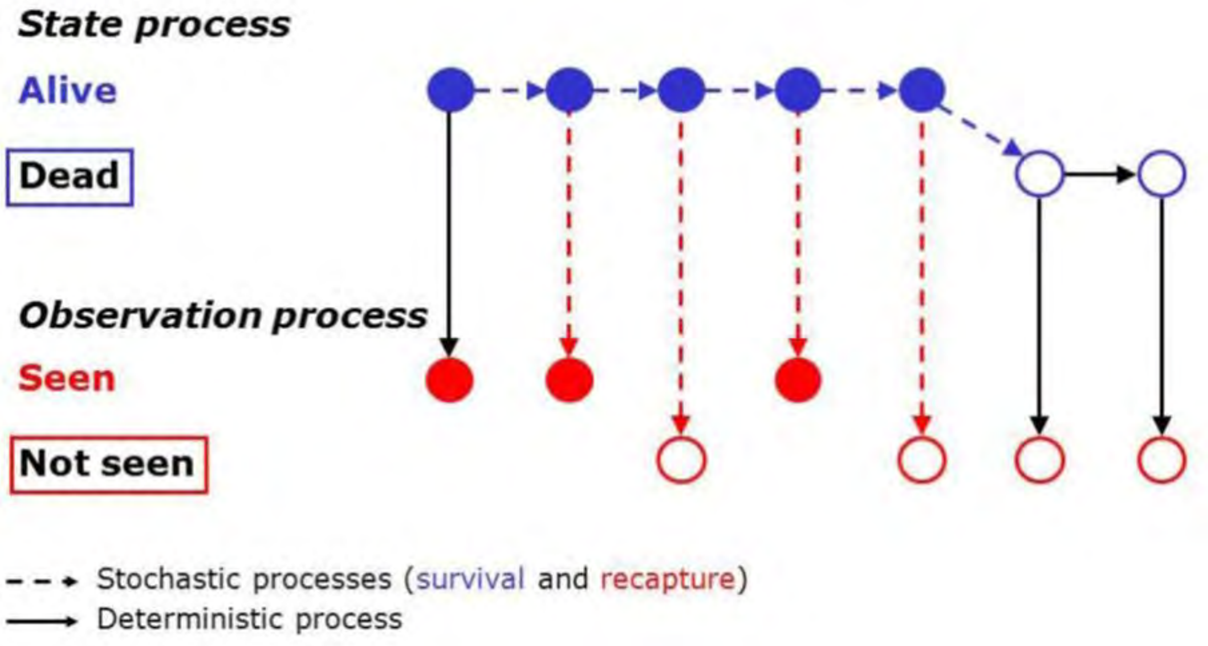

Figure 2. Diagram of a state-space formulation of an encounter history of an individual. The true state of the individual is 1111100 (blue circles) and the observed state of the individual is 1101000 (red circles; figure from Kéry & Schaub 2012).

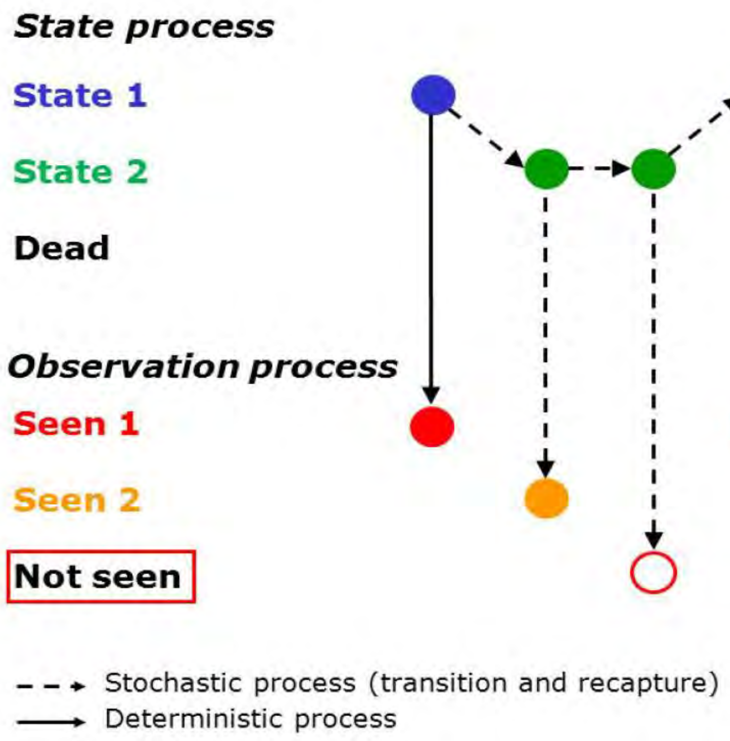

Figure 3. Diagram of a multi-state state-space definition of an encounter history in which a distinction is made between the different states of a captured individual, e.g. location or breeding status. The movement between states is modelled, and estimated, as a transition probability. Thus, a multi-state model enables the state-specific estimation of survival (blue, green, and black circles, each representing a state) and recapture (red, orange, and open circles) probabilities (figure from Kéry & Schaub 2012).

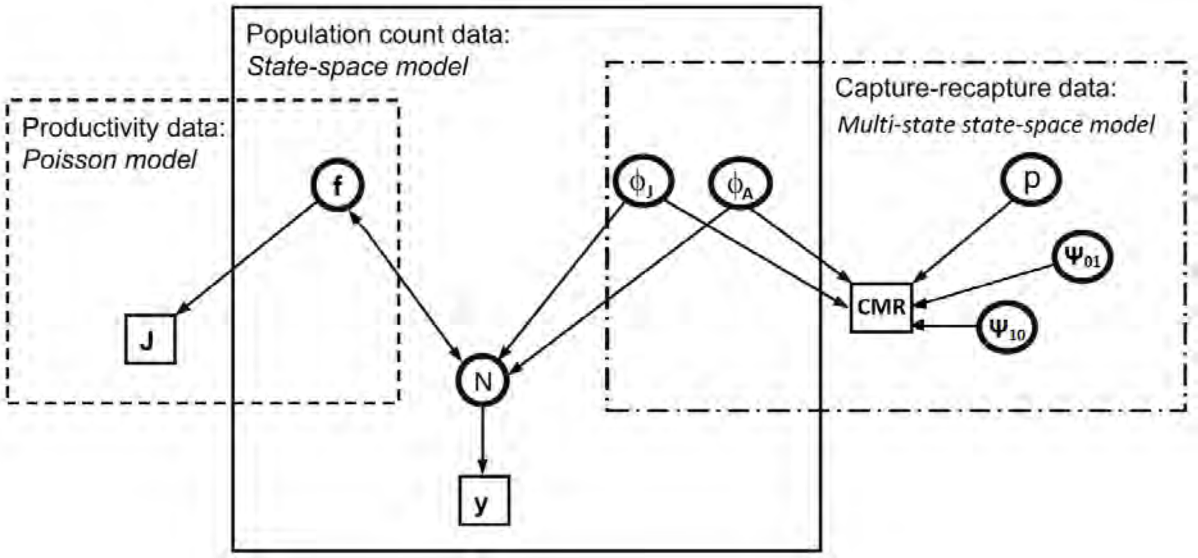

Figure 4. Directed acyclic graph of the integrated population model used in Chapter 5 in this thesis. The circles represent estimated parameters and the squares the data. The rectangles represent the different likelihoods. The circles in overlapping rectangles are the parameters shared by the different likelihoods. The arrows indicate the dependence of the nodes. *J* - productivity data; *y* - count data; *CMR* - capture-mark-recapture data; *f* - fecundity; *N* - population size; ϕ_J : juvenile survival; ϕ_A - adult survival; *p* - recapture; Ψ_{10} - temporary emigration; Ψ_{01} - temporary immigration.

Chapter 2

Climatic influences on survival of migratory African Reed Warblers *Acrocephalus baeticatus* in South Africa

Photo Dieter Oschadleus

Climatic influences on survival of migratory African Reed Warblers *Acrocephalus baeticatus* in South Africa

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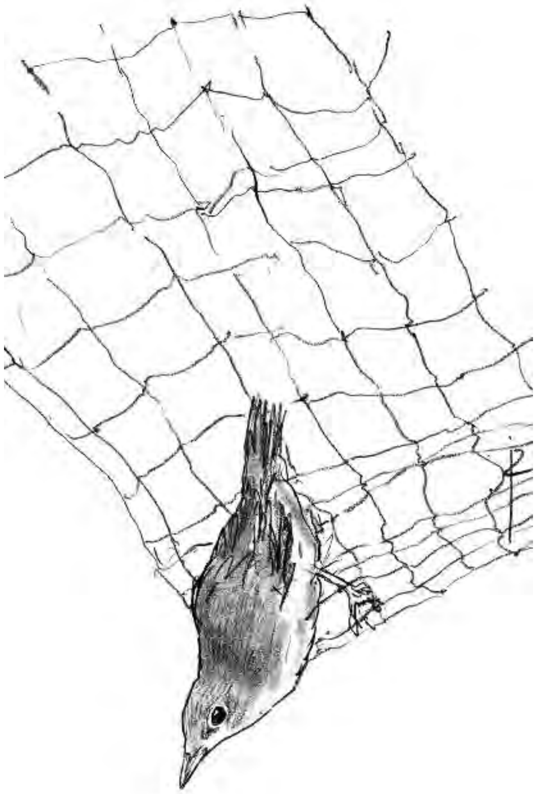
The focus of most research on the influence of recent climate change on birds has been on the northern hemisphere. Climate change has been different in the southern hemisphere, prohibiting extrapolation from northern research findings – and inference regarding future climate change – to species living there. We investigated the correlation between climatic conditions and survival of a migratory population of African Reed Warblers *Acrocephlaus baeticatus* in Paarl, South Africa. We used temperature and rainfall in its breeding area, and Normalized Difference Vegetation Index (*NDVI*) in its wintering area, Central Africa around the Congo Basin. We fitted capture-mark-recapture models for open populations to a 12-year ringing dataset (1998–2010). After accounting for transience – this species exhibits high breeding site fidelity – with a 'Time-Since-Marking' model we found a mean survival probability of 0.79 ± 0.04 SE. Rainfall and *NDVI* did not influence survival in this dataset. Mean temperature (Aug–Apr) had a positive effect on survival: an increase of 1.6°C was associated with an increase of annual survival from 0.69 ± 0.05 to 0.88 ± 0.03. Higher temperatures could have increased local survival by providing more food and breeding habitat, thereby increasing adult body condition and reducing foraging costs, predation and territorial conflicts. Even though we would need data on abundance and reproduction to quantify the effects of climatic conditions on population growth, we found a clear effect of climatic variation on a key demographic parameter, adult survival.

Key words: breeding area, capture-mark-recapture, Cormack–Jolly–Seber, environmental fluctuation, migration, Normalized Difference Vegetation Index, transience, wintering area



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The earth's surface was warmer in the past three decades than in any previous decade since 1850 (IPCC 2013). This period was likely the warmest in the past 1400 years in the Northern Hemisphere (IPCC 2014). Recent climate change has been linked to many different aspects of avian ecology and biology (see reviews by Parmesan 2006, Leech & Crick 2007, Travis *et al.* 2013). For species whose range is limited by climatic tolerance, a climate that moves outside that tolerance forces them to track their climate niche (Peterson 2003). Tingley *et al.* (2009) compared century-old ranges with current ranges of 53 bird species in the Sierra Nevada mountains (California) and found that 48 species had moved following their climate niche in response to a warmer and wetter climate. In North America and Great Britain species with a southern breeding distribution have benefited from global warming, which allowed them to expand their ranges northward by an average of 60 km over 26 years (26 species) and 19 km over 20 years (59 species), respectively (Thomas & Lennon 1999, Hitch & Leberg 2007). Common breeding birds across Europe with little high temperature tolerance suffered population declines over 1980–2005, when the average temperature increased by 0.9°C (Jiguet *et al.* 2010). European migrants wintering in sub-Saharan Africa that have not advanced their arrival date at their breeding grounds, where springs have advanced over the past 50 years, have also decreased in abundance (Saino *et al.* 2011). Some species have shown enough phenotypic plasticity to adapt to recent climate change. A century ago White Stork *Ciconia ciconia* arrival on their breeding grounds differed per region in mountainous Slovakia, with earlier arrivals in warmer and lower regions (Gordo *et al.* 2013). Breeding success of early arrivals was higher than that of late arrivals. Since the late 1970s – after global warming commenced – spatial variation in arrival date mostly disappeared and breeding success no longer depends on timing, probably due to a more even spread of food supply over the breeding season (Gordo *et al.* 2013). In the UK sedentary Long-tailed Tits *Aegithalos caudatus* survived better in years with warmer springs and autumns – in four decades their population has more than doubled (Gullett *et al.* 2014).

Most studies of the impacts of recent climate change have focussed on the northern hemisphere, particularly on the northern, temperate region (Felton *et al.* 2009, Chambers *et al.* 2013, IPCC 2014, but see Kent *et al.* 2014). Since the northern hemisphere has warmed three times as fast over land as the southern hemisphere (IPCC 2007), gathered inference cannot easily be extrapolated to the southern hemisphere (Chambers *et al.* 2013). Globally the warming trend will likely continue in the first half of this century, and the probability increases to 'virtually certain' for the latter part of the century (IPCC 2013). The most conservative scenarios predict a global increase of at least 1.5°C by the end of the century (IPCC 2014). Confidence in the forecasts regarding changes in drought conditions and precipitation amounts and frequency is lower and varies per region. Climate change forecasts predict that regions in the southern hemisphere will experience extreme temperatures at a lower overall increase in temperature than the northern hemisphere, i.e. at an earlier stage of the forecasted global warming, and these will lead to more evaporation than identical increases in temperature in the northern hemisphere (Beaumont *et al.* 2011, Sherwood & Fu 2014).

To assess the impacts of future climate change on species and individual populations we need to determine the effect(s) of climatic conditions on demography (Robinson *et al.* 2007). The effects can be complex. Herfindal *et al.* (2015) found that warmer Aprils increased breeding success of female Goshawks *Accipiter gentilis* in Denmark, but negatively affected life-time reproductive success of the female's hatchlings of those years. Easier breeding conditions would also allow lower quality females to breed, which might have introduced an inferior component to that year's cohort (with poorer hunting skills).

Apart from reproduction and dispersal, the other key demographic parameter that influences population size is survival (Baillie & Schaub 2009). In the Arctic, warmer sea surface temperatures were negatively correlated with survival in three colonies of Little Auks *Alle alle* (Hovinen *et al.* 2014). This effect, with a time lag of one and two years, was likely caused through a lower food supply of lesser quality. Determining the factors that influence survival is more complex for migratory birds, because migrants are exposed to environmental conditions in their breeding area, during migration in flight and at stop-over sites, and in their wintering area (Newton 2004). In the UK, survival of Sedge Warblers *Acrocephalus schoenobaenus* was strongly correlated with rainfall in their Sahelian wintering grounds (Peach *et al.* 1991), but survival of Eurasian Reed Warblers *Acrocephalus scirpaceus* was not (Thaxter *et al.* 2006). Nonetheless, Ockendon *et al.* (2014) found that rainfall in the Sahel did have a strong impact on the abundance of both species.

With this study we aim to add to the evidence of the impacts of climate change on birds in the southern hemisphere. We investigated the correlation of survival of a migratory population of the African Reed Warbler *Acrocephalus baeticatus* with climatic conditions in the breeding area in South Africa and the wintering area in Central Africa. Since the 1950s temperatures have been rising across South Africa (Kruger & Shongwe 2004, Midgley *et al.* 2011), particularly in the Western Cape (Warburton *et al.* 2005), and the dry periods have become longer and more intense (Kusangaya *et al.* 2014). This warming trend is predicted to continue: until 2050 by 1–2°C in the coastal areas and 3–4°C in the interior, after 2050 by 3–4°C in the coastal areas and 6–7°C in the interior (Midgley *et al.* 2011) affecting the western parts of southern Africa most rapidly (Midgley *et al.* 2003). Precipitation is forecasted to decrease in the southwest of South Africa (Niang *et al.* 2014). In Central Africa the changes in mean annual temperature are expected to be relatively smaller than the predicted average 2+°C over the entire continent by the middle of this century and 4+°C by the end of

Adult African Reed Warbler caught and ringed in South Africa (Photo Dieter Oschadleus).

the century (Niang *et al.* 2014). For some regions in Central Africa with sufficient data over 1986–2005 to serve as baseline precipitation is forecasted to increase from the mid-21st century onwards, but the different climate scenarios do not agree for many regions in this area (Niang *et al.* 2014).

The African Reed Warbler is a partial intra-African migrant that breeds in wetlands south of the Sahara (Urban *et al.* 1997). Populations below 26°S are migratory; they are thought to migrate to Central Africa during the austral winter (June–Aug; Dean 2005). During the breeding season the African Reed Warbler breeds and forages for insects in moist or wet habitat (Urban *et al.* 1997), but during the non-breeding season it is less dependent on water: it forages in thick patches of shrubs and grasses away from water (Harrison 1997). In South Africa the African Reed Warbler is relatively common and at present of no conservation concern (Dean 2005). However, the precarious state of South Africa's wetlands – 65% threatened and 48% critically endangered – combined with the forecasted increase in open water evaporation and duration of dry spells could drastically alter the status of this species in the 21st century (Midgley *et al.* 2011, Driver *et al.* 2012). An added factor could be deteriorating conditions in the wintering area due to the forecasted increase in temperature (Christensen *et al.* 2007).

The African Reed Warbler is closely related to the Eurasian Reed Warbler, or even conspecific depending on the method used to determine genetic distance (Fregin *et al.* 2009, 2012). These closely related reed warblers conform to global patterns of life history variation among birds (see Jansen *et al.* 2014) for a comparison of their published demographic rates): northern, temperate species generally have low survival and high reproductive success, while southern, temperate species exhibit the opposite with higher survival and smaller clutch sizes (Ghalambor & Martin 2001; an example of closely related New World warblers in Salgado-Ortiz *et al.* 2008). Eurasian Reed Warblers have increased their seasonal reproductive success in response to warmer springs by advancing their breeding phenology, thus lengthening their breeding season (Halupka *et al.* 2008). We investigated climatic effects on survival of their southern, temperate counterparts, the African Reed Warblers. We analysed a 12-year capture-mark-recapture dataset collected through a public ringing scheme at Paarl in the Western Cape of South Africa. In addition to temperature, we investigated a potential effect of rainfall on survival. Both climatic variables could impact survival indirectly via a direct effect on breeding sites (reed beds) and food supply (insect abundance). The peak of the rainfall at the breeding grounds occurs in June–Aug, when most birds are at their wintering grounds, and as such may affect survival in the subsequent breeding season. We therefore not only considered effects of rainfall in the current breeding season (Aug–Apr; year t), but also in the previous season ($t-1$).

Rainfall and temperature data were not available for the wintering grounds in Central Africa. We used the Normalized Difference Vegetation Index (*NDVI*) instead. This index is a measure of net primary productivity – a higher value signifies a greener environment (Pettorelli *et al.* 2005). *NDVI* is strongly correlated with rainfall and to a lesser degree with temperature (Wang *et al.* 2001, Pettorelli 2012). *NDVI* is particularly useful when the wintering area is large and not clearly delineated by recaptures or recoveries (Thaxter *et al.* 2006, Balbontín *et al.* 2009) as is the case for the African Reed Warbler. Therefore, we used *NDVI* of areas around the Congo Basin as a proxy for climatic conditions in the wintering area hypothesizing that in years with greener (wetter) winters survival would be higher.

METHODS

Ringing data

Adult African Reed Warblers were captured in mist-nets by licensed ringers (citizen scientists) according to the South African Ringing Unit protocol (SAFRING; de Beer *et al.* 2001) in and around Paarl Bird Sanctuary, a sewage works of 45 ha situated in the Western Cape of South Africa (33°43'S, 18°58'E; Figure 1). In the 12-year period between 1998 and 2010, 851 birds were captured between August and the following April, yielding 263 recaptures. August was chosen as the beginning of a capture occasion, because reed warblers start arriving from their wintering grounds during August and September to breed in the south-western Cape; they remain in their breeding grounds until March/April (Hockey *et al.* 1989). The resighting data were pooled over Aug–Apr to estimate annual survival (Appendix 2).

Captured individuals were aged by the volunteers, but at present no comprehensive guide exists to age South African bird species (de Beer *et al.* 2001). Therefore, SAFRING deemed data pertaining to age classes other than adult not reliable enough for use. Too few individuals of this sexually monomorphic species were sexed for use in the survival analysis.

Conditions in the breeding area

Temperature and rainfall were used as indicators of the environmental conditions in the breeding area. Temperature and rainfall were obtained from the weather station at Paarl via the Climate Systems Analysis Group, University of Cape Town. Millimetres of monthly rainfall were aggregated over Aug–Apr. Monthly mean temperatures (degrees Celsius) were averaged over Aug–Apr. The derived estimates were used as covariates in the estimation of survival (Figure 2A and 2B; Appendix 2).

Over the study period mean temperature (Aug–Apr) did not show a discernible trend (Pearson's product moment correlation: $r = -0.10$ (95% CI –0.66–0.53), $t_9 = -0.30$, $P = 0.77$). Rainfall did show a weak decreasing trend (Spearman's rank correlation test: $r_s = -0.45$, $S = 320$, $P = 0.16$).

Conditions in the wintering area

Given the uncertainty of the location of the wintering area in Central Africa, we selected three areas around the Congo Basin: East, South and West (Figure 1). Normalized Difference Vegetation Index (*NDVI*) was used as an indicator of environmental conditions in the wintering area. *NDVI* is a satellite-derived index of vegetation quality that uses the normalized difference between the near-infrared (*NIR*) and red (*RED*) wavelengths reflected from the Earth's surface:

$$NDVI = (NIR - RED)/(NIR + RED)$$

(see Pettorelli *et al.* 2005 for details). The values typically range from near zero (e.g. soil, dying vegetation) to 1 (green vegetation). We used the MODIS MOD13C2 *NDVI* product (monthly values per 0.05 degree grid cells), downloaded from the Land Processes Distributed Active Archive Centre (LP DAAC), located at the U.S. Geological Survey (USGS) Earth Resources and Science (EROS) Centre (lpdaac.usgs.gov). Monthly anomalies per land cell (monthly *NDVI* minus monthly *NDVI* mean of the entire study period) were calculated for each wintering season (May–July), then averaged per season per block. A positive anomaly indicated a wetter (greener) than average season, a negative anomaly a drier than average.

The derived anomalies were used as covariates in the estimation of survival (Figure 2C; Appendix 2). MODIS data were available from 2000, so we estimated survival for 1998–1999 independently using an extra parameter. We fitted the blocks (Figure 1) separately, because the mean annual *NDVI* anomalies of East and South of the Congo Basin (EOCB, SOCB) were weakly correlated with each other (Pearson's product moment correlation: $r = 0.65$ (95% CI 0.03–0.91), $t_8 = 2.40$, $P = 0.04$), the other blocks were not correlated ($r \leq 0.45$, $P \geq 0.19$).

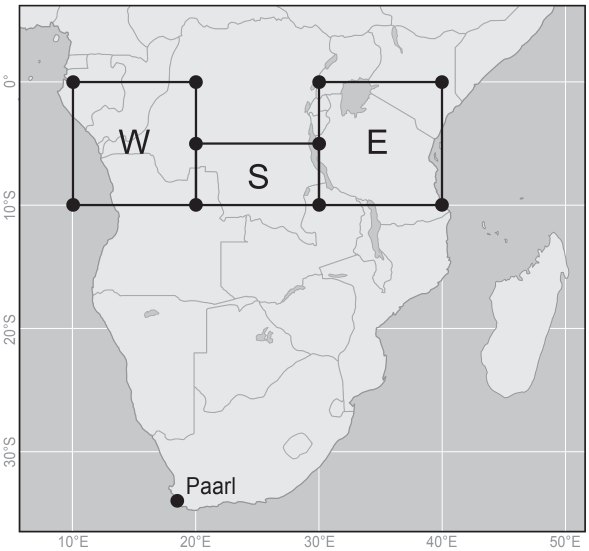

Figure 1. Capture location of the African Reed Warbler (Paarl) and its wintering area divided into three blocks in Central Africa: East (E), South (S) and West (W) of the Congo Basin. The decimal latitude and longitude of the north-west and south-east corner of each block were as follows: E 0.00°/10.00°, –9.83°/20.13°; S –4.50°/20.13°, –9.83°/30.28°; W 0.00°/30.28°, –9.83°/40.34°.

Capture-mark-recapture analyses

We used capture-mark-recapture models for open populations, which separate survival probability from recapture probability, to estimate apparent or local adult survival (hereafter survival) – 'apparent' because mortality cannot be separated from permanent emigration (Lebreton *et al.* 1992). To determine a general starting model that fitted the data a goodness-of-fit (GOF) test was performed of a Cormack–Jolly–Seber (CJS; Cormack 1964, Jolly 1965, Seber 1965) model with time-dependent survival (Φ) and recapture (p) ($\Phi(t)p(t)$) with program U-CARE 2.3.2 (Choquet *et al.* 2009). The overall GOF test was significant (χ^2_{32} = 56.04, $P_{\text{two-tailed}} = 0.005$) as a result of the directional z-test for transience of Test3.SR ($z = 3.75$, $P_{\text{two-tailed}} = 0.0002$). The result indicated that more birds than expected were seen only once, which violates the assumption of the CJS model that every marked individual has the same recapture probability (Lebreton *et al.* 1992). Mist nets can only be placed at the edge of reed beds, where a territorial bird like the African Reed Warbler that nests safely away from the edge only occasionally forages (Urban *et al.* 1997, Eising *et al.* 2001). This behaviour could result in an overabundance of transients (Buckland & Baillie 1987). Passerine ringing data often show transience, i.e. non-local birds with an apparent survival probability of zero after initial capture (Pradel *et al.* 1997). Not accounting for transience causes underestimation of survival for newly marked birds during the first period because that estimate is based on a mixture of transient and resident birds (Buckland & Baillie 1987).

Subsequently, we fitted a 'Time-Since-Marking' (TSM) model, in which initial capture is treated as a separate 'age' class from recapture (*a2*; Pradel *et al.* 1997). The transient effect was modelled as constant over time in *a2*, with time as an additive effect in $a2 + t$ and as an interactive effect in $a2 \times t$ ($= a2 + t + a2 \times t$). The median c-hat GOF, implemented in program MARK (White & Burnham 1999), was used to assess the fit of a TSM model with constant *a2* survival and time-dependent recapture $\Phi(a2)p(t)$. Estimated c-hat for this model was 1.09 ± 0.04 SE (0.84–1.35) indicating no further evidence of overdispersion (Lebreton *et al.* 1992) and, therefore, an adequate representation of the structure in the data.

Program MARK 8.0 (White & Burnham 1999) was used for model fitting and R 3.1.1 (R Development Core Team 2014) for data handling, figures and statistical tests. We used simulated annealing to fit the more complex models and report profile likelihood confidence intervals. For the simpler models we used the faster standard Newton–Raphson algorithm after preliminary analyses showed that the two algorithms gave identical results. Corrected Akaike's Information Criterion (*AICc*) was used for model selection (Akaike 1973, Burnham & Anderson 2002). Estimates are shown with their standard errors.

RESULTS

Accounting for transience

To solve lack of fit we accounted for transience before considering climatic covariates. Models 6 and 7 (Figure 2D, Table 1) that accounted for transience showed a considerably better fit than model 9 – the corresponding model that did not account for transience (Δ*AICc*; Table 1). The Time-Since-Marking (TSM) models with time-dependent (t) survival (models 7 and 10) showed parameter estimability problems (the number of estimated parameters was smaller than K in Table 1) due to sparseness of the data (low recapture probability). Model 6 with constant survival including a transient effect and time-dependent recapture was the most parsimonious model without covariates. Estimation of recapture of the last interval was problematic, even though it is theoretically estimable in these models due

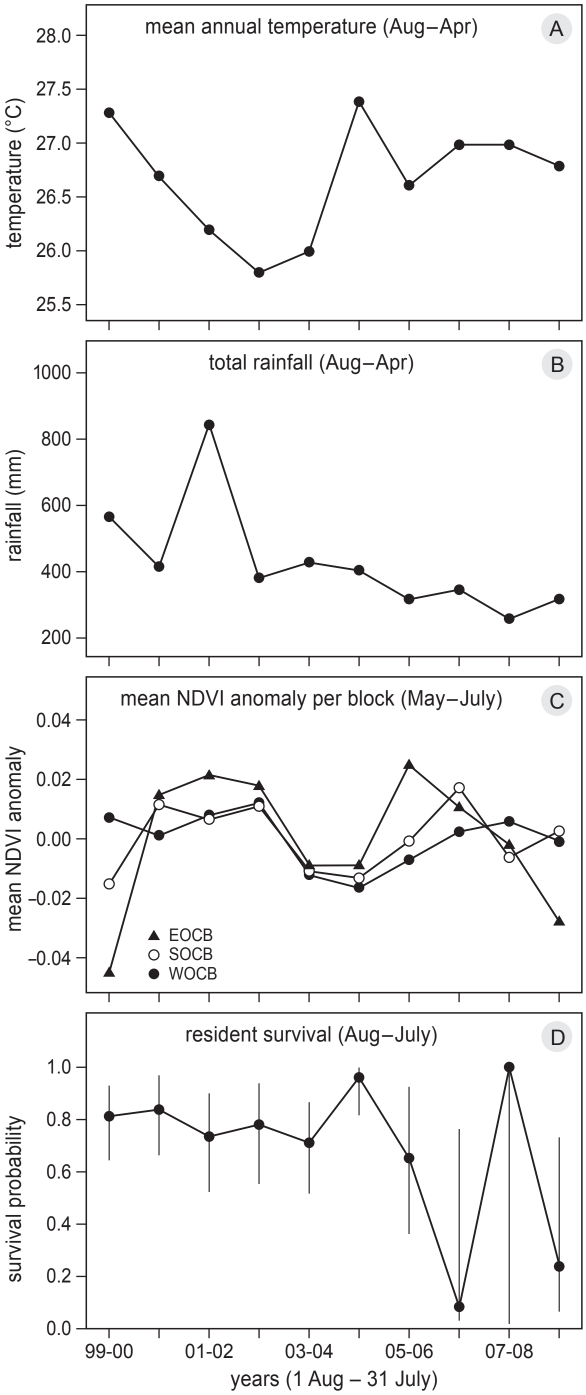

Figure 2. (A) Temperature, (B) rainfall (measured at Paarl, South Africa) and (3) *NDVI* values (1999–2009, for the three spatial blocks East, West and South of the Congo Basin (*EOCB*, *WOCB*, *SOCB*) shown in Figure 1) used as covariates in model 1, 5, 2 to 4 and (D) annual resident survival (model 7, Table 1). Note that we could not separate resident from transient survival during the first year.

Table 1. Models fitted to African Reed Warbler ringing data (1998–2010) from Paarl.

Model	Δ*AICc*	*AICc* weight	*K* ‡	Deviance
1. $\Phi(a2 + \mathrm{temp})p(t)$ §	0.00	0.81	14	179.94
2. $\Phi(a2 + \mathrm{SOCB})p(t)$	6.18	0.04	15	184.06
3. $\Phi(a2 + \mathrm{EOCB})p(t)$	6.23	0.04	15	184.11
4. $\Phi(a2 + \mathrm{WOCB})p(t)$	6.69	0.03	15	184.58
5. $\Phi(a2 + \mathrm{rain})p(t)$	6.76	0.03	14	186.71
6. $\Phi(a2)p(t)$	6.94	0.03	13	188.94
7. $\Phi(a2 + t)p(t)$	7.96	0.02	23	169.20
8. $\Phi(a2 + \mathrm{rain\ prev})p(t)$	8.75	0.01	14	188.04
9. $\Phi(.)p(t)$	13.22	0.00	12	197.27
10. $\Phi(a2 \times t)p(t)$	14.47	0.00	31	158.79

Δ*AICc* = the difference with the smallest *AICc*; *K* = number of theoretically estimable parameters; Φ = survival probability; p = recapture probability; $a2$ = two Time-Since-Marking classes to account for transients; t = time-dependence; × = interaction; . = mean; temp = mean temperature Aug–Apr; *SOCB*/*EOCB*/*WOCB* = mean *NDVI* anomaly May–July for south/east/west of the Congo Basin; rain = total mm Aug–Apr; prev = Aug–Apr of the previous year.
§ *AICc* = 1272.74. ‡ Models 2–4 have an extra parameter, compared to the other covariate models, estimating survival in 1998–1999 for which there was no *NDVI* data.

to the additive transients effect. However, estimability problems at the end of the study period are customary with sparse data (Lebreton *et al.* 1992). All models with a constant recapture probability were less well supported than models 1–10.

Model 6 estimated an initial survival (resident individuals + transients) probability of 0.51 ± 0.06 and a resident survival probability of 0.79 ± 0.04. The proportion of residents was 0.65 (initial survival/resident survival; Pradel *et al.* 1997).

Environmental covariates

We then explored possible causes of temporal variation in survival, replacing the unconstrained time effect in model 7 by covariates: temperature (model 1, Table 1, Figure 2A; model 7, Figure 2D), Normalized Difference Vegetation Index (*NDVI*; models 2–4), rainfall (model 5), and rainfall over the previous year (model 8). Rainfall and mean temperature were not correlated (Spearman's rank correlation test: $r_s = -0.33$, $S = 292.16$, $P = 0.32$). Mean temperature (Aug–Apr) was not correlated with *NDVI* (May–July) of the Central African blocks ($r \leq -0.23$, $P \geq 0.13$) nor was rainfall ($r_s \leq 0.19$, $P \geq 0.61$).

Conditions in the breeding area

The model constraining survival to be a function of temperature was clearly the best model in our set (model 1, Table 1), showing that annual variation in temperature (Aug–Apr) on the breeding grounds had a significant, positive influence on survival (Table 2). Temperature explained 46% of the temporal variation in survival (ANODEV $F_{1,9} = 7.54$, $P = 0.02$). Annual adult survival ranged from 0.69 ± 0.05 during August 2002 – July 2003, when mean temperature (Aug–Apr) was 25.8°C, to 0.88 ± 0.03 during 2004–2005, when mean temperature was 27.4°C (Figure 3). The unconstrained annual estimates from model 7 (Table 1) were less precise, but most 95% confidence intervals of model 1 fell within those of model 7 (Figure 3). The model with the temperature effect was 40 times more likely than the model with unconstrained temporal variation (*AICc* weight model 1/*AICc* weight model 7 = 0.81/0.02; Table 1).

Table 2. Covariate influence on annual adult survival.

Covariate	Model (Table 1)	Regression Coefficient*	SE	95% CI	
				Lower	Upper
Temperature	1	0.76	0.25	0.26	1.25
SOCB	2	–17.60	17.61	–52.10	16.91
EOCB	3	–8.67	9.21	–26.72	9.37
WOCB	4	–13.03	18.79	–49.86	23.81
Rainfall	5	–0.002	0.001	–0.004	0.000
Rainfall prev	8	–0.002	0.001	–0.003	0.002

For details of the covariates, see Table 1. *Slope on the logit scale.

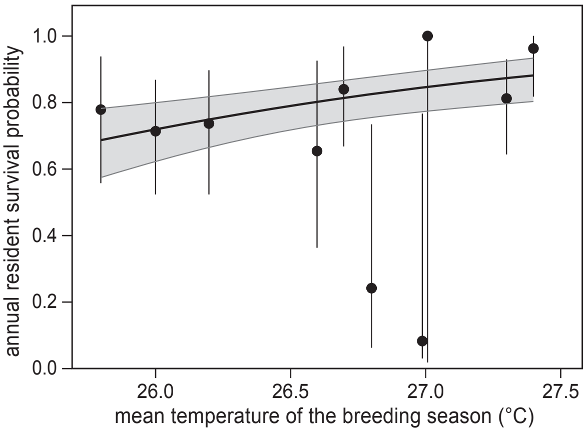

Figure 3. Apparent survival of adult African Reed Warblers in relation to temperature (Aug–Apr) at Paarl (1999–2010). The solid line shows the linear (on the logit scale) relationship between temperature and survival (model 1, Table 1). Grey lines show the 95% confidence interval. The points are the annual survival estimates from model $\Phi(a2 + t)p(t)$ (model 7, Table 1, Figure 2D), the vertical lines their 95% profile likelihood confidence intervals.

Estimated recapture probabilities of model 1 ranged from 0.01 ± 0.009 for Aug–Apr 2007–2008 to 0.54 ± 0.09 during 1999–2000 (omitting 2009–2010 due to estimability problems; see Table A1 for all annual estimates and those of the additive time model 7).

Even though model 5 constraining survival to be a function of rainfall had a marginally lower *AICc* value than the constant model (model 6), the confidence interval for the effect of rainfall included zero (Table 2) and there was therefore little evidence that annual variation in total rainfall during Aug–Apr had any influence on survival, nor of rainfall in the previous year (model 8; Table 2).

Conditions in the wintering area

We found no evidence that annual variation in *NDVI* in the wintering area affected survival (all confidence intervals included zero; Table 2), as models 2 to 4 (Table 1) had only marginally lower *AICc* values than the constant model (model 6). The lower *AICc* value of the covariate models was mostly due to the fact that they estimated survival independently for the first year for which we had no *NDVI* observations. The comparison of *AICc* values therefore includes an element of unconstrained time variation for that year.

DISCUSSION

We found that annual apparent adult survival of the African Reed Warbler population in Paarl was significantly correlated with mean temperature (Aug–Apr) in the breeding area. When the temperature increased by 1.6°C, annual survival increased substantially by 0.19. The mechanism by which climatic conditions influence demographic parameters can be complex and indirect, and is often poorly understood (Gullett *et al.* 2014). For instance, when Gullett *et al.* (2014) linked higher temperatures to increased survival of Long-tailed Tits, direct higher mortality in less favourable weather appeared unlikely as none was observed. Instead, they suspected that severe conditions during breeding forced the parents to invest more in the nest, in foraging and in their own thermo-regulation leading to decreased body condition and, thus, eventually to higher mortality. This mechanism could also explain our findings: a temperature rise lead to increased food availability thus reducing foraging costs and a proliferation of reeds expanding the breeding habitat, thereby reducing territorial disputes and decreasing predation risk in denser and higher reeds (Urban *et al.* 1997, Eising *et al.* 2001, Leisler & Schulte-Hagen 2011). Another mechanism could be increased local survival through reduced emigration: larger reed beds could reduce the need for breeding dispersal. However, as the African Reed Warbler exhibits high breeding site fidelity (Harrison 1997), this explanation appears unlikely.

The African Reed Warbler may initially profit from the forecasted increase in temperature in its breeding area, but the relationship between demography and climate is often non-linear (e.g. Nevoux *et al.* 2008). An increase larger than 1–2°C could well cause a decline in survival of the African Reed Warbler by drying out its breeding habitat. In The Netherlands declining water levels were found to decrease the abundance of water reeds (Graveland 1998).

Our mean adult survival estimate of the migratory African Reed Warbler in Paarl of 0.79 compared closely to the 0.77 estimated over 16 years for a sedentary population in Malawi (Peach *et al.* 2001). Thaxter *et al.* (2006) estimated 0.33 to 0.60 mean survival probability (1988–2004, range of two sites and sexes separately) for the closely related migratory Eurasian Reed Warbler in England. This considerable difference follows the generally accepted paradigm of the latitudinal gradient in survival, where northern, temperate passerines have a significantly lower survival rate than tropical and southern passerines (Martin 1996, Johnston *et al.* 1997, Peach *et al.* 2001, Leisler & Schulte-Hagen 2011(reed warblers)).

Because of the limited duration of our study (10 annual resident survival estimates of which the last three were based on low recapture probabilities), the small sample size (n = 851), and the low number of recaptures (n = 263), we only considered models with a single environmental variable to avoid finding spurious relationships (overfitting; Young & Karr 2011). Using this approach, we were able to identify that mean temperature (Aug–Apr) in the breeding area was the only single variable that was significantly correlated with survival in this species. Rainfall over the current and previous year in the breeding area and *NDVI* in the wintering area were not significant predictors on their own, though it is quite possible that a larger dataset would allow exploration of more complex models and might reveal interacting effects of environmental conditions.

To accurately determine the influence of climatic conditions on population demography we need data pertaining to survival (here capture-mark-recapture data) as well as density (abundance data), fecundity and dispersal (Stenseth *et al.* 2004, Gullett *et al.* 2014). Regarding the latter, the African Reed Warbler has been observed as a cooperative breeder in a study area where the habitat was saturated and dispersal opportunity was severely limited (Eising *et al.* 2001). Similarly, measures of food availability, predation risk, brood parasitism, habitat status and the impact of climate on these would enhance our understanding of what exactly influences which life history trait (see Jansen *et al.* 2014 for more detailed information regarding the African Reed Warbler; for other species, Foppen *et al.* 1999, Yom-Tov *et al.* 2006, Avilés *et al.* 2012). Data on all – or at least more – demographic parameters will also indicate which of the vital rates drive(s) population dynamics (Le Gouar *et al.* 2011, Robinson *et al.* 2012). In a developing country like South Africa, funding for data collection, let alone controlled experiments, is scarce. For most species, especially the common ones, the only data available are those collected by citizen scientists. The protocol for bird ringing could easily be expanded to include data collection of some of the aforementioned variables. However, fecundity and abundance data collection would need a rigorous protocol to ensure the safety of the study species and the reliability of the data.

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SAMENVATTING

Onderzoek naar de effecten van klimaatverandering op vogels is tot nu toe vooral op het noordelijk halfrond verricht. Omdat klimaatverandering zich op het zuidelijk halfrond anders ontwikkelt dan op het noordelijk halfrond kunnen de resultaten van onderzoek op het noordelijk halfrond niet zonder meer geëxtrapoleerd worden naar het zuidelijk halfrond en zijn voorspellingen over de effecten van klimaatverandering moeilijk te vertalen naar zuidelijke soorten. In dit artikel hebben we aan de hand van 12 jaar (1998–2010) vangst-merk-terugvangstgegevens in Zuid-Afrika gekeken naar het verband tussen klimatologische omstandigheden en de overleving van een populatie Kortvleugelkarekieten *Acrocephalus baeticatus* die vanuit het Zuid-Afrikaanse broedgebied aan het begin van de zuidelijke winter naar Centraal-Afrika (Congo-bekken) trekt om daar te overwinteren. De klimatologische factoren die we in beschouwing hebben genomen, zijn temperatuur en regenval in het broedgebied en een "Normalized Difference Vegetation Index" (*NDVI* of groenindex) in het overwinteringsgebied. Als we de lagere overleving in het eerste jaar na de vangst buiten beschouwing laten (mogelijk veroorzaakt door doortrekkers in de vangsten: broedvogels zijn in latere jaren zeer plaatstrouw aan hun broedgebied), is de gemiddelde jaarlijkse overleving 0,79 ± 0,04 (SE). Regenval in het broedgebied en de *NDVI* in het overwinteringsgebied hadden geen effect op de overleving, terwijl de gemiddelde temperatuur tijdens het broedseizoen (augustus–april) een positief effect had op de overleving. Een toename van 1,6°C ging gepaard met een toename van de jaarlijkse overlevingskans van 0,69 ± 0,05 tot 0,88 ± 0,03. Hogere temperaturen leiden mogelijk tot een grotere beschikbaarheid van voedsel en broedhabitat, waardoor er minder lang gefoerageerd hoeft te worden, de vogels in betere conditie verkeren, en de kansen op predatie en territoriale conflicten kleiner zijn. Hoewel we aanvullende gegevens over aantallen en broedsucces nodig hebben om de effecten van klimatologische omstandigheden op de populatiegroei te kunnen bekijken, vinden we een duidelijk effect van klimatologische omstandigheden op een belangrijke demografische parameter, de overleving van volwassen vogels. (TL)

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APPENDIX 1.

Table A1. Annual recapture probability with 95% confidence intervals (model 1 and 7; Table 1).

Capture occasion (Aug–Apr)	Recapture probability model 1	95% CI Lower	95% CI Upper	Recapture probability model 7	95% CI Lower	95% CI Upper
1998–1999	0.54	0.36	0.71	0.54	0.35	0.73
2000–2001	0.14	0.08	0.23	0.15	0.08	0.26
2001–2002	0.15	0.09	0.24	0.16	0.09	0.27
2002–2003	0.17	0.10	0.28	0.16	0.09	0.27
2003–2004	0.17	0.10	0.28	0.16	0.09	0.27
2004–2005	0.22	0.14	0.32	0.18	0.11	0.25
2005–2006	0.21	0.14	0.32	0.24	0.11	0.46
2006–2007	0.08	0.04	0.14	1.00	0.08	1.00
2007–2008	0.01	0.00	0.05	0.02	0.00	1.00
2008–2009	0.00	0.00	0.00	0.00	0.00	0.22

APPENDIX 2.

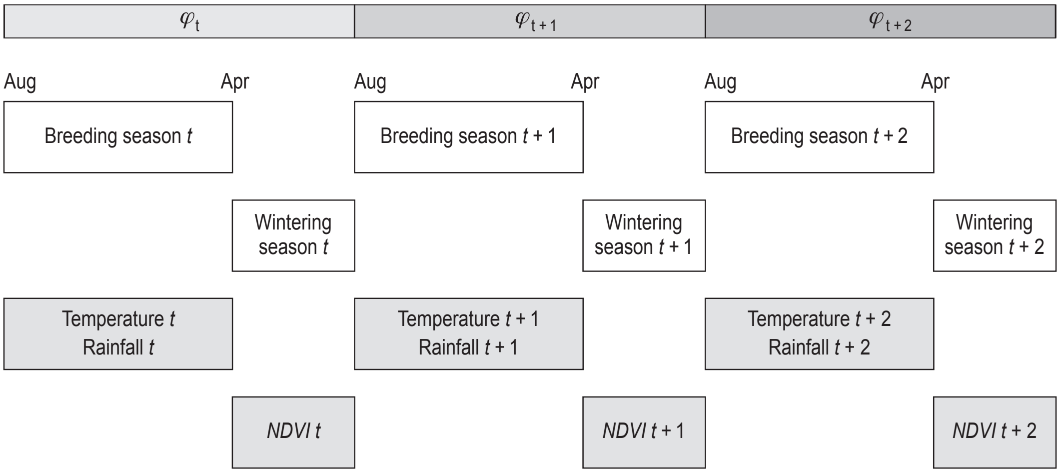

Figure A2. The timeline and intervals of the annual survival estimates and the covariates (light grey) used in the analysis of the capture-mark-recapture data of African Reed Warblers at Paarl (1998–2010).
Φ = survival probability; *NDVI* = Normalized Difference Vegetation Index

Chapter 3

Does seasonality drive spatial patterns in demography? Variation in survival in African Reed Warblers *Acrocephalus baeticatus* across southern Africa does not reflect global patterns

Photo Dieter Oschadleus

Ecology and Evolution

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Does seasonality drive spatial patterns in demography? Variation in survival in African reed warblers *Acrocephalus baeticatus* across southern Africa does not reflect global patterns

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Keywords
Avian life history, capture–mark–recapture, JAGS, multistate state-space, seasonality, spatial variation.

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Abstract

Among birds, northern temperate species generally have larger clutches, shorter development periods and lower adult survival than similarly-sized southern and tropical species. Even though this global pattern is well accepted, the driving mechanism is still not fully understood. The main theories are founded on the differing environmental seasonality of these zones (higher seasonality in the North). These patterns arise in cross-species comparisons, but we hypothesized that the same patterns should arise among populations within a species if different types of seasonality select for different life histories. Few studies have examined this. We estimated survival of an azonal habitat specialist, the African reed warbler, across the environmentally diverse African subcontinent, and related survival to latitude and to the seasonality of the different environments of their breeding habitats. Data (1998–2010) collected through a public ringing scheme were analyzed with hierarchical capture-mark-recapture models to determine resident adult survival and its spatial variance across sixteen vegetation units spread across four biomes. The models were defined as state-space multi-state models to account for transience and implemented in a Bayesian framework. We did not find a latitudinal trend in survival or a clear link between seasonality and survival. Spatial variation in survival was substantial across the sixteen sites (spatial standard deviation of the logit mean survival: 0.70, 95% credible interval (CRI): 0.33–1.27). Mean site survival ranged from 0.49 (95% CRI: 0.18–0.80) to 0.83 (95% CRI: 0.62–0.97) with an overall mean of 0.67 (95% CRI: 0.47–0.85). A hierarchical modeling approach enabled us to estimate spatial variation in survival of the African reed warbler across the African subcontinent from sparse data. Although we could not confirm the global pattern of higher survival in less seasonal environments, our findings from a poorly studied region contribute to the study of life-history strategies.

Introduction

In the 170 years since German explorers first described substantially smaller clutch sizes in South American birds compared with those found in Europe (Skutch 1985), empirical data of a latitudinal gradient in many avian life-history traits have accumulated in both the New World (Yom-Tov et al. 1994; Young 1994; Johnston et al. 1997; Ricklefs 1997; Ghalambor and Martin 2001; Tarwater and Brawn 2010) and the Old World (Moreau 1944; Lack 1968; Rowley and Russell 1991), although few studies have compared survival between the Old World northern and southern hemisphere (Yom-Tov et al. 1992; Peach et al. 2001; Schaefer et al. 2004; Stevens et al. 2013). Southern hemisphere and tropical species, particularly passerines, are characterized by smaller clutch sizes, higher nest predation, several nesting attempts, longer development periods and parental care, and thus higher juvenile survival, and higher adult survival than closely related northern, temperate species of similar body mass (Martin 1996; also see Skutch 1985 and McNamara et al. 2008 for more references). Even though not all studies have found these patterns (Karr et al. 1990; Brawn et al. 1995; Sandercock et al. 2000; Ricklefs and Shea 2007; Blake and Loiselle 2008; Ricklefs et al. 2011), it is still the generally accepted paradigm.

Life-history theory predicts that with limited available resources each individual must balance the energy demands of growth, maintenance, and reproduction, to maximize fitness in its natural and demographic environment (Gadgil and Bossert 1970). How the four components of food supply, reproductive rate, mortality/survival, and population density interact to drive the evolution of life history, and thus explain the latitudinal gradient in life-history strategies, is the subject of lively debate to this day, since the first tentative hypothesis was suggested by Hesse in 1922 (reviews in Martin 1996; Ricklefs 2000; McNamara et al. 2008; Skutch 1985). The three main hypotheses centre on the seasonality of the environment, which shows a latitudinal gradient in day length and climatic extremes with stability around the equator and ever more extremity toward the poles. Lack (1947) proposed that longer day length during the breeding season in the North would enable parents to raise larger broods, leading to the evolution of larger clutch sizes, and correspondingly lower adult survival. Skutch (1949) argued that reproduction rate was adjusted to mortality, which must be higher in the North due to the hazards of migration or winter and lower in the South because of the observed smaller clutch sizes and stable population densities. He also proposed that higher nest predation in the South would select for smaller and thus easier to conceal broods. Ashmole (1963) contended that northern temperate climates – with a highly varying food supply leading to high mortality – would decrease population density during the non-breeding season, and thus decrease food competition during the breeding season, leading to a higher reproductive rate. Findings continue to emerge to support or dispute one or other of these hypotheses (Ricklefs 1980; Dijkstra et al. 1990; Ferretti et al. 2005; Halupka and Greeney 2009; Rose and Lyon 2013). The patterns are apparent across species, but if the hypotheses above hold, that is, types of seasonality select for particular life histories, we should also expect to see the same patterns within genera of closely related species and within species where populations inhabit areas that differ in seasonality. Finding these same patterns would confirm the generality of the paradigm.

The Old World Acrocephalidae family of reed and bush warblers is a phylogenetically homogeneous group and one of the most extensively studied avian groups and as such well suited to comparative studies of life-history strategies (Leisler and Schultze-Hagen 2011). The true reed warblers *Acrocephalus* occur sympatrically in wetlands – a global, azonal habitat that varies in extent, composition, density, and height among biomes (Leisler and Schultze-Hagen 2011; Nel and Driver 2012). Within this genus, the subgroup of six small, plain-backed marsh warblers contains the Eurasian reed warbler (*Acrocephalus scirpaceus*, Hermann) and the African reed warbler (*Acrocephalus baeticatus*, Vieillot), which are deemed sister taxa or conspecific depending on the sample, methodology, and threshold of genetic distance used to separate species (Helbig and Seibold 1999; Fregin et al. 2009, 2012). The difference in research extent between these two insectivorous warblers is striking. Most details of the breeding ecology of the African reed warbler were gathered in a 1-year study in one study area by Eising et al. (2001), and to date, survival was estimated for one population in Malawi (Peach et al. 2001). In contrast, long-term studies have covered most biological and ecological aspects of the Eurasian reed warbler's life history, resulting in findings representative of the species and not merely a "snapshot" of the observed population (Leisler and Schultze-Hagen 2011; Fitzsimmon 2013).

The African reed warbler is a tropical and southern, partial intermediate migrant (migratory roughly below 26°S) thought to migrate to Central Africa during the austral winter (June–August); the Eurasian reed warbler is a northern, temperate long-distance migrant wintering mainly in West and East Africa and as far south as northern Angola with rare sightings in South Africa (Dean 2005; Herremans 2005; Kennerley and Pearson 2010). Apart from nest predation, the comparison between these two species shows patterns consistent with the generally accepted latitudinal trend in avian life-history traits (Table 1; page numbers indicate several sources).

As it now appears that the pattern holds across these very closely related species, a more powerful test of the theory would be to compare populations of a single species occurring in environments with different seasonality. This would facilitate understanding of causal relationships, ecological constraints, population density regulation, and the evolution of life-history traits (Frederiksen et al. 2005; Dhondt 2001; examples Thaxter et al. (2006) and Saracco et al. 2012). Additionally, data collected following one protocol and curated by a single institution would yield well-founded results (Frederiksen et al. 2005). The objective of this study was to investigate spatial variation in adult survival of the African reed warbler found in wetlands across the southern African subcontinent,

Table 1. Comparison of life-history traits of the African reed warbler (ARW) and the Eurasian reed warbler (ERW) sourced from published studies. ?, no data are available.

Trait	ARW	ERW	References
Clutch size (commonly)	2–3	4–5	1
Nest predation per breeding season	20%	28–95%	2
Nesting attempts (after brood fails)	?	1–5	3
Incubation (days)	12–14	9–12	4
Fledging (days)	12–14	10–13	5
Parental care after fledging (days)	?	10–14	6
Juvenile survival (mean probability)	?	0.22	7
Adult survival (mean probability)	0.77	0.51, 0.56, 0.59, 0.61, 0.46, 0.56	8

1. ARW – Urban et al. 1997; Eising et al. 2001; ERW – p. 211 Simms 1985; 2. ARW – Eising et al. 2001; ERW – p. 106 Honza et al. 1998; Halupka et al. 2008; 3. ERW – p. 185 Schultze-Hagen et al. 1996; Halupka et al. 2008; 4. ARW – Urban et al. 1997; Eising et al. 2001; ERW – Simms 1985; Halupka et al. 2008; Kennerley and Pearson 2010; 5. ARW – Urban et al. 1997; Eising et al. 2001; ERW – Simms 1985; Halupka et al. 2008; Kennerley and Pearson 2010; 6. ERW – Kennerley and Pearson 2010; 7. ERW – Coehoorn et al. 2011; 8. ARW – Peach et al. 2001; ERW – p. 213 Simms 1985; Buckland and Baillie 1987; Peach et al. 1990; Coehoorn et al. 2011; Kew and Leech 2013.

which is, relative to its size, one of the most environmentally diverse areas in the world (Allan et al. 1997). We used ringing data collected over 12 years by a public ringing scheme according to the protocol of the South African Ringing Institute (SAFRING) (de Beer et al. 2001). The data encompass 16 major vegetation units within nine bioregions within four biomes (Table 2) located from 21°S to 34°S. We hypothesized that survival would be lower in the north of the latitudinal range than in the south, and that the timing of rainfall, the seasonality of the environment, and the migratory strategy of the different populations would influence survival. We predicted that survival would be higher in the area with austral summer rainfall than in the area with winter rainfall and lowest in the areas with irregular rainfall, where the populations are sedentary (Dean 2005). The breeding season of the African reed warbler starts from August onwards, that is, after the austral winter, when the migratory populations return (Dean 2005). Winter rainfall might provide better breeding habitat, that is, denser, higher, and greener reed beds (Eising et al. 2001), and a good food supply early in the season, but summer rainfall would provide a longer period of adequate food supply for adults, which would also leave migrants fitter for migration (Newton 2006). We expected survival to be highest in the least seasonal environments and higher in migratory than in sedentary populations. Although migration is hazardous (Dobson 1990; Newton 2004, 2006; Leisler and Schultze-Hagen 2011), these species tend to have shorter breeding seasons and produce fewer young and sedentary species must endure deteriorating conditions (Alerstam and Högstedt 1982).

Materials and Methods

Data

From August 1998 to July 2010, 9921 individual adult African reed warblers (11,598 captures) were caught in mist nets throughout the year in southern Africa (12 capture occasions August–July). These captures were made by licensed ringers according to the SAFRING protocol but not within a designed geographical scheme. We examined capture effort at each location to avoid bias in the survival estimates through incidental mist netting. Capture effort ranged from 1 day to 120 days during the entire study period. Twenty-one locations were selected where capture effort was 24 days or more from 1998 to 2010 (circles in Fig. 1). Recaptures confirmed earlier observed high breeding site fidelity (Eising et al. 2001). Except for five individuals, recaptures of the same individual between occasions were within a radius of 0.17 decimal degrees (10 min South and East) of the original capture. We, therefore, included captures made within this radius of 0.17 decimal degrees of the 21 high effort locations. The subsequent dataset comprised of 6951 individual adult reed warblers (7,816 captures), of which 701 individuals were recaptured at least once in subsequent occasions. Table S1 lists captures per site per year.

The biomes/bioregions/vegetation units of the locations in South Africa, and one in Botswana by proximity, were extracted with ArcView GIS 3.1 (ESRI 1999) from the latest vegetation map (Mucina and Rutherford 2006); for Namibia the map in Mendelsohn et al. 2003 and for Botswana the map in Allan et al. 1997 were used (Table 2). When locations were within 0.17 decimal degrees of others and all within the same vegetation unit, they were viewed as one site (numbers in Fig. 1). Because no direct measurement of seasonality was available, we used the climate details of the vegetation types and "scored" seasonality by adding up annual precipitation coefficient of variation (APCV), mean annual temperature (MAT), and mean annual frost days (MAFD) (Table 2).

Atlas data indicate that African reed warbler populations are migratory in the south of southern Africa, roughly below 26°S (Harrison 1997; Dean 2005). We used this latitude to separate migratory populations from non-migratory populations. This split locations in Namibia

Table 2. Climate details of the bioregions/vegetation units of the capture sites of the African reed warbler and estimated mean survival during 1998–2010.

Biome	Bioregion	Vegetation unit	Sites (Fig. 1)	Timing P	MAP (mm)	APCV (%)	MAT (°C)	MAFD (days)	Seasonality "score"[1]	Φ	95% CRI
Desert	*Central–western Plains[2]		2	Irregular	<50	>100	17.0	0	+	0.69	0.45–0.89
Grassland	Mesic Highveld	Egoli Granite	4	Summer	682	26	16.0	29	±	0.70	0.51–0.87
		Rand Highveld	6	Summer	654	27	15.8	28	±	0.72	0.50–0.89
		Soweto Highveld	7	Summer	662	27	14.8	41	+	0.53	0.34–0.75
		Wakkerstroom Montane	8	Summer	902	22	14.1	31	±	0.65	0.45–0.85
		Eastern Free State Sandy	11	Summer	701	26	13.6	51	+	0.49	0.18–0.80
	Dry Highveld	Carletonville Dolomite	5	Summer	593	28	16.1	37	+	0.83	0.62–0.97
		Winburg Grassy Shrubland	12	Summer	495	31	15.3	41	+	0.71	0.51–0.88
	Sub-escarpment	KZN Highland Thornveld	9	Summer	752	25	16.5	15	–	0.80	0.59–0.95
		Northern KZN Moist	10	Summer	836	23	16.2	20	–	0.59	0.34–0.82
Savanna	# Arid woodland		1	Summer	250–650	?	?	?	?[3]	0.57	0.35–0.79
	Sub-escarpment	Ngongoni Veld	13	Summer	888	22	17.7	2	–	0.76	0.58–0.91
	Central Bushveld	Dwaalboom Thornveld	3	Summer	551	29	19.4	19	±	0.49	0.25–0.75
Fynbos	Southwest Fynbos	Swartland Alluvium	15	Winter	656	27	17.1	3	–	0.65	0.34–0.90
	WC Renosterveld	Swartland Shale	14	Winter	430	32	17.2	3	–	0.57	0.36–0.79
		Swartland Granite	16	Winter	520	30	16.3	3	–	0.75	0.57–0.89

P, precipitation; MAP, mean annual precipitation; APCV, annual variation precipitation coefficient; MAT, mean annual temperature; MAFD, mean annual frost days; Φ, mean survival; CRI, credible Interval; KZN, KwaZulu-Natal; WC, west coast; +, high; ±, intermediate; -, low; ?, not available.

[1] Seasonality was "scored" by adding up APCV, MAT, and MAFD (range 41.9–117.0). These values were binned into low (41.9–50), intermediate (50–80), and high (80–117).

[2] Fog (visibility ≤1000 m) 100–125 days per year. This could indicate a less seasonal environment than expected based on the seasonality "score".

[3] Because the climatic details were not available, this site was omitted from Fig. 3.

References: *Mendelsohn et al. 2003; #Allan et al. 1997; Mucina and Rutherford 2006.

and Botswana (sites 1–3, Fig. 1) from locations in South Africa, resulting in 1,021 nonmigratory captures versus 6,795 migratory captures.

Data analysis

We used capture–mark–recapture (CMR) models for open populations to estimate apparent adult survival probability (hereafter survival), "apparent" because mortality and permanent immigration are confounded. The models assume individual homogeneity in survival and recapture and no lost or missed marks, and condition on first capture (Lebreton et al. 1992). We first pooled the data from all sites and assessed goodness-of-fit (GOF) of the global Cormack–Jolly–Seber model (i.e., fully time-dependent survival ϕ_t and recapture p_t ($\phi_t p_t$)) with Program U-CARE 2.3.2 (Choquet et al. 2009). The directional *z*-test for transience (3.SR) was significant ($P = 0$). Transients, as opposed to residents, are individuals with a zero survival probability after initial capture (Pradel et al. 1997). By necessity, mist nets are placed along the edge of reed beds. In large patches of suitable habitat capture at the edge, where a territorial bird like the African reed warbler that nests in close proximity to conspecifics (Urban et al. 1997; Eising et al. 2001) only occasionally forages, might result in low recapture while placement in the middle of breeding territories (e.g., fragmented reed beds) would net much higher numbers, leading to an excess of individuals that are only captured once (Buckland and Baillie 1987). Passerine mist-netting data often show transience and not accounting for it will lead to underestimation of survival (Buckland and Baillie 1987). With the removal of 3.SR, the overall GOF no longer showed lack of fit ($P = 0.23$).

We used multistate capture–recapture models (Gimenez et al. 2007) to account for transience and to investigate our hypotheses (sites grouped according to rainfall

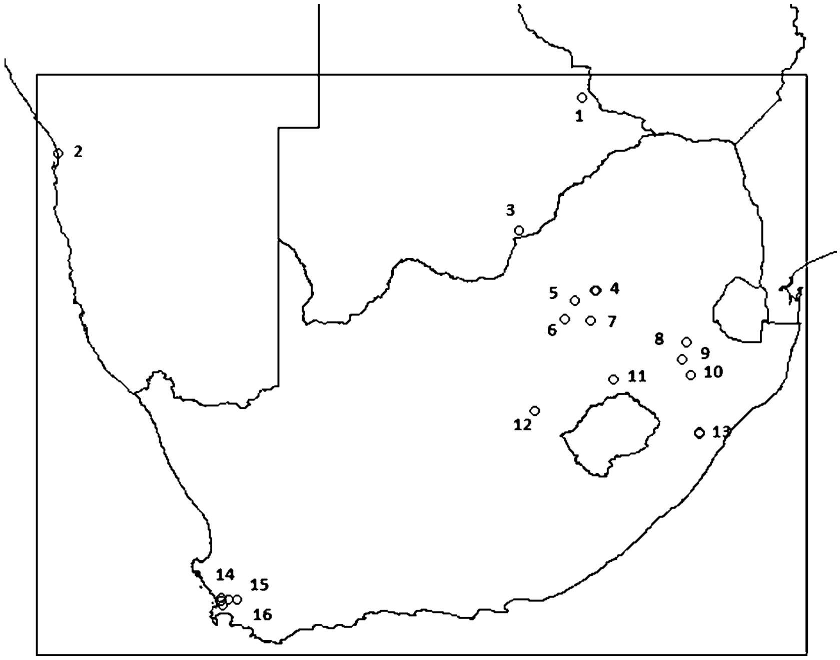

Figure 1. Mist-netting locations analysed in this study of the African reed warbler in southern Africa (1998–2010). The numbers indicate capture sites pooled by proximity within one vegetation unit. Sites 1, 4, and 13 are two locations each less than 0.17 decimal degrees apart; site 14 contains three locations less than 0.17 degrees apart.

timing, vegetation units and migratory strategy). We considered a three-state model where the state transition matrix is given by

	True state (t + 1)		
True state (t)	Initial	Resident	Dead
Initial	0	$\phi * \psi$	$1-(\phi * \psi)$
Resident	0	ϕ	$1-\phi$
Dead	0	0	1

(ϕ – survival, ψ – transition probability) and the observation matrix by

	Observed state (t + 1)		
True state (t)	Seen as *I*	Seen as *R*	Not seen
Initial (*I*)	0	0	1
Resident (*R*)	0	p	1-p
Dead	0	0	1

(p– recapture probability). We then developed a hierarchical model with additive random site and year effects to quantify the spatial and temporal variation in survival (the sparse data prohibited the use of an interactive model):

$$\text{logit}(\phi_{s,t}) = \mu + \eta_s + \varepsilon_t$$

where $\phi_{s,t}$ is the survival probability from time t to t + *1* in site s; μ is the overall mean survival on the logit scale. η_s and ε_t are the site and year random effects, respectively, that are independently normally distributed (i.e., $\eta_s \sim N(0, \sigma^2_\eta)$, and $\varepsilon_t \sim N(0, \sigma^2_\varepsilon)$). σ^2_η and σ^2_ε are the spatial and temporal variations (on the logit scale) in survival. Testing our hypotheses required estimating mean survival across groups of sites with similar rainfall regime or migratory status. We calculated these survival rates from the posterior distributions of the site-specific survival rates.

We treated the residence probability (ψ) constant over time, but allowed it to differ among sites. Because the data were sparse, we used a single random time effect to model spatio-temporal variation in recapture probability at all sites. That is,

$$\text{logit}(\text{p}_{s,t}) = \beta + \gamma$$

where $\text{p}_{s,t}$ is the recapture probability at time t in site s, β is the overall mean recapture on the logit scale. γ is the spatio-temporal random effect that is independently normally distributed (i.e., $\gamma \sim N(0, \delta^2_\gamma)$, and δ^2_γ is the spatio-temporal variation in recapture probability (on the logit scale). Residence and recapture probability were considered nuisance parameters.

We implemented the models in a Bayesian framework (King et al. 2010; Kéry and Schaub 2012), assuming noninformative priors for all parameters. We specified uniform priors (U[-5,5]) for the overall mean logit survival and recapture probabilities, a uniform prior (U[0,1]) for the residence probability, and uniform priors (U[0,5]) for the standard deviation parameters (see Appendix S1 for details). We ran three independent chains of length

100,000 with a burn-in of 50,000 and a thinning rate of 20. The Brooks–Gelman–Rubin diagnostic statistic (Brooks and Gelman 1998) and the diagnostic plots (trace plots, density plots, and autocorrelation plots) showed no lack of convergence. All the analyses were performed in JAGS 3.3.0 (Plummer 2003) via R package R2jags (Su and Yajima 2012). The R and JAGS code used are available in Appendix S1.

Results

Mean adult survival of the African reed warbler was estimated at 0.67 (95% credible interval (CRI): 0.47–0.85). The estimated spatial and temporal standard deviations of the logit survival were 0.70 (95% CRI: 0.33–1.27) and 1.08 (95% CRI: 0.52–2.35), respectively. Variation in survival was unrelated to latitude (Fig. 2). Survival of populations at the same latitude (rounded to degrees) differed widely, for instance from 0.49 (95% CRI: 0.18–0.80) to 0.80 (95% CRI: 0.59–0.95) at 28°S (Fig. 2). Estimated survival per vegetation unit differed considerably with a minimum of 0.49 (95% CRI: 0.18–0.80) in Eastern Free State Sandy Grassland and Dwaalboom Thornveld and a maximum of 0.83 (95% CRI: 0.62–0.97) in Carletonville Dolomite Grassland, but there was no relationship between survival and seasonality (Table 2; Fig. 3). Survival did not differ significantly, or widely, between rainfall regimes: 0.66 (95% CRI: 0.46–0.83) in the winter rainfall (peak May–August) areas (sites 14–16, Fig. 1, Table 2), 0.65 (95% CRI: 0.50–0.82) in the summer rainfall areas (sites 1, 3–13), and 0.69 (95% CRI: 0.51–0.87) in the irregular rainfall area (site 2). On average, migratory populations (sites 4–16) tended to survive better than sedentary populations (sites 1–3), but the difference was not significant as reflected by the overlap of the 95% credible intervals (migratory: 0.67 (95% CRI: 0.52–0.84); sedentary: 0.59 (95% CRI: 0.39–0.78)).

The estimated residence probability varied from a range of 0.25 (95% CRI: 0.04–0.74) for site 15 to 0.86 (95% CRI: 0.65–0.99) for site 4. Because of the sparseness of the data, most residence probability estimates, and a few survival estimates, showed low precision (wide CRIs). The estimated mean recapture probability was 0.12 (95% CRI: 0.08–0.15) with a spatio-temporal standard deviation on the logit scale of 1.21 (95% CRI: 0.97–1.50).

Discussion

The African subcontinent lends itself well to comparative studies of avian life histories as it covers nine terrestrial biomes with a wide range of climate regimes (Mucina and Rutherford 2006). As a habitat specialist of azonal wetlands, the African reed warbler was a suitable candidate to investigate the influence of environmental seasonality on life-history traits. We found substantial variation in survival among 16 vegetation units within four biomes located between 21°S and 34°S ranging from 0.49 to 0.83 (Table 2). Our findings (Fig. 2) did not reflect the global interspecific pattern of higher survival toward lower latitudes as found, for instance, by Peach et al. (2001) for African and European insectivores and Stevens et al. (2013) for Afrotropical and similar-sized temperate species. The latitudinal band in our study may have been too narrow to detect such a latitudinal gradient, but there was no indication of a trend in the expected direction. Moreau (1944) compared published clutch sizes between

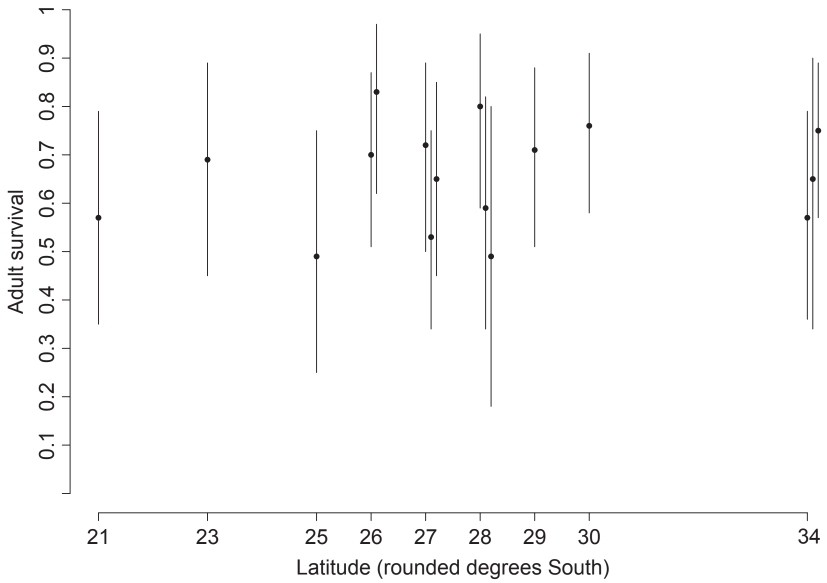

Figure 2. Adult survival of the African reed warbler at capture sites across southern Africa (mean 1998–2010). Sites at the same rounded latitude were separated to show the 95% credible intervals (vertical lines).

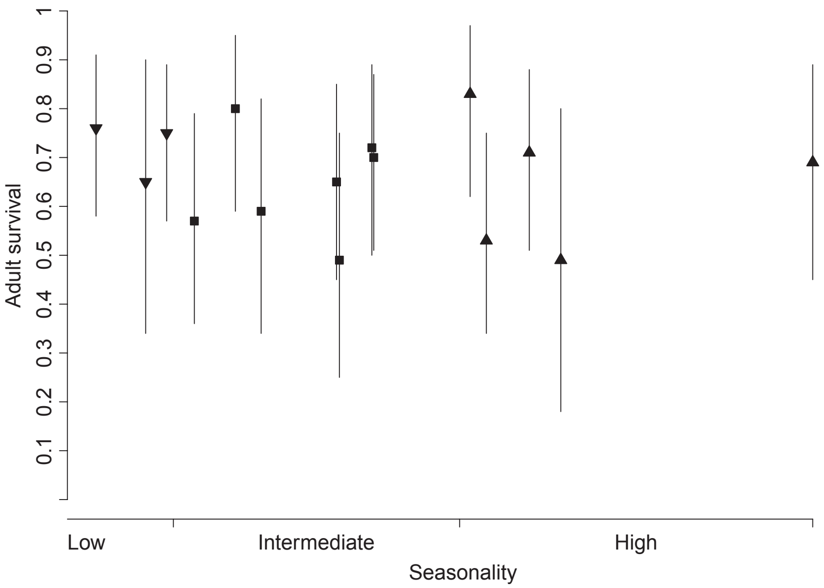

Figure 3. Adult survival of the African reed warbler in environments with varying seasonality (mean survival 1998–2010; 95% credible interval as vertical lines). Site 1 in arid woodland was omitted due to unavailable climatic data. Seasonality was "scored" by adding up annual precipitation variation, mean temperature, and frost days (see Table 2 for details).

the equator and South Africa and concluded that there was evidence for a real but slight latitudinal gradient. Saracco et al. (2012) found spatial variation in survival across the North American continent for the common yellowthroat *Geothlypis trichas* – another partially migratory and similar-sized warbler found mainly in reed beds (Dunn and Alderfer 2008; Sinclair and Ryan 2009). Although the ranges of estimated survival rates for yellowthroats in North America and reed warblers in southern Africa overlap (0.35–0.61 vs. 0.49–0.83), the extremes do conform to the general trends of higher survival of southern hemisphere species compared with northern, temperate species (Brawn et al. 1999; Francis et al. 1999).

Our study did highlight variation in survival at the landscape scale like studies by Ricklefs and Shea (2007), Blake and Loiselle (2008), and Saracco et al. (2012). As the latitudinal seasonality (lower in the South, little in the Tropics and high in the northern, temperate zone) underpins the main hypotheses of the latitudinal gradient in life-history strategies (Moreau 1944; Lack 1947; Skutch 1949; Ashmole 1963), we predicted lower survival in less seasonal environments. We found no such pattern in the substantially differing environments of the African reed warbler populations (Table 2; Fig. 3) or between the different rainfall regimes (Table 2).

There are many potentially interacting influences on life-history traits (Martin 2004; McNamara et al. 2008). Saracco et al. (2012) suggested that part of the spatial variation in survival may be due to life-history differences between sedentary and migratory populations. They found a trend similar to the one we found for the African reed warbler: higher survival among migratory populations than among sedentary populations. By leaving for the wintering grounds when conditions get tough, migratory populations might increase their survival chances to such an extent that it compensates for the added mortality of migration, whereas sedentary populations are exposed to prevailing conditions in situ all year round (Alerstam 1993). Another explanation could be that these birds invest relatively more in reproduction at the expense of survival (Martin 1996; Ricklefs 2000). Thaxter et al. (2006) proposed availability of suitable dispersal habitat as a reason for the spatial differences they found in male Eurasian reed warbler survival in England. Dispersing males would lower resident apparent survival estimates. In the divergent vegetation units across southern Africa, proximity of dispersal habitat could be as different as the environments of the study populations. Eising et al. (2001) observed cooperative breeding with unrelated helpers in the ordinarily monogamous African reed warbler in saturated habitat in an environment with little dispersal opportunity. Less-strenuous breeding could increase annual survival of the breeding pair, and breeding in a group could be safer, for everybody, than breeding alone (Riehl 2013). Another factor – linked to reed beds as breeding habitat – found to influence adult survival is brood parasitism, due to the cost of defense against the parasite and the higher costs of raising the parasite's chick (Leisler and Schultze-Hagen 2011). Stokke et al. (2007); found a positive relationship between host density and the parasitism rate among 16 Eurasian reed warbler populations in Europe. Parasitism risk increased with decreasing distance of tree-top perches – from which the female cuckoo surveys potential victims – to Eurasian reed warbler breeding populations (Welbergen and Davies 2009). More extensive and "pure" reed beds were the least parasitized (Leisler and Schultze-Hagen 2011). Brood parasitism in African reed warbler nests by Klaas's Cuckoos *Chrysococcyx klaas* has been observed in East Africa (Urban et al. 1997).

This study revealed large spatial variation in survival in divergent environments across the African subcontinent and an indication of variation due to migratory strategy. Even with sparse data (average recapture similar to its sister taxon – Buckland and Baillie 1987), our hierarchical modeling approach was able to estimate spatial variation with fairly high precision. We did not find a clear pattern of higher survival in less seasonal environments. As seasonality can only be regarded as a proxy for food supply, quantitative data on this combined with additional data on, for example, dispersal and brood parasitism potential in the vegetation units could aid understanding of the ecological constraints that influence a life-history trait that is a major driver of population dynamics (Baillie and Schaub 2009). Incorporating recording of distance to the nearest dispersal habitat and tree presence within the reed beds into the existing protocol of CMR data collection would be relatively simple. In this manner, a geographically uncoordinated public ringing scheme across a vast subcontinent – where resources for detailed field studies are scarce – could extract important information, as our study already showed, and contribute to the study of life-history strategy and its evolution from a relatively poorly studied region (Martin 1996).

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Conflict of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. The R and JAGS code used for the African reed warbler survival analysis.

Table S1. Captures per site per occasion of the African reed warbler (1998–2010) in southern Africa.

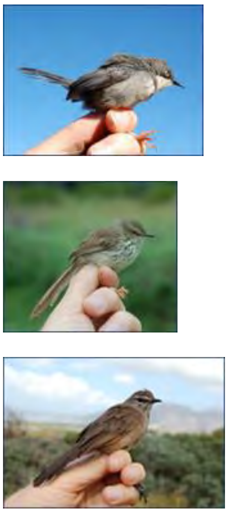
Chapter 4

Synchronicity in survival of avian insectivore assemblages in a wetland and fynbos in South Africa

Photo Mark Brown

Photos Dieter Oschadleus

Photo Penn Lloyd



Abstract

Recent climate change has impacted many ecological communities and individual species. Future climate change is forecasted to increase climatic variation, in particular the occurrence of extreme events. It is, therefore, imperative to understand how climatic variation influences population dynamics and species assemblages, especially in already fragile habitats that will come under ever greater pressure as this century unfolds. I investigated synchronicity in survival in response to climatic variation of two avian insectivore assemblages, one in a wetland and one in fynbos in South Africa. Sympatric species experience the same biotic environment (interactions) and abiotic stochasticity (climate). Ringing data of four wetland species covering 1999-2013 and three fynbos species covering 2000-2007 were analysed - separately - in a hierarchical model with an asynchronous (species-specific) variance component and a synchronous (common) variance component. These components from a model without and one with a climatic covariate enabled the estimation of the forcing effect of the climatic variation as a synchronizing and desynchronizing agent. As hypothesized, synchronicity at the more seasonal wetland was substantially larger than at the climatically more stable fynbos site: 0.50 (95% Credible Interval: 0.01-1.92 on the logit scale) and 0.03 (0.00001-0.19). As was the asynchronicity: wetland range 0.30 (0.0003-1.65) to 1.15 (0.002-5.53), fynbos range 0.06 (0.00004-0.34) to 0.15 (0.0002-0.90). However, we did not find clear evidence of climatic forcing. The time-series could have been too short to include extreme climatic variation, especially at the fynbos site. Our findings did quantify the dynamics within the species assemblages and provided the first survival estimates of several African endemics including two with a severely restricted range. Additional data on abundance and fecundity would enable a better understanding of population dynamics and the potential influence of environmental stochasticity on those dynamics.

Introduction

Sympatric, trophically similar species do not live in isolation, they are part of an ecological community (Begon *et al.* 2006). They might compete for similar resources and they are all subject to the same environmental conditions. Based on 100 original time series from communities in biomes across the globe spanning 1874-2014, Dornelas *et al.* (2014) found, contrary to expectations, that the species richness of the assemblages had remained constant, but that the species composition had changed 10% per decade. This accelerating species turnover in which species were often replaced by functionally dissimilar species has the potential to change ecosystems as a whole or even result in new ecosystems. What drives community dynamics, and the methodology of determining the mechanisms, is still hotly debated by population ecologists (see Hubbell 2001; reviews in Houlahan *et al.* 2007; Ernest *et al.* 2008; Loreau & de Mazancourt 2008; Ranta *et al.* 2008; Gonzalez & Loreau 2009; Matthews & Whittaker 2014; Colorado & Rodewald 2015). If species assemblages are driven by inter-specific competition, population sizes/growth rates would be negatively correlated resulting in compensatory dynamics (Houlahan *et al.* 2007). If competition is the sole driving force - and the community is at full carrying capacity, it would lead to stochastic zero-sum dynamics: the total abundance of all species in the assemblage remains constant but a decrease in the abundance of one species would give rise to an identical increase in the abundance of the other species (Gonzalez & Loreau 2009). If species assemblages are instead driven by a common response to environmental fluctuation, the correlation between species' abundance would be positive. The response of all species in the assemblage would be synchronous. Competition-driven communities would respond asynchronously to environmental fluctuations (Lahoz-Monfort *et al.* 2011).

Since stochasticity (demographic and environmental) and non-stationarity are a fact of life, complete synchronization is hardly ever reached in species assemblages (sympatric synchronicity) or in allopatric populations of a single species (spatial or allopatric synchronicity; Cazelles & Stone 2003; Engen & Sæther 2005). Even when the scale of climatic variation is large enough to encompass a meta-population of one species, life-history differences amongst the subpopulations could reduce spatial synchronicity (Ringsby *et al.* 2002). Most research has focussed on spatial synchronicity in abundance (Robinson *et al.* 2013; reviews in Bjørnstad *et al.* 1999, Hudson & Cattadori 1999, and Koenig 1999). Grenfell *et al.* (1998) found density-dependent spatial synchronicity caused by climatic variation in two sheep populations. Ims & Steen (1999) hypothesized and subsequently demonstrated (Ims & Andreassen 2000) significant spatial synchronicity in vole populations in Norway forced by avian predators. Using a novel modelling approach on existing abundance data Cazelles & Stone (2003) confirmed previous speculations of cyclic spatial synchronicity in populations of crabs, lynxes and three species of gamebirds. Spatial synchronicity of 29 species of passerines in

North America varied in spatial range: populations of some species exhibited spatial synchronicity over a larger area than others (Jones *et al.* 2007). In Britain spatial synchronicity of 53 common birds was positively correlated with both natal and breeding dispersal distance (Paradis *et al.* 1999).

Empirical evidence of sympatric synchronicity is rare (Robinson *et al.* 2013). Studies of synchronicity in species assemblages are scarce despite the increasing use of conservation management aimed at groups of similar species (Sauer & Link 2002). Raimondo *et al.* (2004) found synchronicity in abundance in almost a third of pairs of sympatric butterfly species that utilized the same food as larvae and looked alike as adults. The latter meant that they offered a similar search image to generalist predators. In this manner predation acted as a synchronizing agent. Houlahan *et al.* (2007) conducted a meta-analysis of 41 datasets of diverse taxonomic groups, some at several spatial scales, to determine community abundance covariance (the sum of all pair-wise covariances). They found mainly positive community covariance, i.e. sympatric synchronicity. Their results also indicated a scale-dependence in community covariance: at a smaller scale negative covariance, i.e. sympatric asynchronicity, was more prevalent. A breeding seabird species assemblage off the coast of Scotland displayed synchronous responses to climatic variation in population growth rates and in reproductive success (Robinson *et al.* 2013).

Population dynamics themselves are governed by survival, reproduction, and dispersal (Caswell 2001). Each of these can be influenced by inter- and/or intra-specific competition and/or correlate with environmental fluctuation and other vital rates (Houlahan *et al.* 2007). Reynolds *et al.* (2011) discovered spatial synchronicity in survival in colonies of common guillemots *Uria aalge* with overlapping wintering areas. Colonies that wintered in different areas did not display this synchronicity. Variation in survival of white stork *Ciconia ciconia* populations in Germany and Poland was also correlated with the environmental conditions at the same wintering area, causing spatial synchronicity (Schaub *et al.* 2005). Grosbois *et al.* (2006) estimated that allopatric, unconnected populations of blue tits *Cyanistes caeruleus* were synchronized in temporal variation in survival in response to climatic variation, although survival itself varied widely. Local climatic conditions that were correlated on the scale of the study meta-population acted as both synchronizing and desynchronizing agent on survival of Atlantic puffins *Fratercula arctica* in four colonies (Grosbois *et al.* 2009). Climatic variation could have affected primary production on the meta-population scale resulting in spatial synchronicity. At the colony scale that same variation could have affected the main prey species, which differed per colony, resulting in spatial asynchronicity. Lahoz-Monfort *et al.* (2011) found a similar situation in a sympatric analysis - using an adaptation of the Grosbois *et al.* (2009) multi-species, spatial synchronicity model - of survival of three auk species: most temporal variation in survival was synchronous amongst the species and largely explained by climatic variation, but that same climatic variation also explained the asynchronous part of the survival variation to differing degrees for each species. Using this same model they (Lahoz-Monfort *et al.* 2013) investigated sympatric synchronicity in reproductive success of a 5-species seabird assemblage. All species showed a long-term reproduction decline, but little synchronicity in reproductive success. What there was, was mostly explained by climatic variation, which explained the asynchronicity to a lesser and varying degree per species.

Based on 4218 vertebrate populations of 1411 species (dominated by avian species) Collen *et al.* (2009) estimated a global decline in species' abundance. (Sub)tropical species declined faster than temperate species. Thirty-one indicators used to assess the state of global biodiversity - including population trends, extinction risk, habitat extent and quality, and community composition - all pointed to an increase in global biodiversity loss (Butchart *et al.* 2010). Climate change forecasts predict warmer/more frequent hot days and nights, higher frequency, intensity and/or amount of heavy precipitation, and a higher occurrence and/or magnitude of extreme high sea levels with likely probability for the early 21st century (IPCC 2013). That probability increases for the late 21st century. Global decreases in abundance and biodiversity combined with a rapidly changing climate dictate the need for a better understanding of how climate affects populations and communities, especially those in already fragile and threatened habitats.

Inchausti & Halley (2003) investigated the relationship between population abundance and quasi-extinction time - time lapsed until a 90% decrease in abundance - in 554 populations of 123 animal species. Increased and increasing temporal variability in abundance decreased quasi-extinction time. There is growing empirical evidence that population growth rate is most sensitive to the least variable vital rate (Pfister 1998; Sæther *et al.* 2000; Altwegg *et al.* 2007; Schmutz 2009). When climatic variability increases and extreme events become more frequent, the variability of vital rates is likely to increase (Boyce *et al.* 2006). Southern, temperate birds have higher survival than their northern, temperate counterparts (Yom-Tov *et al.* 1992; Peach *et al.* 2001; Stevens *et al.* 2013): they trade off current reproductive success against survival (Ghalambor & Martin 2001). Combining this 'line of reasoning' it would appear that survival is potentially the most influential vital rate in the context of population dynamics to study in southern, temperate birds.

I investigated synchronicity in survival in relation to climatic variation in two avian insectivore assemblages, one in a wetland (four species, 1999-2013) and one in fynbos (three species, 2000-2007) in South Africa. Because common species are probably more important for ecosystem functioning than rare species (Collen *et al.* 2009), I selected common species. These species are relatively short- to medium-lived (longevity range based on ring recoveries at least ~5.5 - 10.5 years; South African Bird Ringing Unit). They are all African endemics, two species are restricted to South

Africa and a part of Namibia (Hockey *et al.* 2005). The fynbos biome is endemic to South Africa and a global biodiversity hotspot (see Cowling *et al.* 2003 for details). Almost a third of the fynbos biome has already been lost through anthropogenic habitat alteration, of the remaining only 4% is still pristine (Huntley & Barnard 2012). Fynbos climate has become drier and warmer in the past century and this trend is forecasted to continue with a high risk of severe droughts (Altwegg *et al.* 2014; Niang *et al.* 2014). Huntley & Barnard (2012) predicted that fynbos bird assemblages will lose 30-40% of their species by 2085 in response to climate change. At present, 65% of the wetlands in South Africa are threatened and 48% critically endangered (DEA 2011). The study site wetland is located in the austral summer (Dec-Feb) rainfall area, where a delay in the onset of the rains has already been observed (Niang *et al.* 2014). Groundwater recharge is forecasted to decline, which will increase the pressure on already scarce freshwater resources by a rapidly expanding human population (Kusangaya *et al.* 2014; Niang *et al.* 2014). Over the past 50 years mean annual temperature has risen by ~1 ^{0}Celsius (DEA 2013). It is forecasted to rise by 3-6 ^{0}C by the end of the 21st century, faster than the global mean (Niang *et al.* 2014). An increase in extreme rainfall events and longer dry spells has been observed and is forecasted to continue (DEA 2013; Niang *et al.* 2014).

Based on the different seasonality of the study sites – the wetland is more seasonal than the fynbos site (Fig. 1) - I expected more temporal variation in survival and lower species-specific mean survival at the wetland than at the fynbos site conform Life History Theory (Lack 1947; Skutch 1949; Ashmole 1963). Since climatic variation is larger in the more seasonal environment, we expected the assemblage as a whole to respond more synchronously to the potentially larger forcing strength of the climatic variation at the wetland, i.e. the synchronous or common component of the variation in survival was expected to be larger at the wetland than at the fynbos site. For this reason I also expected more synchronicity than asynchronicity in survival at the wetland, and the reverse at the fynbos site. I suspected that the relatively stable climate at the fynbos site combined with the short study period (8 years) would make detection of a correlation between climate and survival difficult, because the latter would decrease the chances of including periods with extreme weather (relative to the climatic stability; Altwegg *et al.* 2006; Gimenez *et al.* 2006). The less functionally similar species assemblage at the fynbos site, which was stratified by height in both nesting and foraging habitat, combined with the low seasonality led me to suspect that the asynchronous variance components - species-specific variance - would be smaller for all species than at the wetland. At the fynbos site the number of breeding territories of all species was fairly stable over the study period and a small proportion of facultative cooperative breeding pairs had helpers suggesting that the assemblage was at carrying capacity (P. Lloyd pers. comm.; Lloyd *et al.* 2009). Despite this I did not expect compensatory dynamics to play a significant role in any asynchronous variation at either site, because prey species and nesting sites differed to varying extents in each habitat (Hockey *et al.* 2005) and both sites were managed in a manner that suggests that there was no resource limitation (H.D. Oschadleus pers. comm.).

Materials and Methods

Study sites

The wetland at Darvill is a Bird Sanctuary that is part of the Darvill Waste Water Works (~0.7 km^2) in KwaZulu-Natal Province in the east of South Africa (29°36'S, 30°26'E). The wetland consists of four big ponds and three narrow, long strip ponds - all man-made - bordered by reeds and surrounded by disturbed grassland and thornveld dominated by exotic trees and shrubs, and small patches of indigenous forest (Prins 2013). It is located in Midlands Mistbelt Grassland (vegetation unit in bioregion Sub-escarpment Grassland in biome Grassland; Mucina & Rutherford 2006) at 613 metres above sea level. The water level in the ponds is allowed to fluctuate, but the ponds never run dry (M. Brown pers. comm.). Reed beds have not been cut during the study period (M. Brown pers. comm.).

The fynbos site at Koeberg is a 2.6 km^2 area situated in the 29 km^2 Koeberg Nature Reserve in the Western Cape Province in the west of South Africa (33°41'S, 18°27'E), designated in 1991. The reserve neighbours a nuclear power plant on a low-lying coastal plain. It is Hopefield Sand Fynbos (in bioregion Southwest Fynbos in biome Fynbos) characterized by evergreen, rush-like restios endemic to South Africa with ericoid and proteoid shrubs resembling heathland (Mucina & Rutherford 2006; see Nalwanga *et al.* 2004 for more details). Fynbos regenerates through natural fire, but fires at this site are controlled by the nuclear power plant managers (H.D. Oschadleus pers. comm.; Nalwanga *et al.* 2004).

The two study sites differ in seasonality and rainfall regime (Fig. 1). The more seasonal site at Darvill has a subtropical climate with summer rainfall (Dec-Feb): daily minimum temperatures ranged from -9.0 to 26.0 °Celsius (mean ± standard deviation: 12.2 ± 6.2), maximum temperatures from 10.6 to 41.6 °C (26.9 ± 5.1), and daily total rainfall from 0.0 to 115.5 millimetres (2.1 ± 6.6) - 1999 to 2009. At Koeberg the Mediterranean climate with winter rainfall (June-Aug) is more temperate: daily minimum temperatures ranged from 3.9 to 23.0 °C (12.8 ± 3.4), maximum 10.4 to 38.2 °C (20.6 ± 4.6) and daily rainfall 0.0 to 50.4 millimetres (1.0 ± 3.3) - 2000 to 2007.

Study species

The study species at the Darvill wetland are:

Lesser Swamp-Warbler	*Acrocephalus gracilirostris* (Hartlaub; LSW)
Levaillant's Cisticola	*Cisticola tinniens* (Lichtenstein; LC)

Tawny-flanked Prinia	*Prinia subflava* (Gmelin; TFP)
Spectacled Weaver	*Ploceus ocularis* (A. Smith; SW)

At the Koeberg fynbos:

Bar-throated Apalis	*Apalis thoracica* (Shawn and Nodder; BTAP)
Karoo Prinia	*Prinia maculosa* (Boddaert; KAPR)
Karoo Scrub-Robin	*Cercotrichas coryphoeus* (Vieillot; KARO).

These seven common passerines are mainly insectivorous, resident and sedentary, year-round territorial, monogamous and solitary nesters that share parental care (Hockey *et al.* 2005). LC incubating sex is unknown; incubation only by the female of TFP and the three species at Koeberg (Tarboton 2001; Hockey *et al.* 2005 when no other source is mentioned). KARO is a facultative cooperative breeder, most pairs breed without helpers (Lloyd *et al.* 2009). The species are hosts of obligate brood parasites: LC and TFP by the cuckoo finch *Anomalospiza imberbis* (Cabanis) and SW, BTAP, KAPR, and KARO by *Chrysococcyx* cuckoos (LSW unknown but unlikely; H.D. Oschadleus pers. comm.). SW is the only sexually dimorphic species.

At the wetland site the species nest above/near water apart from SW that usually nests in trees. They forage low down in vegetation above/near water apart from SW that forages mostly in trees. At the fynbos site the species nest and forage in shrubs/bushes at different heights (from high to low: BTAP, KAPR, KARO; nest-site partitioning details in Nalwanga *et al.* 2004). Table 1 lists divergent life history details.

Data

At the wetland at Darvill adult birds were captured by licensed citizen scientists following the South African Bird Ringing Unit protocol (de Beer *et al.* 2001). From 1999 to 2013 (capture occasion Oct-Sep - based on the start of the breeding season) 1753 individuals were captured (446 recaptures) - LSW 562 individuals (198 recaptures), LC 586 individuals (119), TFP 364 individuals (59), and SW 241 individuals (70).

At the fynbos site at Koeberg adult breeding birds, and KARO helpers, were ringed as part of a long-term study (for the ringing protocol see Lloyd *et al.* 2014). Birds were captured during the entire year, but resighting was confined to the breeding season Aug-Oct. From 2000 to 2007 (occasion Jan-Dec) 698 individuals were captured (1130 resightings) - BTAP 132 individuals (245 resightings), KAPR 205 individuals (365), and KARO 361 individuals (520).

Data analysis

I used capture-mark-recapture/resight models for open populations to estimate apparent, or local, adult survival (hereafter 'survival'; Lebreton *et al.* 1992). Since we cannot distinguish permanent emigration from mortality, survival estimates pertain to the study site only. First, I conducted a goodness-of-fit test in program U-CARE 2.3.2 (Choquet *et al.* 2009) of the global Cormack-Jolly-Seber model (CJS; Cormack 1964; Jolly 1965; Seber 1965) - time-dependent survival and recapture $\phi(t)p(t)$ - of the datasets per species. CJS models assume homogeneity of survival and recapture for all individuals and no trap response (previous captures do not influence subsequent capture; Lebreton *et al.* 1992). For all species the global tests were not significant indicating that the CJS model fitted the structure of the data (LSW: $\chi^2_{43} = 35.57$, $P = 0.78$; LC: $\chi^2_{42} = 31.32$, $P = 0.89$; TFP: $\chi^2_{27} = 10.82$, $P = 0.998$; SW: $\chi^2_{32} = 20.64$, $P = 0.94$; BTAP: $\chi^2_{15} = 7.14$, $P = 0.95$; KAPR: $\chi^2_{11} = 8.92$, $P = 0.63$; KARO: $\chi^2_{16} = 5.00$, $P = 0.996$).

Then I pooled the species data per site to investigate the (a)synchronicity of survival of the species assemblage in each habitat. I used a hierarchical model with two temporal random effects and a species-specific intercept - following Lahoz-Monfort *et al.* (2011), who adapted the multi-site model from Grosbois *et al.* (2009) and incorporated the separation of variance by Loison *et al.* (2002) into their methodology:

$$\text{logit}(\phi_{S,\,t}) = \mu_S + \varepsilon_S(t) + \delta(t) \qquad \text{(eqn 1)}$$

where $\phi_{S,\,t}$ is the survival probability of species S from year t to year $t + 1$, μ_S is mean survival of species S on the logit scale, $\varepsilon_S(t)$ the temporal effect of species S on the logit scale, and $\delta(t)$ the temporal effect common to all species on the logit scale. The two random terms are assumed to be uncorrelated and have independent distributions: $\varepsilon_S(t) \sim N(0, \sigma^2_S)$ and $\delta(t) \sim N(0, \sigma^2_\delta)$. σ^2_S is the temporal variance per species representing the asynchronous component of the variance and σ^2_δ the temporal variance common to all species - the synchronous variance component.

How synchronous one species is with the other species in a particular habitat can be estimated by an intra-class correlation coefficient (ICC):

$$\text{ICC}_S = \frac{\hat{\sigma}^2_\delta}{\hat{\sigma}^2_\delta + \hat{\sigma}^2_S} \qquad \text{(eqn 2)}$$

ICC_S denotes the amount of temporal variance in survival of species S accounted for by the synchronous temporal variance common to all species. The smaller the ICC_S the more asynchronous the survival of that species is to the survival of the other species.

To investigate how much of the asynchronicity ε_S and the synchronicity δ in survival was caused by climatic fluctuation I added a time-dependent environmental covariate as a fixed effect to the total variance model. The covariates and their values were the same for each species per study site. Sparseness of data - as evidenced by the uncertainty of the results of the total variance models - precluded the investigation of covariate interaction during an occasion or season, additive effects or of stabilizing selection ($x + x^2$). By comparing this residual variance model – after accounting for environmental covariates – with the total variance model I could then estimate:

$$C_\delta = 1 - \frac{\hat{\sigma}^2_\delta\,(\text{res})}{\hat{\sigma}^2_\delta\,(\text{total})} \qquad \text{(eqn 3)}$$

$$C_S = 1 - \frac{\hat{\sigma}^2_S\,(\text{res})}{\hat{\sigma}^2_S\,(\text{total})} \quad \text{per species} \qquad \text{(eqn 4)}$$

These coefficients quantify the influence of climatic fluctuation on the synchronous variation δ (C_δ) common to all species and on the asynchronous variation ε_S (C_S) specific to each species. See Lahoz-Monfort *et al.* (2011) for a more detailed description of the analysis.

Because the data were sparse and recapture/resighting probability p was considered a nuisance parameter, I modelled p with one species-temporal random effect:

$$\text{logit}(p_{S,t}) = \beta + \gamma \qquad \text{(eqn 5)}$$

where $p_{S,t}$ is the recapture/resighting probability of species S at time t, β is the overall mean recapture probability on the logit scale, and γ is the species-temporal variation on the logit scale.

I implemented the models in a state-space formulation in a Bayesian framework (Gimenez *et al.* 2007; Kéry & Schaub 2012) with non-informative priors for all parameters. We specified uniform priors for species-specific mean survival and overall mean recapture/resighting - U[0, 1], and for the standard deviations of the survival and recapture/resighting variance components - U[0, 5]. I ran all models with three chains. For the species assemblage models (species data pooled) I ran 100,000 iterations discarding the first 50,000. Because there was more autocorrelation in the Darvill simulations, I only used every 20th iteration (thinning) for the Darvill data (posterior distribution of 7500 iterations) and every 10th iteration for the Koeberg data (posterior distribution of 15,000 iterations). Regression coefficient priors were specified as U[-10, 10] for Darvill and U[-5, 5] for Koeberg. The CJS models per species ran with 50,000 iterations, a burn-in of 25,000 and a thinning rate of 20 for Darvill and 10 for Koeberg with priors U[0, 1] for survival and recapture/resighting.

Models were run in WinBUGS 1.4 (Spiegelhalter *et al.* 2003) from R 2.15.3 (R Core Team 2012) using R2WinBUGS 2.1-18 (Gelman *et al.* 2011). I checked the Brooks–Gelman–Rubin diagnostic statistic (Brooks & Gelman 1998) and trace, density, and autocorrelation plots to confirm convergence.

Climatic covariates

As all study species are non-migratory, I used weather variables over the whole year and the seasonal extremes: minimum temperature (tmin) during the austral winter (June-Aug), maximum temperature (tmax) during the austral summer (Dec-Feb), and rainfall (ppt) during the rainy season, i.e. austral summer at Darvill and austral winter at Koeberg. Because the capture occasions at Koeberg ran from Jan to Dec, I only used tmax of Jan and Feb. I explored both current occasion and previous occasion (lag 1) values to examine potential direct and indirect (lag 1) effects on survival. Temperatures were averaged and rainfall summed. I also investigated the effect of variation in rainfall (standard deviation), because days with heavy rainfall have been steadily increasing in both rainfall regimes in South Africa while the mean has not changed (Easterling *et al.* 2000a). All values were standardized (units of standard deviation).

Wetland weather data

The weather station at Darvill was operational until 27 March 2010, which meant that temperature data were missing for occasions 2009-2010, 2010-2011, and 2011-2012. Data for the entire period were available from a weather station at Pietermaritzburg (PMB; 29°37'S, 30°24'E) - 4.5 km away in a built-up area at 673 masl (60 m higher than Darvill). Daily tmax per calendar year at Darvill and PMB (1994-2009) were correlated (Pearson's product moment correlation: t_{14} = 3.75, P = 0.002, cor = 0.71 (95% confidence interval (CI): 0.33-0.89)), as were mean tmin winter and tmax summer ($P \leq 0.001$, cor ≥ 0.73). Daily tmin per calendar year was not correlated (t_{14} = -0.02, P = 0.98, cor = -0.006 (95% CI: -0.50-0.50)). Therefore, we used annual (1 Oct-30 Sep) and seasonal (extremes, see above) current and previous year means of PBM tmin and tmax, and the same of the Darvill data for the available occasions. To account for the missing occasions in the Darvill data we used an extra species-specific parameter:

$$\text{logit}(\varphi_{S,\,t}) = \mu_S + \beta1*\text{covar} + \beta2_S*\text{missing} + \varepsilon_S(t) + \delta(t) \qquad \text{(eqn 6)}$$

where 'missing' was zero for available data and '1' for missing data, as well as models that assumed that conditions were average during those occasions, i.e. Darvill data for the first eight occasions and zero for the remaining three. Rainfall data at Darvill were available until 31 Dec 2012, which covered the period needed for the analysis (until Sep 2012).

Neither the Darvill nor the PMB data showed any discernible trend over the respective periods (mean tmax and total ppt per occasion - Pearson's product moment correlation: $P \geq 0.06$; mean tmin

PMB: t_{13} = 3.75, P = 0.02, cor = -0.59 (95% CI: -0.85 to -0.12)). Mean tmin and tmax at PMB were weakly correlated (t_{13} = 3.18, P = 0.007, cor = 0.66 (95% CI: 0.23-0.88); PMB mean tmin/total ppt, PMB mean tmax/total ppt, and Darvill pairs: $P \geq 0.16$)

The data were obtained from the Climate Systems Analysis Group (CSAG), University of Cape Town. CSAG applies a 95% annual availability threshold for rainfall (data available for ≥ 347 days) and a 90% threshold for temperature (≥ 328 days). Apart from rainfall during occasion 2001-2002 at PMB (337 days) all climatic covariates were based on sufficient data.

Fynbos weather data

The data did not show any discernible trend over 1999-2007 (Pearson's product moment correlation: $P \geq 0.09$). Mean tmin and tmax per occasion were not correlated with total ppt per occasion ($P \geq$ 0.74), but were strongly correlated with each other (t_7 = 6.00, $P < 0.001$, cor = 0.91 (95% CI: 0.64-0.98)). Since we used one covariate at a time, this did not pose a problem (i.e. multi-collinearity; Grosbois *et al.* 2008).

Data were obtained from the weather station at Eskom's Koeberg Nuclear Power Station. Data for Jan 2002 were missing due to a system's failure.

Results

I found considerably more temporal variation in apparent adult survival of the four species in the wetland at Darvill - the more seasonable habitat (Fig. 1) - than of the three species in the fynbos at Koeberg (Figs 2 & 3).

At the wetland mean survival over 1999-2012 was 0.66 (95% credible interval (CRI): 0.54-0.78) for the lesser swamp-warbler (LSW), 0.55 (0.41-0.71) for the Levaillant's cisticola (LC), 0.51 (0.37-0.67) for the tawny-flanked prinia (TFP), and 0.66 (0.50-0.84) for the spectacled weaver. At the fynbos site mean survival over 2000-2006 was 0.77 (95% CRI: 0.69-0.84) for the bar-throated apalis (BTAP), 0.72 (0.65-0.78) for the Karoo prinia (KAPR), and 0.79 (0.73-0.84) for the Karoo scrub-robin (KARO).

Mean recapture probability at the wetland was 0.21 (95% CRI: 0.17-0.25) with a variance on the logit scale of 0.28 (95% CRI: 0.08-0.59). At the fynbos site mean resighting probability was much higher at 0.94 (95% CRI: 0.91-0.97) as was the variance of 0.66 (95% CRI: 0.08-2.04). Low recapture at the wetland resulted in less precision (95% CRIs in Fig. 2) of the survival estimates compared to the precision of the fynbos estimates (95% CRIs in Fig. 3), where the precision was least for 2000 when few birds were ringed (P. Lloyd pers. comm.).

Both asynchronous (species-specific) and synchronous (common) variation were higher at the wetland than at the fynbos site resulting in larger intra-class correlation coefficients per species (total variance model; Table 2). However, the precision of both components of the variation (standard deviation on the logit scale) was not high at either location (95% CRIs of σ^2_δ and σ^2_S; Table 2). At the wetland the intra-class correlation coefficients (ICC_S) were more precise than those at the fynbos site (95% CRIs; Table 2). The spectacled weaver (SW) was least synchronous with the other species of the wetland species assemblage at Darvill. This species exhibited the largest species-specific temporal variation (asynchronicity σ^2_S) in survival, larger than the interspecific temporal variation (synchronicity σ^2_δ), resulting in the smallest ICC (Table 2). At the fynbos site the bar-throated apalis showed the largest asynchronicity in survival (σ^2_S; Table 2). The three species in this seasonally more stable habitat (Fig. 1) all exhibited more asynchronicity than synchronicity in survival.

We did not find any clear drivers of the variation in survival during the study periods at either site. Table 3 shows the two covariates that did account for a small portion of both variance components at Darvill (residual variance models; Table 2; all covariates in Table A1 in Appendix). Mean minimum temperature during winter (June-Aug, range 6.3 - 8.5 ^{0}C; data from the weather station at Pietermaritzburg) was positively correlated with survival (Table 3) and explained 10% of the inter-specific temporal variation (C_δ; Table 2). Note that most credible intervals spanned zero. We only present the species-specific coefficients C_S that did not span zero, those of the Levaillant's cisticola (LC; Table 2). The mean minimum winter temperature explained 41% of the variation in survival specific to this species (asynchronicity) during 1999-2012. The mean maximum temperature during summer (Dec-Feb, range 27.9 - 31.0 ^{0}C; data from Darvill weather station; residual variance model) explained 7% of the temporal variation common to the species assemblage (C_δ) and was negatively correlated with survival of LC (Table 3). It explained 48% of the asynchronous variation exhibited by this species (C_S; Table 2).

Discussion

I investigated synchronicity in local adult survival in two avian insectivore assemblages in habitats of differing seasonality. As expected I found substantially more variation in survival at the more seasonal wetland than at the fynbos site (Figs 2 & 3). The larger temporal variance was exhibited in both the synchronous (common) variance component (σ^2_δ total variance model Darvill: wetland 0.50, fynbos 0.03; Table 2) and the asynchronous (species-specific) component (σ^2_S total variance model Darvill: range wetland 0.30-1.15, fynbos 0.06-0.15). The species with the largest asynchronous variation was the spectacled weaver (1.15). As this species does not usually forage and nest in or at the edge of the ponds is might experience a different microhabitat with different (levels of) influences, for example predation and/or food availability.

Contrary to expectation I did not find clear evidence of climatic forcing at the wetland, i.e. as an explanation for the large synchronicity in survival. The larger climatic variation at the wetland did not account for most of the larger asynchronicity exhibited by the four species either. This particular wetland is not a natural environment: its water levels are managed, the pools never run dry and reed beds have not been cut during the study period. The latter has been observed to influence arthropod communities, with species-specific responses (negative/positive; Schmidt *et al.* 2005). Perhaps these beneficial - from the insectivore perspective - anthropogenic changes have decreased the environmental variation experienced by the insectivores to such an extent that the abiotic part of that variation, i.e. climatic variation, alone did not result in unfavourable conditions (Boyce *et al.* 2006; Russell *et al.* 2009).

At high density, populations are more susceptible to climatic variation and this density-dependence can be non-linear through a density threshold above which the climatic variation has an impact, but below which the population continues to increase (Grenfell *et al.* 1998; Hudson & Cattadori 1999; Stenseth *et al.* 2004; review in Sæther *et al.* 2004). While investigating the relationship between different climatic covariates and survival in three geographically separated populations of blue tits in the Mediterranean region, Grosbois *et al.* (2006) found that the population at the highest density was most sensitive to climatic variation. In an insular population of orange-crowned warblers *Oreothlypis celata* off the coast of California adult survival was not correlated with density or rainfall, but reproductive success was correlated with both (Sofaer *et al.* 2014).

Climatic variation could impact population dynamics not through a correlation with adult survival but with other vital rates. In Britain adverse weather had a limited effect on adult survival of several common resident bird species, but it did correlate negatively with juvenile survival (Robinson *et al.* 2007). Juvenile survival contributed substantially to the population dynamics (Robinson *et al.* 2004; Freeman *et al.* 2007; Robinson *et al.* 2014). Six bird species in the arid Karoo in South Africa laid larger clutch sizes after substantial rainfall (Lloyd 1999). In two sympatric *Lagopus* ptarmigan populations in the Yukon spring temperature affected different vital rates: in one species temperature correlated positively with reproductive success, in the other species with adult survival (Wilson & Martin 2010).

Minimum winter (PMB weather station) and maximum summer temperature (Darvill) separately explained only a fraction of the synchronous variation (10% and 7% respectively; C_δ in Table 2), possibly because temperature data of the study site itself was not available for the entire study period. Many studies have found an influence of seasonal extremes on avian survival (e.g. Gullett *et al.* 2014; spatial climatic forcing: Hovinen *et al.* 2014). However, Robinson *et al.* (2007) argued that the use of (seasonal) mean climatic covariate values might ignore species' physical tolerance. By using covariates that are most likely to impact survival directly, i.e. extreme weather events like prolonged periods of heavy rainfall or frost, or heat waves, the probability of detecting a strong effect increases. Additionally, mean climatic values might mask the occurrence of extreme events, which - unlike the mean - might correlate with survival (Easterling *et al.* 2000b; Parmesan *et al.* 2000; Beniston 2015). Although the wetland did experience medium frost (≤ -5 ^{0}C), exceptionally hot days (≥ 40 ^{0}C) and heavy rainfall (≥ 50 mm), these extreme events were too rare during the study period to use as covariates. Climate can correlate non-linearly with survival indicating a climatic threshold of a species (e.g. Altwegg *et al.* 2006; Gimenez *et al.* 2006; Nevoux *et al.* 2008; Ballerini *et al.* 2009). Our data were too sparse to investigate such thresholds, which also prevented investigation of additive or interactive effects. Interaction was plausible at the wetland with its summer rainfall regime.

Parmesan *et al.* (2000) and Grosbois *et al.* (2008) emphasised the need for a thorough understanding of species' annual life cycles when investigating potential impacts of climate on vital rates, for example the timing of moult, the period of highest mortality and highest activity, to increase temporal correspondence between response and explanatory variables (see also Sæther *et al.* 2004; Grosbois *et al.* 2006). The only life cycle event timing known for all four wetland species by approximation is the start of the breeding season (Oct) in the middle of spring. Thus, it would appear more likely that winter climate correlates with reproduction, not with survival.

As to the asynchronicity in survival at the wetland: the spectacled weaver (SW) was the least synchronous with the other species at the wetland (lowest ICC_S total variance model Darvill; Table 2). This species is only captured because it roosts in the reed beds (H. D. Oschadleus pers. comm.), its foraging and nesting habitat do not overlap with the other species (both in nearby woodland). Lesser swamp-warbler (LSW) and tawny-flanked prinia (TFP) were similarly asynchronous (σ^2_S 0.30 and 0.31 respectively, total variance model Darvill; Table 2) and most synchronous with the other species (ICC_S 0.66 and 0.68, total variance model Darvill; Table 2) - in that a large part of their temporal variation in survival was explained by the common variance (σ^2_δ total variance model Darvill; Table 2). Unlike the Levaillant's cisticola (LC), which only forages low down in vegetation, these species forage at all heights and, thus, might experience similar pressures/influences (Hockey *et al.* 2005).

Little is known of even the basic vital rates of African birds. I present the first survival estimates for LC and SW. Peach *et al.* (2001) estimated survival in a rural garden in Malawi (1974-1989). Their 0.56 mean survival for LSW fell within the 95% CRI of the estimated 0.54 to 0.78, as did their 0.60 estimate for TFP (this study - 95% CRI: 0.37-0.67). Their 0.70 estimate for the southern brown-throated weaver *Ploceus xanthropterus* was similar to the estimated 0.66 for SW, but that species breeds in reed beds and breeds singly or in colonies (Hockey *et al.* 2005). Their estimate of 0.53 for the red-faced cisticola *Cisticola erythrops*, a species of habitat similar to LC (Hockey *et al.* 2005), was close to the estimated 0.55.

Although the synchronizing effect of climate was negligible, the desynchronizing effect was discernible for one species. Separately, mean minimum winter and maximum summer temperature explained almost half of the asynchronicity in survival of the Levaillant's cisticola (C_S LC; Table 2). LC differed in survival from the common pattern because colder winters decreased and warmer summers increased survival (Table 3). This species has a smaller micro foraging habitat than the two other species that forage in/near water and its diet appears narrower (Hockey *et al.* 2005). The diet of LSW consists of invertebrates and, possibly, small frogs, and TFP's diet encompasses invertebrates and aloe nectar. LC restricts its diet to small insects. This narrower feeding niche could make this species more susceptible to an influence on its survival of adverse (winter) and good (summer) conditions via prey availability. Sufficient prey availability in the summer could be important to 'pay for' the cost of its rapid wing moult post-breeding (early summer; Hockey *et al.* 2005) leaving it in good shape afterwards. LSW takes 2 - 3 months for a complete moult, timing unknown. TFP only moults its primaries post-breeding.

The absence of a correlation with climatic variation at the fynbos site was as expected based on the temperate climate and the short study period. Perhaps an added factor lay in the stratification of nesting and foraging habitat of the three species at this site. Species could experience different microclimates at these different heights, which were not captured by the covariates pertaining to the entire study site (Hubbell 2005). The synchronous component of the variance (σ^2_δ total variance model Koeberg 0.03; Table 2) was smaller than all asynchronous components (σ^2_S total variance model Koeberg: range 0.06-0.15). I did not expect the stable climate to exert a forcing effect. The bar-throated apalis exhibited the largest asynchronicity in survival (σ^2_S total variance model Koeberg 0.15) resulting in the smallest intra-class correlation coefficient (ICC_S total variance model Koeberg 0.28; Table 2). In general this species prefers woodlands, which offer cover for concealment, and somewhat wetter areas, e.g. scrubs along drainage lines (Day 1997; Hockey *et al.* 2005). This habitat preference could also have resulted in its small sample size (see Data section). Karoo prinia and Karoo scrub-robin prefer drier habitat.

Lloyd *et al.* (2014) provided the only other estimates of survival for these species, but they used the same data to estimate mean survival. Their estimates were almost identical to this study's estimates of mean survival. Peach *et al.* (2001) estimated survival of the yellow-breasted apalis *Apalis flavida*, a species with similar habitat preferences, at 0.68, which was similar to the lower start point of the credible interval of this study's estimate of 0.69.

Several studies investigating survival between the more seasonal northern, temperate and the seasonally more stable southern, temperate region found empirical evidence of a latitudinal gradient in survival (Yom-Tov *et al.* 1992; Ricklefs 1997; Ghalambor & Martin 2001; Peach *et al.* 2001). Jansen *et al.* (2014) tested whether this paradigm was also valid in populations of the African reed warbler *Acrocephalus baeticatus*, a species that breeds in azonal wetlands across the seasonally diverse African subcontinent. They did not find a correlation between survival and seasonality of the habitat. However, they used published values of climatic variables. This study was not able to correlate climatic variation with survival, but I did find higher survival in the less seasonal fynbos site than at the more seasonal wetland. I do need to put in a caveat against this inference: the fynbos findings of high survival were based on resighting data of breeders, whereas the wetland findings were based on recapture data of adult individuals. This difference in methodology combined with the difference in study periods (wetland 14 capture occasions, fynbos 8) prohibited a statistical comparison. Non-breeding adults have been found to have lower recapture and lower survival (Nichols *et al.* 1994; Cam *et al.* 1998; Sandercock *et al.* 2000), and pre-breeding adults larger dispersal, which could potentially increase mortality (Ricklefs 2000).

Recent climate change has already had a noticeable effect on species and communities across the globe (Parmesan & Yohe 2003; Parmesan 2006). Forecasted climate change with the potential to increase correlation between vital rates and to increase both spatial and sympatric synchronicity makes the understanding of the influence of climatic variation on population dynamics more imperative than ever (Boyce *et al.* 2006; Altwegg *et al.* 2014). We need to determine which vital rate(s) are most sensitive to climatic variation (Coulson *et al.* 2001; Morris *et al.* 2008). A first priority would be to establish which vital rate influences population dynamics most (Caswell 2001; Loison *et al.* 2002). Besides ringing data, data on abundance, fecundity and dispersal are needed, ideally data on predation, brood parasitism and food availability as well. Apart from the obvious influences of these latter types of data on vital rates, these data could clarify (trophic) interactions. Climate change could alter species' interactions, and different trophic levels could react differently to climatic variation (Both *et al.* 2009; Cornelissen 2011; Jamieson *et al.* 2012). In South Africa, ringing data are the only widely available data, collected by citizen scientists following the SAFRING protocol. The other types of data would need clearly defined protocols as well to prevent disturbance of the study species and to insure quality and potential for comparison.

Studies of sympatric synchronicity aid the understanding of how species assemblages function and how/if climatic variation acts as synchronizing and desynchronizing agent on the particular vital rate of the individual species (Lahoz-Monfort *et al.* 2011; Robinson *et al.* 2013). This study did not find a clear correlation between survival and climatic variation, but it did quantify the (a)synchronicity in survival in two species assemblages in fragile habitat and it provided the first survival estimates of the Levaillant's cisticola and the spectacled weaver. The use of an integrative climate index could improve the possibility of finding a correlation with climatic variation while minimizing the number of covariates modelled (Grosbois *et al.* 2006; Grosbois *et al.* 2008). As the study species are all common and found in large areas of South Africa, a similar study in a different, preferably more seasonal, habitat could confirm this study's findings. Wetlands are well-suited because they are azonal and South Africa is one of the most geographically diverse countries in the world relative to its size (Allan *et al.* 1997).

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Table 1. Life history details of the study species.

Location habitat	Species	Length (cm)[1]	Mean weight (g)[1]	Clutch size	Incubation period (days)	Nestling period (days)	Fledgling period (days)[1]
Darvill	LSW	17-18	15	2-3[1]	13-14[1]	?	10-14
wetland	LC	12-15	12	2-5[1]	11-14[1]	14-15[1]	?
	TFP	10-15	10	2-5[1]	13-14[1]	10-20[1]	?
	SW	15-16	30	1-4[1]	13-14[2]	15-19[1]	14+
Koeberg	BTAP	12-13	11	2.9[3]	15.2[5]	14.6[6]	?
fynbos	KAPR	13-15	10	3.7[3]	13.1[5]	13.5[6]	?
	KARO	17	19	1-44	144	13-171	28+

LSW, lesser swamp-warbler; LC, Levaillant's cisticola; TFP, tawny-flanked prinia; SW, spectacled weaver; BTAP, bar-throated apalis; KAPR, Karoo prinia; KARO, Karoo scrub-robin; ?, unknown.

[1] Hockey *et al.* 2005; [2] Tarboton 2001 ; [3] Martin *et al.* 2006; [4] Lloyd *et al.* 2009; [5] Martin *et al.* 2007; [6] Martin *et al.* 2011 (reference 1+2 from southern Africa; 3-6 from Koeberg).

Table 2. Estimated synchronous (common) and asynchronous (species-specific) variance at Darvill (wetland - 1999-2012) and at Koeberg (fynbos - 2000-2006), and intra-class correlation (ICC) coefficients of the total variance model and the two residual variance models with significant covariates (Darvill only).

Model	Location	Synchronous variation σ^2_δ (95% CRI) [1]	Species	Asynchronous variation σ^2_S (95% CRI) [1]	ICC$_S$ = σ^2_δ / ($\sigma^2_\delta + \sigma^2_S$)
$\phi_S(t) = \mu_S + \varepsilon_S(t) + \delta(t)$	Wetland	0.50 (0.01, 1.92)	LSW	0.30 (3e-4, 1.65)	0.66 (0.02, 1.00)
(total variance)			LC	0.46 (1e-3, 2.15)	0.57 (0.02, 1.00)
			TFP	0.31 (2e-4, 1.97)	0.68 (0.03, 1.00)
			SW	1.15 (2e-3, 5.53)	0.43 (0.01, 1.00)
	Fynbos	0.03 (1e-5, 0.19)	BTAP	0.15 (2e-4, 0.90)	0.28 (1e-4, 0.99)
			KAPR	0.06 (4e-5, 0.34)	0.40 (4e-4, 1.00)
			KARO	0.09 (1e-4, 0.55)	0.36 (3e-4, 1.00)
$\phi_S(t) = \mu_S$ + tmin winter + $\varepsilon_S(t) + \delta(t)$	Wetland	0.45 (4e-3,1.86)	LSW	0.43 (3e-4, 2.28)	0.57 (0.01, 1.00)
(residual variance)			LC	0.27 (2e-4, 1.65)	0.66 (0.02, 1.00)
			TFP	0.46 (4e-4, 2.88)	0.59 (7e-3, 1.00)
			SW	1.14 (2e-3, 5.90)	0.44 (3e-3, 1.00)
Part of the variance accounted for by tmin winter		$C_\delta = 0.10$	C_S LC = 0.41 [2]		
$\phi_S(t) = \mu_S$ + tmax summer + $\varepsilon_S(t) + \delta(t)$	Wetland	0.47 (4e-3, 1.93)	LSW	0.45 (4e-4, 2.53)	0.59 (0.01, 1.00)
(residual variance)			LC	0.24 (2e-4, 1.44)	0.68 (0.02, 1.00)
			TFP	0.47 (3e-4, 2.83)	0.59 (0.01, 1.00)
			SW	0.79 (1e-3, 4.09)	0.49 (0.01, 1.00)
Part of the variance accounted for by tmax summer		$C_\delta = 0.07$	C_S LC = 0.48 [2]		

CRI, credible interval; species abbreviations as in Table 1; tmin winter, mean minimum temperature June-Aug at Pietermaritzburg; tmax summer, mean maximum temperature Dec-Febr at Darvill.

[1] On the logit scale.

[2] Only the variance component for those species for which the 95% credible intervals of the regression coefficients did not include zero (Table 3) are shown.

Table 3. Covariate influence on annual adult survival of the four species at the Darvill wetland 1999-2012 (two separate models).

Covariate	Species	Regression Coefficient [1]	SD	95% CRI	
				Lower	Upper
tmin	LSW	2.20	1.68	-0.75	5.99
winter	LC	3.72	1.71	0.70	7.47
PMB	TFP	1.11	1.72	-2.05	4.73
	SW	-0.81	2.23	-5.36	3.60
[2] tmax	LSW	-0.73	1.87	-4.59	2.94
summer	LC	-3.55	1.82	-7.58	-0.17
Darvill	TFP	-1.59	2.14	-6.07	2.55
	SW	3.64	2.75	-1.89	8.95

[1] On the logit scale.

[2] Model that assumed that conditions were average during occasions 2009-2010 until 2011-2012.

SD, standard deviation; CRI, credible interval; tmin winter PMB, mean minimum temperature June-Aug at Pietermaritzburg; tmax summer, mean maximum temperature Dec-Feb; species abbreviations as in Table 1.

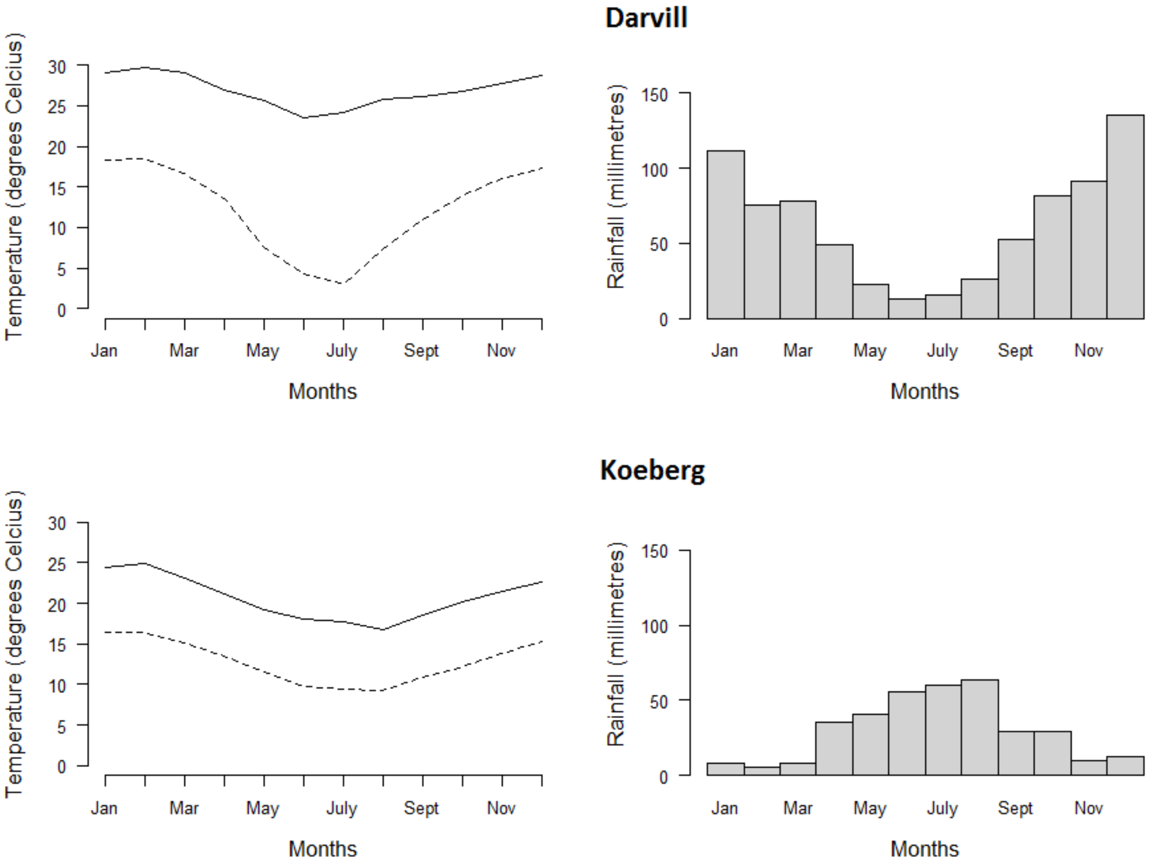

Figure 1. Mean minimum (dashed lines) and maximum (solid lines) temperatures, and mean total rainfall per month at the wetland at Darvill and at the fynbos site at Koeberg. Temperature means at Darvill pertain to 1999-2009 and rainfall on 1999-2012. The Koeberg means pertain to 2000-2007.

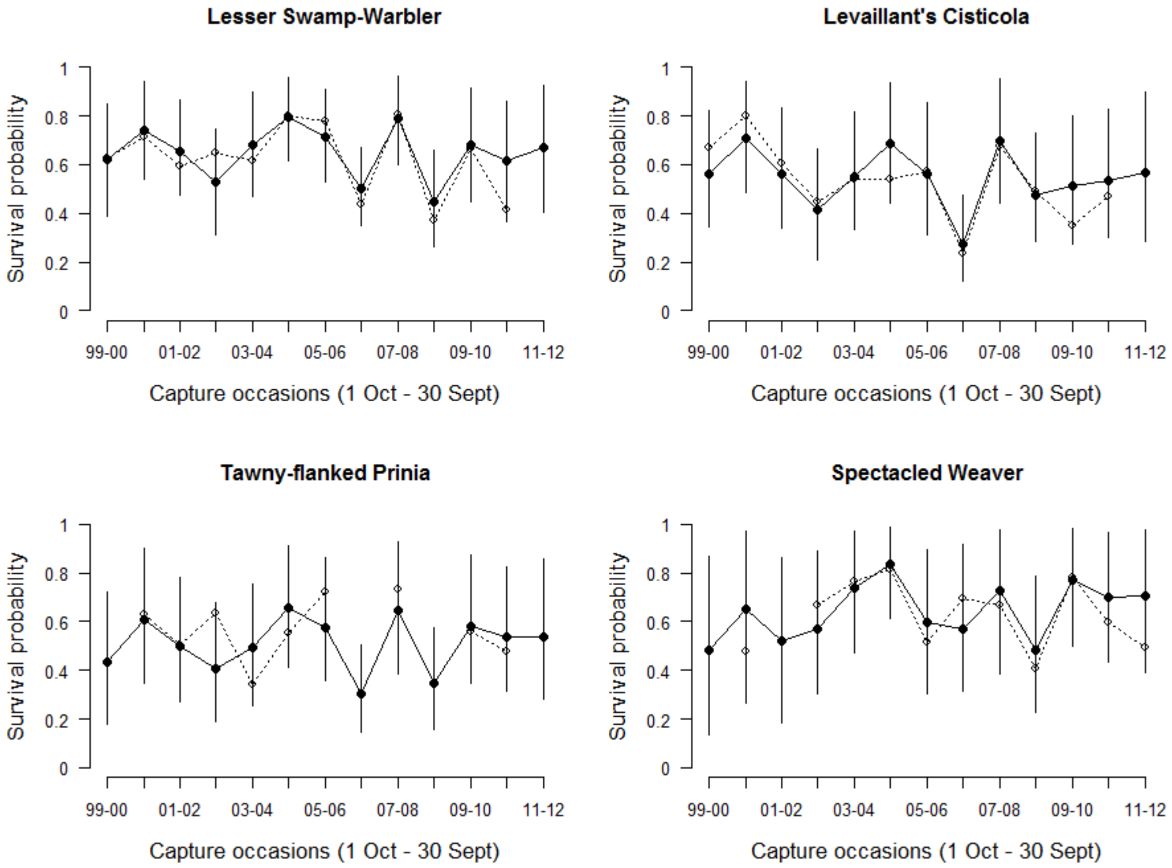

Figure 2. Annual apparent adult survival per species at Darvill (wetland, 1999-2012) estimated with the total variances model (no covariates; solid lines). Vertical lines represent the 95% credible intervals. Dashes lines and open point estimates are survival estimates from the fully time-dependent model run per species. Only those estimates with a standard deviation less than half the estimate (fairly high precision) are shown.

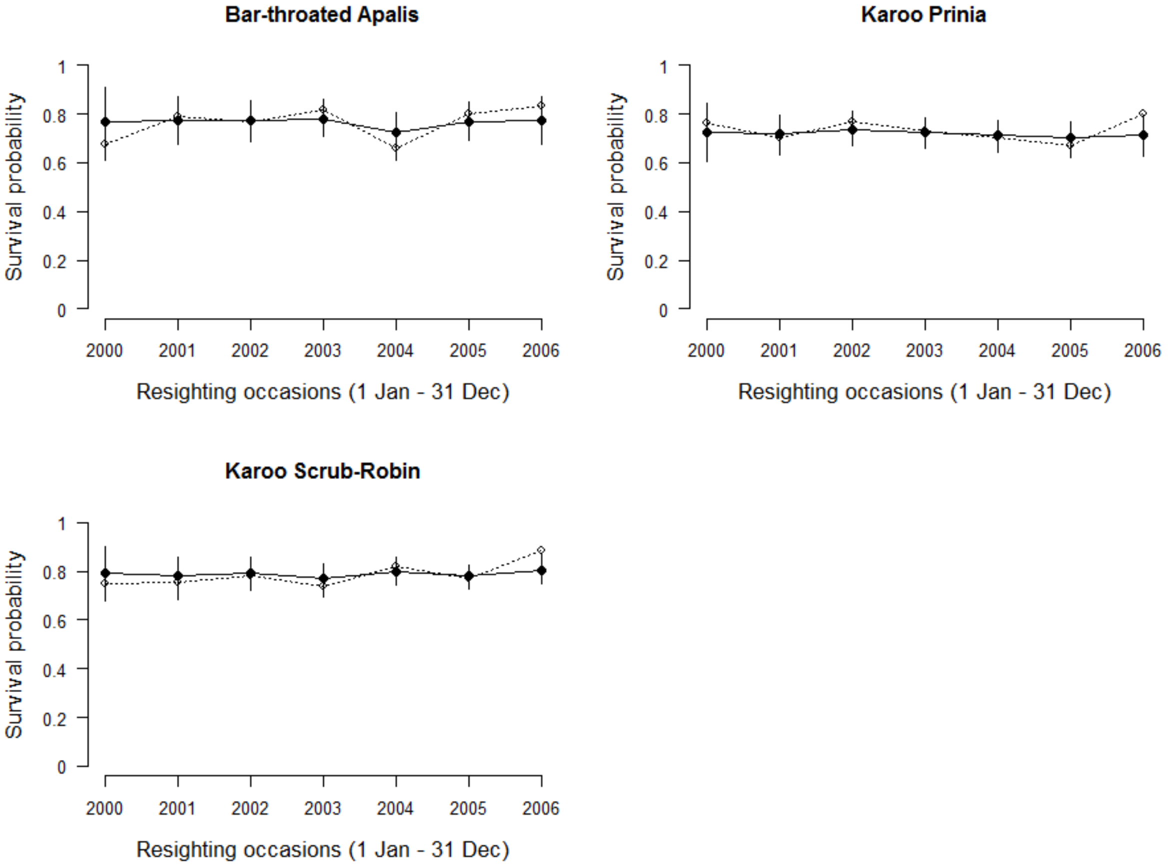

Figure 3. Annual apparent adult survival per species at Koeberg (fynbos, 2000-2006) estimated with the total variance model (no covariates; solid lines). Vertical lines represent the 95% credible intervals. Dashes lines and open point estimates are survival estimates from the fully-time dependent model run per species.

Appendix

Table A1. Covariates used in separate models (residual variance models) for the Darvill wetland (1999-2012) and the Koeberg fynbos (2000-2007).

Location	Model	Covariate [1]	Species	Regression Coefficient [2]	'Missing' parameter [3]	SD	95% CRI	
							Lower	Upper
Darvill wetland	1	tmin year	LSW	-0.60		3.87	-8.14	7.21
		PMB	LC	3.71		3.67	-4.70	9.52
			TFP	0.21		4.08	-7.95	8.09
			SW	-0.93		4.66	-9.08	8.29
	2	tmin year lag 1	LSW	-0.33		3.84	-8.11	6.87
		PMB	LC	3.93		3.33	-3.24	9.28
			TFP	2.53		3.53	-4.76	9.01
			SW	-3.51		4.30	-9.52	6.43
	3 [4]	tmin winter	LSW	2.20		1.68	-0.75	5.99
		PMB	LC	3.72		1.71	0.70	7.47
			TFP	1.11		1.72	-2.05	4.73
			SW	-0.81		2.23	-5.36	3.60
	4	tmin winter lag 1	LSW	-1.30		1.64	-5.02	1.54
		PMB	LC	0.87		1.60	-2.60	4.03
			TFP	-0.29		1.82	-4.22	3.13
			SW	-4.90		2.36	-9.42	-0.43
	5 [3]	tmin year	LSW	4.35		6.11	-9.28	14.08
		Darvill	LC	1.42		6.90	-12.28	13.59
			TFP	3.39		6.74	-11.06	14.18
			SW	3.78		7.53	-12.52	14.46
			LSW		0.25	2.19	-2.31	7.66
			LC		0.86	2.40	-2.13	8.31
			TFP		3.23	3.14	-1.05	9.54
			SW		4.14	3.13	-0.96	9.64
	6 [5]	tmin year	LSW	2.79		4.57	-7.11	9.55
		Darvill	LC	0.84		5.09	-8.92	9.21
			TFP	2.13		4.96	-8.14	9.58
			SW	2.28		5.28	-8.69	9.68
	7	tmin year lag 1	LSW	-2.33		5.46	-12.77	8.81
		Darvill	LC	-3.48		5.46	-13.36	8.15
			TFP	3.43		5.66	-8.29	13.65
			SW	1.26		6.99	-12.73	13.42
			LSW		0.57	2.47	-2.27	8.20
			LC		1.25	2.73	-2.13	8.97
			TFP		3.32	3.15	-1.21	9.57
			SW		4.32	3.19	-1.13	9.69
	8	tmin year lag 1	LSW	-2.12		4.13	-9.22	6.46
		Darvill	LC	-3.36		3.98	-9.48	5.39
			TFP	2.87		4.26	-6.72	9.49
			SW	1.43		4.94	-8.57	9.35
	9	tmin winter	LSW	2.96		2.62	-2.07	8.42
		Darvill	LC	5.10		2.82	-0.74	9.59
			TFP	3.43		2.76	-2.04	8.88
			SW	0.29		3.26	-6.32	6.86
			LSW		-0.26	0.98	-2.12	1.89
			LC		-0.46	0.99	-2.51	1.51
			TFP		1.40	1.36	-0.85	4.50
			SW		2.47	1.49	-0.48	4.87

Table 4 continued.

Location	Model	Covariate [1]	Species	Regression coefficient [2]	'Missing' parameter [3]	SD	95% CRI	
							Lower	Upper
Darvill wetland	10	tmin winter Darvill	LSW	2.20		2.33	-2.16	7.30
			LC	3.84		2.59	-1.11	8.97
			TFP	3.72		2.64	-1.35	9.04
			SW	0.44		3.28	-6.11	7.31
	11	tmin winter lag 1 Darvill	LSW	-3.47		2.20	-7.83	1.08
			LC	-1.31		2.69	-6.99	4.07
			TFP	-0.50		2.60	-5.53	5.11
			SW	-3.14		3.04	-8.77	3.09
			LSW		0.22	2.25	-2.21	7.84
			LC		0.93	2.51	-2.19	8.59
			TFP		3.26	3.12	-0.98	9.57
			SW		3.94	3.25	-1.34	9.63
	12	tmin winter lag 1 Darvill	LSW	-3.37		2.00	-7.54	0.42
			LC	-1.78		2.27	-6.67	2.52
			TFP	-0.36		2.47	-5.35	4.90
			SW	-2.92		2.96	-8.83	2.88
	13	tmax year PMB	LSW	0.82		3.76	-6.72	8.22
			LC	-4.57		3.42	-9.69	2.94
			TFP	-1.77		3.79	-8.84	6.25
			SW	5.65		3.22	-2.13	9.81
	14	tmax year lag 1 PMB	LSW	2.16		3.75	-5.17	10.03
			LC	4.97		3.97	-2.80	12.76
			TFP	3.53		4.04	-4.33	11.75
			SW	-1.79		5.52	-12.56	9.61
	15	tmax summer PMB	LSW	-0.77		2.19	-5.17	3.56
			LC	-3.62		2.21	-8.29	0.49
			TFP	-2.04		2.62	-7.32	2.97
			SW	3.49		3.05	-3.01	9.08
	16	tmax summer lag 1 PMB	LSW	1.19		2.31	-3.35	5.94
			LC	0.74		2.51	-4.18	6.12
			TFP	0.12		2.68	-5.33	5.42
			SW	3.41		3.04	-3.07	8.94
	17	tmax year Darvill	LSW	1.03		3.45	-5.84	7.95
			LC	-3.94		3.48	-11.16	2.78
			TFP	0.07		3.91	-7.67	8.02
			SW	7.30		3.95	-0.37	14.34
			LSW		0.13	1.48	-1.86	3.66
			LC		-0.24	0.92	-2.00	1.71
			TFP		2.59	2.74	-0.71	9.29
			SW		4.84	2.90	-0.01	9.70
	18	tmax year Darvill	LSW	0.72		2.84	-4.96	6.52
			LC	-3.76		2.75	-8.93	2.07
			TFP	-0.67		3.21	-6.96	5.89
			SW	5.79		2.81	-0.61	9.80
	19	tmax year lag 1 Darvill	LSW	2.99		3.68	-3.96	11.26
			LC	-0.11		3.98	-8.06	8.27
			TFP	3.22		4.05	-4.71	11.65
			SW	5.05		5.15	-5.40	13.97
			LSW		0.43	2.45	-2.51	8.13
			LC		1.48	2.91	-2.20	9.07
			TFP		3.36	3.19	-1.28	9.53
			SW		4.11	3.23	-1.25	9.73

Table 4 continued.

Location	Model	Covariate [1]	Species	Regression coefficient [2]	'Missing' parameter [3]	SD	95% CRI Lower	95% CRI Upper
Darvill wetland	20	tmax year lag 1 Darvill	LSW	2.33		2.90	-3.40	8.21
			LC	-0.41		3.17	-6.78	6.18
			TFP	2.72		3.30	-4.28	8.66
			SW	3.13		3.96	-5.54	9.46
	21	tmax summer Darvill	LSW	-0.85		1.90	-4.86	2.92
			LC	-3.88		1.94	-7.95	-0.16
			TFP	-1.33		2.20	-5.88	2.97
			SW	3.50		2.68	-1.83	8.79
			LSW		-0.21	0.91	-1.80	1.80
			LC		-0.36	0.79	-1.92	1.28
			TFP		1.46	1.36	-0.80	4.56
			SW		2.36	1.48	-0.45	4.86
	22 [4]	tmax summer Darvill	LSW	-0.73		1.87	-4.59	2.94
			LC	-3.55		1.82	-7.58	-0.17
			TFP	-1.59		2.14	-6.07	2.55
			SW	3.64		2.75	-1.89	8.95
	23	tmax summer lag 1 Darvill	LSW	1.59		2.01	-1.91	6.23
			LC	-0.15		2.04	-4.14	4.30
			TFP	1.83		2.25	-2.24	6.69
			SW	4.12		2.85	-1.22	10.42
			LSW		0.46	2.58	-2.75	8.28
			LC		0.99	2.57	-2.51	8.54
			TFP		3.37	3.20	-1.34	9.52
			SW		4.13	3.23	-1.22	9.66
	24	tmax summer lag 1 Darvill	LSW	1.44		1.78	-1.92	5.23
			LC	-0.14		1.84	-3.64	3.68
			TFP	1.63		2.10	-2.49	6.01
			SW	3.78		2.40	-0.98	8.59
	25	total ppt year Darvill	LSW	0.01		0.01	-0.01	0.03
			LC	0.02		0.01	-0.01	0.05
			TFP	0.00		0.01	-0.02	0.02
			SW	-0.01		0.01	-0.04	0.02
	26	total ppt year lag 1 Darvill	LSW	0.002		0.01	-0.02	0.03
			LC	0.005		0.01	-0.02	0.03
			TFP	0.002		0.01	-0.02	0.02
			SW	-0.004		0.01	-0.03	0.02
	27	total ppt summer Darvill	LSW	0.01		0.03	-0.04	0.07
			LC	0.05		0.03	-0.001	0.10
			TFP	-0.01		0.03	-0.06	0.04
			SW	-0.01		0.03	-0.07	0.06
	28	total ppt summer lag 1 Darvill	LSW	0.001		0.02	-0.05	0.05
			LC	0.03		0.03	-0.02	0.07
			TFP	0.02		0.03	-0.03	0.07
			SW	-0.01		0.03	-0.08	0.06
	29	SD ppt year Darvill	LSW	1.85		1.69	-1.78	5.06
			LC	0.46		1.72	-2.69	4.23
			TFP	0.04		1.76	-3.37	3.53
			SW	0.39		2.16	-3.77	4.92
	30	SD ppt year lag 1 Darvill	LSW	-0.49		1.67	-3.72	3.06
			LC	2.22		1.71	-0.90	5.58
			TFP	0.15		1.86	-3.57	3.84
			SW	-0.75		2.14	-4.73	3.75

Table 4 continued.

Location	Model	Covariate [1]	Species	Regression coefficient [2]	'Missing' parameter [3]	SD	95% CRI	
							Lower	Upper
Darvill wetland	31	SD ppt summer Darvill	LSW	1.39		1.44	-1.05	4.61
			LC	2.76		1.33	0.29	5.62
			TFP	0.50		1.41	-2.20	3.37
			SW	0.21		1.93	-3.38	4.24
	32	SD ppt summer lag 1 Darvill	LSW	-0.88		1.16	-3.11	1.50
			LC	1.28		1.13	-0.90	3.57
			TFP	0.05		1.30	-2.51	2.59
			SW	-1.34		1.67	-4.58	1.93
Koeberg fynbos	33	tmin year	BTAP	-1.03		1.99	-4.51	3.10
			KAPR	-1.04		1.63	-4.15	2.49
			KARO	0.74		1.90	-3.19	4.38
	34	tmin year lag 1	BTAP	0.47		1.85	-3.36	3.93
			KAPR	0.05		1.48	-2.71	3.10
			KARO	0.55		1.62	-2.85	3.74
	35	tmin winter	BTAP	-0.32		1.32	-2.76	2.77
			KAPR	-0.31		0.88	-1.84	1.68
			KARO	0.79		1.04	-1.14	2.94
	36	tmin winter lag 1	BTAP	0.56		1.02	-1.41	2.65
			KAPR	0.13		0.73	-1.30	1.63
			KARO	-0.01		0.90	-1.69	1.87
	37	tmax year	BTAP	-1.24		2.44	-4.81	4.12
			KAPR	-0.76		2.14	-4.44	3.72
			KARO	1.87		2.07	-3.06	4.81
	38	tmax year lag 1	BTAP	0.66		2.16	-3.74	4.58
			KAPR	-0.02		1.75	-3.61	3.57
			KARO	0.14		1.97	-3.77	4.18
	39	tmax summer	BTAP	0.00		1.29	-2.62	2.87
			KAPR	0.27		0.92	-1.48	2.29
			KARO	0.54		1.08	-1.52	2.93
	40	tmax summer lag 1	BTAP	1.13		1.04	-1.02	3.24
			KAPR	0.06		0.86	-1.77	1.79
			KARO	-0.56		1.04	-2.42	1.41
	41	total ppt year	BTAP	-0.001		0.01	-0.02	0.02
			KAPR	-0.001		0.01	-0.02	0.01
			KARO	0.01		0.01	-0.01	0.02
	42	total ppt year lag 1	BTAP	0.01		0.01	-0.01	0.03
			KAPR	0.01		0.01	-0.01	0.02
			KARO	0.01		0.01	-0.01	0.02
	43	total ppt winter	BTAP	0.01		0.02	-0.03	0.05
			KAPR	0.01		0.02	-0.03	0.04
			KARO	0.01		0.02	-0.03	0.04
	44	total ppt winter lag 1	BTAP	0.02		0.02	-0.02	0.06
			KAPR	0.01		0.02	-0.01	0.05
			KARO	0.01		0.02	-0.03	0.05
	45	SD ppt year	BTAP	-0.58		1.02	-2.69	1.60
			KAPR	0.07		0.80	-1.42	1.78
			KARO	0.52		0.88	-1.11	2.48
	46	SD ppt year lag 1	BTAP	0.69		0.98	-1.03	2.79
			KAPR	0.15		0.72	-1.24	1.74
			KARO	0.18		0.83	-1.32	1.93

Table 4 continued.

Location	Model	Covariate [1]	Species	Regression coefficient [2]	'Missing' parameter [3]	SD	95% CRI Lower	95% CRI Upper
Koeberg fynbos	47	SD ppt winter	BTAP	-0.07		0.96	-1.82	2.04
			KAPR	0.31		0.73	-1.04	1.92
			KARO	0.14		0.80	-1.32	1.90
	48	SD ppt winter lag 1	BTAP	0.57		1.03	-1.36	2.74
			KAPR	0.41		0.76	-1.10	1.98
			KARO	0.04		0.89	-1.54	2.09

[1] PMB/Darvill indicate the weather station.

[2] On the logit scale.

[3] (Model with an) extra parameter (on the logit scale) to account for the missing covariate data from the Darvill weather station during occasions 2009-2010 until 2011-2012.

[4] Table 3.

[5] Model using Darvill weather data that assumed that conditions were average during occasions 2009-2010 until 2011-2012.

SD, standard deviation; CRI, credible interval; tmin, mean minimum temperature; lag 1, previous year; winter, June-Aug; tmax, mean maximum temperature; summer, Dec-Feb for Darvill wetland and Jan-Feb for Koeberg fynbos; total ppt, total millimetres rainfall; species abbreviations as in Table 1.

Chapter 5

The drivers of population dynamics of the Sociable Weaver *Philetairus socius*

Photo René E. van Dijk

Photo Max Loubon

Photo René E. van Dijk

Abstract

Population dynamics have evolved to be most sensitive to the least variable demographic rate. The forecasted increase in climatic variation and in the frequency and intensity of extreme events could increase the variability of demographic rates with potentially detrimental effect on populations. It is, therefore, crucial to understand population dynamics and to determine the effect of climatic stochasticity on demographic rates. I investigated the population dynamics and the influence of climatic extremes on the demographic rates of a population of 25 colonies of sociable weavers *Philetairus socius* near Kimberley (South Africa) during 1993-2014. Sociable weavers are colonial cooperative breeders endemic to (semi-)arid savanna in Namibia and South Africa. Using an integrated population model I estimated a mean fecundity of 0.65 (95% credible interval: 0.39-0.99) fledglings per adult female per year, mean juvenile survival of 0.43 (0.32-0.55), and mean adult survival of 0.66 (0.61-0.71). I determined that fecundity contributed most to the variation in population growth rate over the study period. Although many colonies were declining, the population did not show a trend. Projecting the population model five years into the future indicated that the population will recover. I did not find any climatic correlates at the population level. A separate analysis of the most data-rich colony showed a clear declining trend. The colony's near future included an increasing extinction probability from 0.05 in 2014 to 0.33 in 2018. In this colony extreme heat was negatively correlated with juvenile survival and extreme cold with adult survival and fecundity. The climate indices explained more than half of the temporal variation of these demographic parameters. Both climatic extremes could have reduced food supply by forcing birds to seek thermal refuge in nest chambers for longer periods, thus decreasing foraging time. Rainfall was negatively correlated with adult survival. More rainfall would increase breeding opportunities via food supply allowing more adults to breed independently and for longer, thus increasing the demands on adults. There is some evidence that colonies respond differently to climatic stochasticity. This could explain the absence of climatic correlates at the population level. The findings of this study suggest that more and increasingly extreme climatic events could have an adverse effect on this population of sociable weavers, especially since more climatic variation has the propensity to synchronize colony responses.

Introduction

Population dynamics, the fluctuation in population size over time, are driven by births, deaths, and dispersal (Begon *et al.* 2006), which translate into the demographic or vital rates fecundity, survival, emigration, and immigration (Caswell 2001). Population dynamics are affected by demographic stochasticity, i.e. random changes in the demographic rates of single individuals in a population, and environmental stochasticity, which causes random changes in the demographic rates of all individuals in a population (Schmutz 2009). The former acts independently on individuals, and only affects the population dynamics of small populations perceptibly; the latter acts at the population level and affects the population dynamics of both small and large populations (Lande *et al.* 2003).

The population growth rate is not equally sensitive to changes in each vital rate, although increased variation in any vital rate does tend to decrease population growth rate (Tuljapurkar *et al.* 2003). Pfister (1998) investigated sensitivity in populations of plants, invertebrates, reptiles, and birds and found a negative correlation between variance and sensitivity, i.e. the smaller the variation in a demographic rate, the greater the sensitivity of the population growth rate to changes in that demographic rate. Schmutz (2009) found a similar pattern when examining adult survival in 62 bird populations. Pfister (1998) inferred that life histories have evolved to buffer that demographic rate against environmental variability (see also Gaillard & Yoccoz 2003, who called this canalization against temporal variability).

Environmental stochasticity in the form of climatic variation, including extreme weather events like heavy rainfall and heat waves, has been increasing since 1950 and is forecasted to increase further in the 21st century, including an increase in both frequency and intensity of extreme events (IPCC 2014). Climatic variability could increase to such an extent that the variability of canalized traits increases substantially, which could have severe consequences for populations and increase their risk of extinction (Tuljapurkar *et al.* 2003; Boyce *et al.* 2006; Schmutz 2009). Because of the non-linear relationship between vital rates and population growth, populations could decline as a result of increasing variation in the canalized demographic rate without changes in its mean (Boyce *et al.* 2006). Understanding how environmental stochasticity influences demographic rates and, thus, affects population dynamics has, therefore, become of increasing importance (reviews in Jenouvrier 2013 and Frederiksen *et al.* 2014).

Many studies have found that demographic rates respond differently to climatic variation. For example, variation in juvenile survival of asp vipers *Vipera aspis* in the Jura mountains of Switzerland was strongly influenced by variation in winter temperature while the canalized demographic rate adult survival was not (Altwegg *et al.* 2005). In Britain adult survival of blackbirds *Turdus merula*, which had the greatest impact on observed population growth rate, was negatively influenced by dry summers and cold winters, but juvenile survival and fecundity were not (Robinson *et al.* 2012). Conversely, greater snow goose *Chen caerulescens atlantica* juveniles survived better when summers were warmer, but adult survival was not affected by temperature (van Oudenhove *et al.* 2014). Blue cranes *Anthropoides paradiseus* survived better when the late breeding season was wetter, but fecundity was higher when the early breeding season was wetter (Altwegg & Anderson 2009).

I investigated the population dynamics of 25 colonies, treated as one population, of sociable weavers *Philetairus socius* at Benfontein near Kimberley in the Northern Cape in South Africa during 1993 to 2014. The sociable weaver is a small, mainly insectivorous, passerine endemic to the arid and semi-arid savanna of South Africa and Namibia (Maclean 1973a). The study area is located at the eastern edge of the distribution of the sociable weaver. This distribution is closely associated with that of the stiff dry grasses (mainly *Stipagrostis*) that the sociable weaver needs to build its unique 'haystack' communal nest structures (Maclean 1973b). A colony can house from 2 to 500 individuals in its individual nest chambers. The sociable weaver is an obligate cooperative breeder, at Benfontein 30-80% of breeding pairs had one to five helpers (Covas 2002; Covas *et al.* 2006). Breeding is initiated in response to rainfall with a minimum of six days between the first good rains and laying of the first egg (Maclean 1969, 1973c). The breeding season can last up to nine months (Maclean 1973c). Parental care of fledglings lasts up to six weeks and juveniles delay dispersal from their natal colony until they are at least four months old and generally do not leave during their first year (Covas 2002; Covas *et al.* 2004a).

Over the past 50 years extreme rainfall events have increased significantly in South Africa, but there was little evidence of a long-term annual trend (Mason *et al.* 1999; DEA 2013). The same period saw an identical pattern in hot and cold extremes - with the latter decreasing, although longer time series do seem to indicate a warming trend (DEA 2013; Kruger & Sekele 2013). Forecasts based on unmitigated climate scenarios predict a 5-8 $^{\mathrm{o}}$Celsius increase in the interior of South Africa by the end of the 21st century (DEA 2013). In the Kimberley region mean austral summer rainfall is forecasted to decrease from the mid-21st century onwards (Hulme *et al.* 2001). Additionally, spring rainfall is forecasted to decrease at the end of the 21st century indicating a delayed onset of the summer rains (Niang *et al.* 2014).

The aim of this study was to determine the drivers of population dynamics of the sociable weaver population at Benfontein, i.e. the influence of vital rates on population growth rate and the influence of climatic stochasticity on those vital rates. Based on Altwegg *et al.*'s (2014) findings that the population growth rate of this species is least sensitive to changes in fecundity I expected fecundity to contribute most to the observed variation in population growth rate. Additionally, I carried out a population viability analysis to investigate the near future of this declining population (Altwegg *et al.* 2014).

Birds have a relatively high body temperature and can experience evaporative water loss of more than 5% of their body mass per hour, when temperatures rise to 30 °C and above, particularly small species with their large surface to volume ratio (McKechnie & Wolf 2010; Gardner *et al.* 2015). They become dehydrated quickly, even if there is enough water available. Because the large nest mass provides insulation (White *et al.* 1975; Bartholomew *et al.* 1976), sociable weavers can avoid the dangers of heat stress and dehydration by taking refuge in their nest chambers during the hottest parts of the day (Maclean 1973e). Above average temperatures would increase the length of those periods, thus decreasing foraging time. As summer occurs in the middle of the breeding season I hypothesized that extreme heat would have a more detrimental effect on survival of juveniles as they are either fledglings still being fed by their parents, who have less time to forage, or recently independent individuals who will be less efficient at foraging. Less foraging time for parents would also have an adverse effect on fecundity as less food would decrease nestling fitness and, hence, their survival to fledging. Sociable weavers also return to their nests in extreme cold (Maclean 1973e). As winter (Jun-Aug) coincides with the end of the breeding season and is always a time when food is scarce and nestlings die of starvation (Maclean 1973c), I hypothesized that extreme cold would increase nestling starvation and, thus, decrease fecundity, as well as decrease adult survival at the end of a taxing season for breeders. By this time the juveniles of the earlier broods would have gained foraging experience, so I did not expect a large negative effect on their survival. In semi-arid habitat rainfall determines food supply and the length of the breeding season (Maclean 1973c; du Plessis *et al.* 1995; Allan *et al.* 1997; Lloyd 1999; Dean & Milton 2001). I hypothesized that rainfall would have a positive effect on fecundity and juvenile survival, but a negative effect on adult survival through the sustained effort required of a lengthier breeding season.

Altwegg *et al.* (2014) found large spatiotemporal variation in survival and fecundity in a population of 17 colonies at the study site. This suggests that colonies respond differently to environmental stochasticity. To investigate this I included a separate analysis of the only colony that was active during the entire study period 1993-2014 and large enough to yield adequate sample sizes.

Materials and Methods

Study area and field methods

The study area of approximately 20 km^2 is part of Benfontein Game Farm, ca. 6 km south-east of Kimberley in the Northern Cape Province of South Africa (28°52'S, 24°51'E). It is located in the

Savanna biome and Eastern Kalahari Bushveld bioregion, and consists of semi-arid Kimberley Thornveld characterised by warm, wet summers (Dec-Feb) with erratic rainfall and dry, cold winters (Jun-Aug) with frequent frost (Mucina & Rutherford 2006). During the study period of 17 July 1993 to 12 June 2014 (first and last capture) minimum daily temperature ranged from -8.5 to 24.9 ^{o}Celsius (mean ± standard deviation: 10.1 ± 6.8), maximum daily temperature from 5.0 to 40.9 ^{o}C (26.7 ± 6.3), and daily rainfall from 0.0 to 88.6 millimetres (1.2 ± 4.8). Average annual rainfall was 437.4 mm (± 119.3) over 1993-2013. The annual number of days when the temperature dropped below zero ranged from 8 to 48. Annual mean maximum and minimum temperature and rainfall did not show a temporal trend (Pearson's product moment correlation: $P > 0.06$).

The study area is open and flat, dotted with camelthorn trees *Acacia erioloba* and the groundcover consists mainly of *Stipagrostis* grasses with much bare soil (Covas 2002; Mucina & Rutherford 2006).

The study area encompasses 53 colonies of sociable weavers with varying starting dates and periods of occupancy (Fig. 1, Table A1). Since 1993 colonies have been captured by placing a mist net around the nest tree before dawn and flushing the birds into the net (Covas *et al.* 2004a). Captured birds were processed following the South African Bird Ringing Unit protocol (de Beer *et al.* 2001; see Covas *et al.* 2004a for a detailed description). Individuals of several smaller colonies were captured with hand nets (Spottiswoode 2007). From 1993 to 1998 1 to 2 colonies were captured every month - the majority of colonies twice but some colonies up to five times over the course of a breeding season (Altwegg *et al.* 2014), i.e. usually Sep-Apr depending on rainfall (Covas *et al.* 2008); from 1998 to 2000 during 1 to 2 months at the start and at the end of the breeding season; from 2001 to the present only once before the start of the breeding season (Covas *et al.* 2002, 2011). Not all active colonies were captured every season (bold numbers in Table A1 indicate missing colony size information for some years) and none were captured during seasons 1997, 2006 and 2007. More than 70% of resident colony members were caught during a colony capture (Covas *et al.* 2008). Escaped adults were counted and those targeted by specific studies were later caught with hand nets (Covas *et al.* 2006; Spottiswoode 2007).

Breeding was monitored by examining all nest chambers in a colony every 3 to 4 days during the breeding season (Covas *et al.* 2011; Paquet *et al.* 2015). Sociable weaver nestlings fledge between day 21 and 24 (Maclean 1973c). Since disturbance after day 17 causes the nestlings to fledge prematurely, productivity was measured as the number of nestlings alive at day 17 (Covas *et al.* 2008). Nestlings were ringed at day 17 and assumed to survive to fledging (Covas *et al.* 2008). Not all nestlings observed alive at day 17 were ringed (R. Covas pers. comm.). From 1993 to 1998 nestlings were also ringed before day 17 (proportion unknown; R. Covas pers. comm.).

Individuals were aged depending on the size of their black bib, juveniles moult into adult plumage with a fully-developed black bib at ca. four months (Maclean 1973c; Covas *et al.* 2004a). Hereafter, 'juveniles' refers to all individuals in their first year, 'nestling' is used specifically to refer to those individuals that have not fledged and 'fledgling' to dependent juveniles and as a measure of productivity (see also Capture-mark-recapture data).

Data

I selected data pertaining to 25 colonies in the meta-population of 53 colonies for this analysis (hereafter 'population'; Fig. 1). The other colonies were too small and/or not studied long enough to include in this study. Colony 2 was the only colony that was active during the entire study period with enough data to analyse separately. No data were collected during breeding seasons 2006 and 2007. The count and productivity data from the different colonies were aggregated per year and subsequently treated as observations of one population, as were the capture-mark-recapture data. Therefore, colony identity was not retained.

Capture-mark-recapture data

I used capture-mark-recapture (CMR) data of adults and juveniles. Individuals ringed as nestlings were considered juveniles during the season they were ringed in, even if they moulted into adult plumage before the start of the next breeding season or were ringed at the end of a long breeding season. The latter would have survived day 17 to 30 - the period of highest mortality for juveniles (Paquet 2013) - before next season's colony captures. The sociable weaver is a monomorphic species that can only be sexed through DNA examination (Doutrelant *et al.* 2004). Only a proportion of the study population was sexed: 587 juveniles (22.8%) and 894 adults (31.7%). Therefore, I had to assume that survival was not sex-dependent.

During breeding seasons 1993-2013 2577 juveniles were ringed (1257 recaptures) and 2821 adults (2517 recaptures). No individuals were captured during season 1997, 2006 and 2007 and no adults during 2005. For colony 2 451 juveniles were ringed (82 recaptures) and 442 adults (219 recaptures).

Population counts

Colony size was determined by adding the number of escaped adults to the number of adults captured during the colony capture. If a colony was captured more than once a year, a mean was used (Spottiswoode 2007). In 1997 the resident colony members were counted, not captured. Colony sizes ranged from 3 to 211 individuals. Not all colonies were captured from the start of the study period (see Table A1). Therefore, I treated the addition of 'new' colonies as permanent immigration into the study population (see Data analysis - Integrated population model).

The population model used in this analysis is female-based. Doutrelant *et al.* (2004) investigated the sex ratio at the study site and found no difference from parity. Therefore, 50% of the sum of the annual colony counts represented the annual number of females in the study population (hereafter 'population count'; Table A1).

The study period 1993-2013 consisted of 370 potential colony counts, i.e. colony/year combinations, from the first capture of each colony (Table A1). Of those 370 colony/year combinations 65 were zero, because the colonies were not inhabited (Table A1); 42 colony counts were missing. These were interpolated (bold numbers in Table A1). If the gap was one year, a mean was used of the counts of that colony before and after the gap. If the gap was more than one year, I used linear interpolation to estimate the missing colony sizes. This method assumes that the observed colony counts are known points on a straight line, missing counts can then be estimated. The population counts (i.e. the sum across all colonies) were treated as a pre-breeding census and ranged from 164 (2013) to 414 (2009). For colony 2 population counts ranged from 3 (2013) to 106 (1993).

Productivity data

The analysis required productivity data - the number of fledglings produced by the population - of the entire breeding season, which was measured in season 1999 (for 14 out of 19 active colonies), 2000 (16/18), 2010 (14/17), 2011 (13/17), 2012 (14/16) and 2013 (12/12). Because the population count was pre-breeding and survival cannot be estimated for the last year of the study (Lebreton *et al.* 1992), productivity data for 2013 were not used in the analysis. Productivity ranged from 12 fledglings in breeding season 2011 to 369 fledglings in breeding season 2013, the maximum of the data used in the analysis was 237 in 1999. For colony 2 productivity ranged from 2 (2011, 2012) to 45 (1999).

Climatic data

Weather data were obtained from the weather station at Kimberley Airport, ca. 10 km from the centre of the study site at the same elevation (courtesy of the South African Weather Service). du Plessis *et al.* (2012) found that birds were not affected by short-term exposure to extreme heat, but that prolonged exposure did reduce their foraging efficiency resulting in a loss in body mass. Therefore, I used the hottest month per interval as a climate index of extreme heat. Maximum daily temperature (degrees Celsius) was averaged per month. Subsequently, the maximum (hereafter 'tmax') was determined of those monthly means in the period of the first month of capture of a season to the month before the next season's first capture (time interval): the seasonal range during the study period was 32.2 to 35.8 ^{0}C. Since the thermoregulatory effect of the nest structure is larger in winter than in summer (Bartholomew *et al.* 1976), I used a more extreme measure of cold than minimum monthly temperature: the maximum number of monthly frost days. The number of frost days (daily minimum temperature below 0 ^{0}C) was aggregated per month and the maximum number of monthly days during the time interval was determined ('frost'): range 9 to 24 days. These climate indices were used in both the survival and fecundity model. Rainfall (millimetres) was aggregated over the time interval (seasonal ppt: 's.ppt'): range 229.9 to 1406.6 mm. Because the time intervals were unequal, total rainfall was divided by the time interval to estimate annual rainfall for the survival model ('a.ppt'): range 270.8 to 793.4 mm. Seasonal rainfall (s.ppt) was used in the fecundity model. All climate indices were standardized (units of standard deviation). Since no data were collected during the breeding seasons 2006 and 2007, the 2005 interval runs from the first month of breeding season 2005 to the month before the first capture of the 2008 breeding season.

None of the climate indices showed a trend over the study period (Pearson's product moment correlation (PC) tmax and frost: $P \geq 0.26$, cor = 0.28/0.11); s.ppt: Spearman's rank correlation test: $P = 0.93$, cor = -0.02). The climate indices were not correlated ($P \geq 0.08$, cor = -0.43 - 0.11).

Data analysis

Survival

To determine a general or structural reference model that fitted the structure in the data (Grosbois *et al.* 2008) a goodness-of-fit (GOF) test was performed in program U-CARE 2.3.2 (Choquet *et al.* 2009) of the global Cormack-Jolly-Seber (CJS) model for open populations (Cormack 1964; Jolly 1965; Seber 1965) for each 'age at initial capture' dataset (juveniles and adults). This model with time-dependent survival and recapture - ϕ(t)p(t) - assumes homogeneity in survival and recapture (Lebreton *et al.* 1992). Because mortality cannot be separated from permanent emigration, estimated survival is apparent or local survival (hereafter 'survival'; Lebreton *et al.* 1992). For both groups the GOF test was significant (Global test: $\chi^2_{123} = 469.88$, $P = 0$). For 'ringed as juveniles' this pertained to the directional z-test for transience (3.SR: $\chi^2_{14} = 143.17$, $P = 0$) and the trap-dependence test (2.CT: $\chi^2_{13} = 71.99$, $P = 3.44\text{e-}10$); for 'ringed as adults' to the transience test ($\chi^2_{15} = 26.25$, $P = 0.04$), the trap-dependence test ($\chi^2_{12} = 139.64$, $P = 0$), and test 3.SM ($\chi^2_{21} = 55.65$, $P = 5.68\text{e-}05$).

Visual inspection of the individual encounter histories revealed a pattern of captures followed by one or more absences. Due to the missing colony captures some individuals (inhabiting certain colonies) were not available for recapture: they temporarily 'emigrated' from the study site by residing at a colony that was not sampled in a particular year (Burnham 1993). Thus, the survey method created an effect of non-random emigration, which will bias survival estimates in an open population model (Kendall *et al.* 1997). Therefore, I used a multi-state model to account for temporary emigration in which recapture is conditional on being present (Fujiwara & Caswell 2002; Kendall & Nichols 2002; Schaub *et al.* 2004; Gimenez *et al.* 2007). Since individuals were not truly absent, survival was modelled as state-independent. The state transition matrix is given by:

	True state (*t*+1)		
True state (*t*)	Present	Absent	Dead
Present	$\phi\ (1 - \Psi_{10})$	$\phi * \Psi_{10}$	$1 - \phi$
Absent	$\phi * \Psi_{01}$	$\phi\ (1 - \Psi_{01})$	$1 - \phi$
Dead	0	0	1

(ϕ = survival, Ψ_{10} = transition from 'present' to 'absent' - temporary emigration, Ψ_{01} = transition from 'absent' to 'present' - temporary immigration) and the observation matrix by:

	Observed state (*t*+1)	
True state (*t*)	Seen	Not seen
Present	p	$1 - p$
Absent	0	1
Dead	0	1

(p = recapture).

Subsequently, I defined a hierarchical model to estimate survival with a mean and random temporal effect per age group (juveniles and adults):

$$\mathrm{logit}(\phi_{Age,\,t}) = \mu_{Age} + \varepsilon_{Age}(t) \qquad \text{(eqn 1)}$$

where $\phi_{Age,\,t}$ is the survival probability per age group from year t to year t+1, μ_{Age} overall mean survival per age group on the logit scale, and $\varepsilon_{Age}(t)$ the temporal random effect per age group on the logit scale. The temporal random term is assumed to have a Normal distribution: $\varepsilon_{Age}(t) \sim N(0, \sigma^2_{Age})$. σ^2_{Age} is the temporal variance in age-specific survival. I report annual survival probabilities as estimated by the model, i.e. not converted into seasonal estimates, to facilitate comparison with other studies.

Because omission of colony captures varied over the years, I treated temporary emigration Ψ_{10} and temporary immigration Ψ_{01} as time-dependent. I had to assume that permanent emigration and immigration from the study area as a whole were balanced, since no data were available on either demographic rate. Sociable weavers rarely move to another colony (Maclean 1973a; Brown *et al.*

2003). Since accounting for movement among the 25 studied colonies would have entailed modelling an extra 600 transition probabilities, this was not feasible with the available data.

Capturing whole colonies at once (see Field methods) might have induced a lack of independence among the residents of a particular colony. The ringing of nestlings before day 17 in a population where 70% or more of all nestlings are depredated by snakes each breeding season (Covas *et al.* 2008) could have created an effect of transience in the dataset 'ringed as juveniles'. Modelling recapture with an individual random effect assured that any residual overdispersion, i.e. not accounted for by the multi-state survival model, would not lead to inflated precision of or a negative bias in the survival estimates (Anderson *et al.* 1994; Kéry & Schaub 2012; Abadi *et al.* 2013). Thus, recapture p was modelled with a mean and individual random effect:

$$\text{logit}(p_i) = \beta + \gamma(i) \qquad \text{(eqn 2)}$$

where p_i is individual recapture, β overall mean recapture on the logit scale, and $\gamma(i)$ the individual random effect on the logit scale. The individual random term is assumed to have a Normal distribution: $\gamma(i) \sim N(0, \sigma^2_\gamma)$. σ^2_γ is the individual variance in recapture on the logit scale.

The GOF test of the colony 2 CMR data was not significant (overall $\chi^2_{48} = 34.30$, $P = 0.93$). Because these data did include missing colony captures (Table A1), survival was modelled as for the whole population (eqn 1), but recapture was modelled with an overall mean and a random temporal effect:

$$\text{logit}(p_t) = \beta + \omega(t)$$

where p_t is temporal recapture, β overall mean recapture on the logit scale, and $\omega(t)$ the temporal random effect on the logit scale. The temporal random term is assumed to have a Normal distribution: $\omega(t) \sim N(0, \sigma^2_\omega)$. σ^2_ω is the temporal variance in recapture on the logit scale.

The transition parameters in the survival model and recapture were considered nuisance parameters.

Fecundity

Fecundity was estimated per adult female, i.e. as an average across breeders and non-breeders, as detailed data on breeding were unavailable. To accommodate the large range of observed productivity fecundity was estimated with a Poison regression:

$$J_t \sim \text{Poisson}(N_t f_t)$$

where J_t is the number of fledglings produced in year t, N_t is the number of estimated adult females at the start of year t - not the observed number of adult females to avoid inclusion of the observation error, and f_t is the fecundity in year t. Fecundity was modelled with a mean and a temporal random effect:

$$\log(f_t) = \alpha + \nu_t \qquad \text{(eqn 3)}$$

where f_t is the fecundity in year t, α overall mean fecundity on the log scale, and v_t the temporal random effect of fecundity on the log scale. The temporal random term is assumed to have a Normal distribution: $v_t \sim \text{Norm}(0, \sigma^2_v)$. σ^2_v is the temporal variance in fecundity on the log scale.

Integrated population model

To link the population size to the demographic rates (age-specific survival and fecundity) I developed a female-based population model with two stages, i.e. the number of 1-year-old females and the number of 2-year-old and older females (Fig. 2). These two stages do not imply a demographic difference: the number of 1-year-old females represents recruitment and allowed me to test the sensitivity of the results to the assumption that all females can be treated the same. There is some evidence that most 1-year-olds do not breed (Covas 2002; Covas *et al.* 2004b).

The projection matrix (Levkovitch matrix; Caswell 2001) is written as:

$$\begin{bmatrix} N_1 \\ N_a \end{bmatrix}_{t+1} = \begin{bmatrix} \phi_J \frac{f}{2} & \phi_J \frac{f}{2} \\ \phi_A & \phi_A \end{bmatrix}_t \begin{bmatrix} N_1 \\ N_a \end{bmatrix}_t$$

where N_1 is the number of 1-year-old females, N_a the number of 2-year-old and older females, ϕ_J juvenile survival, ϕ_A adult survival, and f is the number of fledglings produced per adult female, divided by 2 because the projection matrix only considers females and the sex ratio in the population was even (Doutrelant *et al.* 2004). In this analysis, where the census data is pre-breeding, survival is from year t to t+1 and fecundity pertains to year t. The 'age at first breeding' sensitivity analysis set fecundity of 1-year-olds to zero (upper left hand corner of the matrix, i.e. $\phi_J * f/2 * N_1$). Correlation of the vital rates between the two models would then signify that the 'full' model is robust to this assumption.

The population model was translated into an integrated population model (Besbeas *et al.* 2002, 2003; Schaub *et al.* 2007; Abadi *et al.* 2010; review in Schaub & Abadi 2011) in which N_1 in year t+1 was modelled with a Poisson distribution as:

$$N_{1,\,t+1} \sim \text{Poisson}(N_{1,t}\,\phi_{J,t}\,(f_t/2) + N_{a,t}\,\phi_{A,t}\,(f_t/2)) \qquad \text{(eqn 4)}$$

(see above for parameter explanation). The number of 2-year-old and older females N_a is bounded by zero, when no females survive, and N_a in year t, when all females survive. Therefore, N_a was modelled with a Binomial distribution as:

$$N_{a,\,t+1} \sim \text{Binomial}(N_{1,t} + N_{a,t},\, \phi_{A,t}) \qquad \text{(eqn 5)}$$

To account for the study area expansion when new colonies were added to the study population (Table A1) I added the number of new females to the estimated population size at year t + 1:

$$Ntot_{t+1} = N_{1,t+1} + N_{a,t+1} + \text{new females}_{t+1}$$

Fecundity was estimated based on the estimated number of adult females before the new females were added, thereby ensuring that the model did not try to accommodate this 'surge' in new females. Population growth rate from year t to year $t + 1$ (λ) was based on the estimated population size of year t and year $t + 1$ before the new females were added to avoid treating the new females as population growth:

$$\lambda_t = (N_{1,t+1} + N_{a,t+1}) / (N_{1,t} + N_{a,t})$$

The observation process was modelled with a Normal distribution for the observation error, since I did not assume that the observation error differed between large and small colonies, thus, the population count data (y) was modelled as:

$$y_t = N_{1,t} + N_{a,t} + \text{new colonies}_t + \eta_t$$

where η_t is the temporal random effect, which is assumed to have a Normal distribution: $\eta_t \sim \text{Norm}(0, \sigma^2_\eta)$. The variance σ^2_η is then the observation error.

To investigate which demographic parameter(s) had the greatest impact on the observed population dynamics I conducted a retrospective sensitivity analysis (Caswell 2001). I correlated each simulation of the parameter estimates (posterior distribution) of population growth rate with those of age-specific survival and fecundity. The correlations reported are the posterior modes of those correlations, together with the probability of a positive correlation. The correlations give an indication of the degree of influence of the temporal variation of the respective vital rate on the temporal variation of population growth rate (Robinson *et al.* 2004; Freeman *et al.* 2007; Schaub *et al.* 2012).

To compare the variances of age-specific survival on the logit scale and fecundity on the log scale I back-transformed the variances on the logit/log scale using the Delta method:

$$\sigma^2_\theta = \sigma^2\theta^2(1 - \theta)^2$$

where σ^2_θ is the back-transformed variance, σ^2 the demographic parameter-specific variance on the logit/log scale, and θ the back-transformed mean of the demographic parameter (Powell 2007; Kéry & Schaub 2012).

I conducted a population viability analysis by extending the time indices in the state part of the population model (eqn 4 + 5) and of the priors of survival (eqn 1), recapture (eqn 2), and fecundity (eqn 3). Future estimates of the vital rates can be estimated from the distributions of the means and random effects (Kéry & Schaub 2012). I added 5 years to the study period of 19 years (seasons) to investigate the near future of this declining population and of colony 2 (Altwegg *et al.* 2014). The posterior distribution was used to estimate extinction probability in the near future by estimating the mean of estimated population sizes of zero (before the addition of new colonies).

Climatic correlates

To investigate whether temporal variation in the demographic rates was caused by climatic variation I developed a mixed-effect model by constraining the survival and fecundity rates to be a linear function – on the link scale: logit for survival and log for fecundity – of the climatic covariates in residual variance models using a fixed climatic effect and the random temporal effect. The slope of the standardized covariate (regression coefficient) gives the expected change on the logit/log scale in the demographic rate, when the covariate changes by 1 standard deviation (Grosbois *et al.* 2008). The amount of total temporal variance explained by the climatic variance can then be estimated by comparing the total temporal variance models (eqn 1/eqn 3) with the residual variance models (Loison *et al.* 2002):

$$C = 1 - (\hat{\sigma}^2_\delta \text{ (res)}/ \hat{\sigma}^2_\delta \text{ (total)})$$

where C is the fraction of temporal variance explained by climatic variance, $\hat{\sigma}^2_\delta$ (res) is the temporal variance in the mixed-effect model and $\hat{\sigma}^2_\delta$ (total) is the variance in the model with only a temporal random term.

The CMR and population models were formulated as state-space models (Buckland *et al.* 2004; Gimenez *et al.* 2007). All models were implemented in a Bayesian framework with vague priors for all parameters (Kéry & Schaub 2012). Overall mean age-specific survival and recapture were specified with normal priors with a mean of zero and a precision of 0.0001 bounded by [-10, 10] on the logit scale, as for overall mean fecundity on the log scale; standard deviations of age-specific survival and recapture with uniform priors on the logit scale - U[0, 5], of fecundity on the log scale - U[0, 10], and of the population count - U[0, 50]; temporal transition probabilities in the survival model with U[0, 1] on the probability scale; regression coefficients with U[-5, 5]; initial population sizes of the population with normal priors based on the first population count of 297 with a mean of 100 for N_1 and a mean of 197 for N_a and a precision of 0.001 bounded by [0,] and of colony 2 with a mean of 45 for N_1 and a mean of 71 for N_a.

Models were run with three chains. The total variance model was run with 200,000 iterations, a burn-in of 100,000 and a thinning rate of 20 (posterior distribution of 15,000 iterations); the residual variance models were run with 100,000 iterations, a burn-in of 50,000 and a thinning rate of 20 (posterior distribution of 7,500 iterations), as were the models for colony 2.

Models were run in WinBUGS 1.4 (Spiegelhalter *et al.* 2003) from R 3.1.1 (R Core Team 2014) using R2WinBUGS 2.1-19 (Gelman *et al.* 2011). The Brooks-Gelman-Rubin diagnostic statistic (Brooks

& Gelman 1998), trace, density, and autocorrelation plots of the posterior distributions and the MC errors were checked to confirm convergence.

Results

Survival

In the population mean juvenile survival probability was 0.43 (95% credible interval (CRI): 0.32-0.55) with a temporal variance of 0.77 (0.29-1.83) on the logit scale. Annual apparent juvenile survival probability ranged from 0.21 (0.14-0.28) in 2005-2006 to 0.68 (0.55-0.81/0.54-0.82) in 1995-1996 and 2008-2009 (Fig. 3). Mean adult survival was 0.66 (0.61-0.71) with a temporal variance of 0.21 (0.08-0.48) on the logit scale. Annual adult survival ranged from 0.47 (0.41-0.54) in 2003-2004 to 0.77 (0.68-0.87) in 1996-1997 (Fig. 3). Mean recapture was 0.88 (0.83-0.93) with an individual variance of 2.53 (1.00-5.20) on the logit scale. Temporal emigration ranged from 0.04 (0.001-0.15/0.002-0.12) during 2003-2004 and 2010-2011 to 0.997 (0.989-1.00) during 1996-1997 and 2004-2005. The upper range was clearly caused by the absence of adult captures in the following seasons, which caused a similar but opposite pattern in temporary immigration. Temporary immigration ranged from 0.02 (0.001-0.08) in 1996-1997 to 0.91 (0.75-0.996) in 2009-2010. The model therefore appears to correctly account for the uneven sampling effort. Age-specific survival of colony 2 was similar to that of the population (Fig. A1 in the appendix).

Fecundity

In the population mean fecundity was 0.65 fledglings per female (95% CRI: 0.39-0.99) with a temporal variance of 0.98 (0.41-2.14) on the log scale. Seasonal fecundity ranged from 0.05 (0.03-0.09) in 2011 to 1.68 (0.85-2.78) in 2005 (Fig. 4). Fecundity of colony 2 was similar to that of the population (Fig. A2 in the appendix).

The estimated number of fledglings produced by all females - the product of the estimated number of adults and estimated fecundity - was similar to the observed number of fledglings per season (Fig. 5).

Population dynamics

The pre-breeding population sizes estimated by the integrated population model were close to the observed population counts for both the population and colony 2 (closed circles in Fig. 6; the open circles in the population graph represent the estimated population size before the new colonies were added). The observation error of the population estimates was 193 (0-1117). Recruitment (1-year-old females) ranged from 5 (95% CRI: 1-11) before the start of the breeding season in 2012 to 178 (117-

238) in 2008. Population size of 2-year-old and older females ranged from 110 (94-133) in 2013 to 296 (258-332) in 2009. Mean population growth rate was 0.994 (0.985-1.009) and ranged from 0.75 (0.67-0.90/0.70-0.84) from 2002 to 2003 and 2011 to 2012 to 1.48 (1.27-1.77) from 2004 to 2005.

The IPM was robust to the assumption that 1-year-old females are capable of breeding. When fecundity of 1-year-olds was set to zero, all vital rates and population sizes of 1-year-old (N1) and 2-year-old and older females (Nad) of this IPM and the 'full' IPM were highly correlated ($P < 0.001$, cor range 0.93-0.999; see Fig. A3 for a comparison of fecundity, N1 and Nad of the two IPM's).

The observation error of the colony 2 estimates was 93 (5-339). Mean population growth rate was 0.88 (0.82-0.93) and ranged from 0.46 (0.18-0.81) from 2010 to 2011 to 1.21 (0.69-1.93) from 2005 to 2008 (since there was no data collection at all during seasons 2006 and 2007, this period was ignored in the IPM). The population of colony 2 was clearly declining over the study period 1993-2013 (PC: $t_{17} = -16.23$, $P < 0.001$, cor = -0.97 (95% CI: -0.98 - -0.92); Fig. 6).

The retrospective sensitivity analysis indicated that the growth rate of the population was not influenced by age-specific survival: the 95% credible intervals of the correlation with both vital rates spanned zero (Fig. 7). Fecundity, however, showed a positive correlation with population growth rate indicating that the observed population dynamics were most influenced - relatively as the correlation was not strong (P ($cor > 0$) = 0.56 - by variability in this vital rate (Fig. 7). Back-transformed variance of juvenile survival was 0.046, of adult survival 0.010, and of fecundity 0.051.

Estimated juvenile survival was not correlated with either adult survival or fecundity ($P \geq 0.37$, cor = -0.11-0.22). Adult survival, however, was slightly, negatively, correlated with fecundity (PC: t_{16} = -2.76, $P = 0.01$, cor = -0.57 (95% CI: -0.82 - -0.14).

Projecting the estimation of population size five years into the future indicated that the sociable weaver population will recover (Fig. 8). However, the uncertainty of the projections rapidly increased to such an extent that this inference is rather tenuous. To illustrate, the 95% credible interval (CRI) for the population size of 220 females before the start of breeding season 2018 was 24 to 927. Extinction risk in the near future was zero, i.e. none of the simulations predicted a population size of zero during the projected five years.

The near future of colony 2 appeared one of further decline (Fig. 8). The 95% CRI's indicated that the uncertainty included extinction in all five years (lower 95% CRI = 0, Fig. 8). The extinction risk increased slowly: 0.05 in 2014, 0.11 in 2015, 0.18 in 2016, 0.26 in 2017, and 0.33 in 2018. Mean extinction probability was 0.18 over 2014-2018.

Climatic correlates

The demographic parameters of the population of 25 sociable weaver colonies at Benfontein were not correlated with any of the indices of extreme weather (Table 1). All 95% credible intervals included zero (Table 1). Fig. A4 in the appendix shows the patterns of the demographic parameters and the climatic covariates over the study period.

For colony 2 I did find several climatic indices that explained a considerable fraction of the temporal variance of the demographic rates (C in Table 1). Years that were warmer than average were negatively correlated with juvenile survival (tmax in Table 1). This climate index explained 59% of the temporal variation in juvenile survival (total temporal variance on the logit scale = 0.85 (95% CRI: 0.06-3.12), residual temporal variance = 0.35 (0.00-2.08); C in Table 1). Longer or more 'cold snaps' were negatively correlated with both adult survival and fecundity (frost in Table 1). This climate index explained 58% of the temporal variation in adult survival (total temporal variance = 0.41 (0.01-1.35), residual temporal variance = 0.17 (0.00-0.71)) and 53% of the temporal variance in fecundity (total temporal variance = 0.57 (0.001-1.99), residual temporal variance = 0.27 (0.001-1.15); C in Table 1). Wetter years were negatively correlated with adult survival (ppt in Table 1). This climate index explained 41% of the temporal variation in adult survival (total temporal variance = 0.41 (0.01-1.35), residual temporal variance = 0.24 (0.001-1.00); C in Table 1).

Discussion

This study investigated the population dynamics and the influence of climatic stochasticity on those dynamics of a population of 25 colonies of sociable weavers during 1993-2014. Population growth rate was driven by fecundity during the study period. There was no discernible correlation between climatic variation and population dynamics, but climatic extremes did have a large impact on the vital rates of the largest colony.

The population growth rate of the sociable weaver is most sensitive to variation in survival and least sensitive to variation in fecundity (Altwegg *et al.* 2014). In accordance with Pfister's (1998) life history tenet - the vital rate with the highest sensitivity exhibits the least variation, and vice versa - I found that temporal variation in adult survival was low (0.01) compared to the variation in fecundity (0.05) and that variation in fecundity contributed most to the observed variation in population growth rate. The correlation between fecundity and population growth rate was not strong, which could have been a result of the weak negative correlation between fecundity and adult survival (Doak *et al.* 2005).

The cooperative breeding strategy of the sociable weavers may help to buffer adult survival against environmental stochasticity. During the breeding seasons 1999 and 2000, the findings of

Covas *et al.* (2008) suggested that parents reduced their feeding effort in the presence of helpers. During the breeding seasons 2000 to 2013 Paquet *et al.* (2015) found that survival of younger females was higher in the presence of helpers. In a population of Ground Tits *Pseudopodoces humilis* on the Tibetan Plateau survival of parents with helpers was higher than that of those without helpers (Li *et al.* 2015). At Benfontein females also reduced their reproductive investment in the presence of helpers by laying lighter eggs (Paquet 2013). Russell *et al.* (2007) observed the same strategy in superb fairy-wrens *Malurus cyaneus*. These studies suggest that cooperative breeders trade off fecundity against survival, which would result in low variation in adult survival despite varying environmental stochasticity.

I did not find any climatic correlates at the population level. The assumption that all adult females breed, while in fact - especially after a good breeding season resulting in large recruitment - a large segment of the adult female population might not breed (1-year-olds) regardless of favourable climatic conditions, could have obscured a correlation between fecundity and the environment. If colonies respond differently to climatic stochasticity as suggested by Altwegg *et al.*'s (2014) findings, this would result in an absence of climatic correlates at the population level. This premise is further substantiated by the climatic correlates found for all demographic parameters in colony 2.

As hypothesized, juvenile survival in colony 2 was lower during years with extremely high temperatures; this climate index explained more than half of the temporal variation during the study period. Higher temperatures would force parents, and independent juveniles, to extend their thermal refuge period in the nest structure to avoid hyperthermia and dehydration. This would decrease their foraging time resulting in less food for (in)dependent juveniles. Extreme heat would also increase evaporation of surface water. Collias & Collias (1978) observed that juvenile sociable weavers drank water more frequently than adults and inferred that they might need more water than adults. Fecundity was not correlated with extreme heat. Less food could have had a detrimental effect on the number of nestlings fledging, but Maclean (1973d) and Covas *et al.* (2008) observed that brood failure is high in this species and most of it is attributed to nest predation by snakes. Reduced body condition or starvation through less food of nestlings would then only have had a minor impact on fecundity.

As expected cold snaps were negatively correlated with adult survival and fecundity in colony 2 and explained more than half of the temporal variation in both demographic parameters. Similar to the effect of extreme heat, extreme cold would decrease foraging time at a time when food is generally scarce and adult condition already lessened by the demands of the breeding season. Unlike extreme heat, extreme cold did have a negative effect on fecundity. In winter nestlings are no longer depredated by snakes but many die of starvation (Maclean 1973c). Less foraging time for parents would then increase nestling starvation and, thus, have a discernible effect on fecundity.

Rainfall over the interval was negatively correlated with adult survival in colony 2. Since the main rains fall during summer, when evaporation is high, more rain would increase breeding opportunity through increased food supply (Maclean 1969; Lloyd 1999), which would demand more of a larger proportion of adults over a longer period. The slight negative correlation between adult survival and fecundity appears to support this inference. In food supplemented colonies more individuals bred independently, i.e. not as helpers, and at an earlier age (Covas *et al.* 2004b), and egg laying started three weeks earlier than in control colonies (Spottiswoode 2009). Contrary to expectation, rainfall was not correlated with fecundity itself. Fecundity is the end result of several components, i.e. clutch size, hatching success, fledging success, number of broods and breeding season length (Ricklefs 2000). Such an 'aggregate' would not be directly correlated with rainfall, but via one or more of the underlying components. Covas *et al.* (2008) did find that during 1999 and 2000 in 19 colonies more rainfall increased clutch size, improved fledgling condition of pairs without helpers and increased feeding rates of parents.

The integrated population model (IPM) appeared suitable to determine the population dynamics of the population of 25 colonies as the estimated vital rates were similar to those of earlier studies at Benfontein. The model was robust to the assumption that all adult females could be treated the same even though in reality most females do not yet reproduce when one year old. Estimated mean annual adult survival of 0.66 (0.61-0.71) was also found by Covas *et al.* (18 colonies, 1993-2000; 2004a) and similar to the median of 0.62 of Altwegg *et al.* (17 colonies, 1993-2009; 2014). Brown *et al.* (2003) estimated mean adult survival of 0.66 in colonies of 60 or less individuals and 0.75 for larger colonies for the same sample studied by Covas *et al.* (2004a). This study's mean adult survival compared closely to the 0.63 of the similarly-sized bell miner *Manorina melanophrys*, an Australian colonial cooperative breeder, and of the chimney swift *Chaetura pelagica*, a New World cooperative breeder (Beauchamp 2014). Mean annual juvenile survival of 0.43 (0.32-0.55) was comparable to that of three cooperatively breeding Australian passerines: splendid fairywren *Malurus splendens* - 0.34, red-winged fairywren *Malurus elegans* - 0.41, and white-breasted robin *Eopsaltria geargiana* - 0.28 (Rowley & Russell 1991). Mean annual fecundity of 0.65 (0.39-0.99) fledglings per female was similar to the 0.7 of Altwegg *et al.* (2014) based on four years of data of 17 colonies.

Over the study period mean population growth rate of the population was higher than that of colony 2 (0.994 (0.985-1.009) versus 0.88 (0.82-0.93)). The clear declining population trend and lower population growth rate of the colony could reflect the observed pattern of individuals moving from declining colonies to colonies that are doing better (Altwegg *et al.* 2014). Projecting the IPM five years into the future suggested that the population can be expected to increase slightly, although the uncertainty of the estimated future population sizes was large (Fig. 8). After the first projected year the upper limits of the 95% credible intervals were larger than the largest colony size ever observed in this species, i.e. 500 individuals (Maclean 1973a). However, the probability that the population will go extinct was zero. This optimistic picture of the near future of the population could be an artefact of the underlying assumption of the prediction IPM that the demographic processes remain similar to those observed during the study period, i.e. varied around the 1993-2013 mean. The near future of colony 2 appears less bright with an increasing extinction risk (0.05 in 2014 to 0.33 in 2018).

Understanding population dynamics and the effects of environmental stochasticity on the different vital rates has become progressively more important in a world of increasing climatic variation and extremes (Tuljapurkar *et al.* 2003; Boyce *et al.* 2006; IPCC 2014). This study found that variation in fecundity - the demographic rate to which population growth rate is least sensitive (Altwegg *et al.* 2014) - contributed most to observed variation in population growth rate in accordance with life history theory (Pfister 1998; Schmutz 2009). The vital rates of the population were not affected by climatic extremes, but those of a large colony were. If colonies respond differently to the environment, the forecasted increasing climatic variation could synchronize the responses of colonies and, thus, increase the entire population's extinction risk (Bateman *et al.* 2011; Schaub *et al.* 2015). An increase in hot extremes could severely decrease recruitment in this population, since juvenile survival in colony 2 was negatively influenced by periods of extreme heat. Though this could be offset by a forecasted decrease in cold extremes that had a detrimental effect on both adult survival and fecundity in colony 2. Rainfall is forecasted to decrease and commence later (Hulme *et al.* 2001; Niang *et al.* 2014), which would be beneficial to adults, since rainfall had a negative influence on adult survival in colony 2, but coupled with the positive effect of rainfall on clutch size and fledgling condition (Covas *et al.* 2008) less and later rainfall could result in a negative impact on population growth rate through decreased fecundity. Even though total rainfall is forecasted to decrease, extreme rainfall events are likely to continue to increase (Mason *et al.* 1999; DEA 2013; Niang *et al.* 2014). Higher temperatures would then increase humidity, which would put the unique nest mass of this colonial breeder at risk of fermentation (Bartholomew *et al.* 1976).

Although the savanna biome is forecasted to expand in South Africa (DEA 2013), increases in climatic variation and particularly extreme events could adversely affect a habitat specialist like the sociable weaver and a population at the edge of the species' distribution. Investigations into the response of all colonies of this meta-population to climatic stochasticity - in a yet to be developed multi-state integrated population model - and the effects of climatic variation on savanna grasses - essential to the construction of the nest masses - would clarify the future of this species.

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Table 1. Covariate influence on demographic parameters of sociable weavers at Benfontein (1993-2013). Each covariate was fitted in a separate model, simultaneously for the three demographic parameters.

Population	Demographic rate	Covariate	Regression Coefficient[1]	SD	95% CRI		C[2]
					Lower	Upper	
Population	Juvenile survival	tmax	-0.21	0.26	-0.72	0.32	
		frost	-0.03	0.24	-0.46	0.51	
		ppt[3]	-0.02	0.26	-0.54	0.50	
	Adult survival	tmax	0.01	0.13	-0.24	0.25	
		frost	-0.10	0.12	-0.34	0.15	
		ppt[3]	0.13	0.13	-0.13	0.38	
	Fecundity	tmax	-0.23	0.26	-0.76	0.28	
		frost	-0.37	0.24	-0.86	0.09	
		ppt[4]	0.25	0.25	-0.25	0.74	
Colony 2	Juvenile survival	tmax	-0.65	0.34	-1.33	-0.005	0.59
		frost	0.36	0.38	-0.41	1.09	
		ppt[3]	-0.18	0.43	-1.03	0.70	
	Adult survival	tmax	0.18	0.30	-0.38	0.81	
		frost	-0.40	0.20	-0.79	-0.01	0.58
		ppt[3]	-0.48	0.21	-0.88	-0.05	0.41
	Fecundity	tmax	-0.07	0.39	-0.85	0.67	
		frost	-0.45	0.22	-0.90	-0.01	0.53
		ppt[4]	-0.12	0.38	-0.81	0.64	

[1] On the logit scale; [2] Fraction of temporal variance of the demographic parameter explained by the climate index; [3] Annual total; [4] Interval total.

SD, standard deviation; CRI, credible interval; tmax, maximum of monthly maximum temperature over the interval; frost, maximum of monthly number of frost days over the interval; ppt, total rainfall.

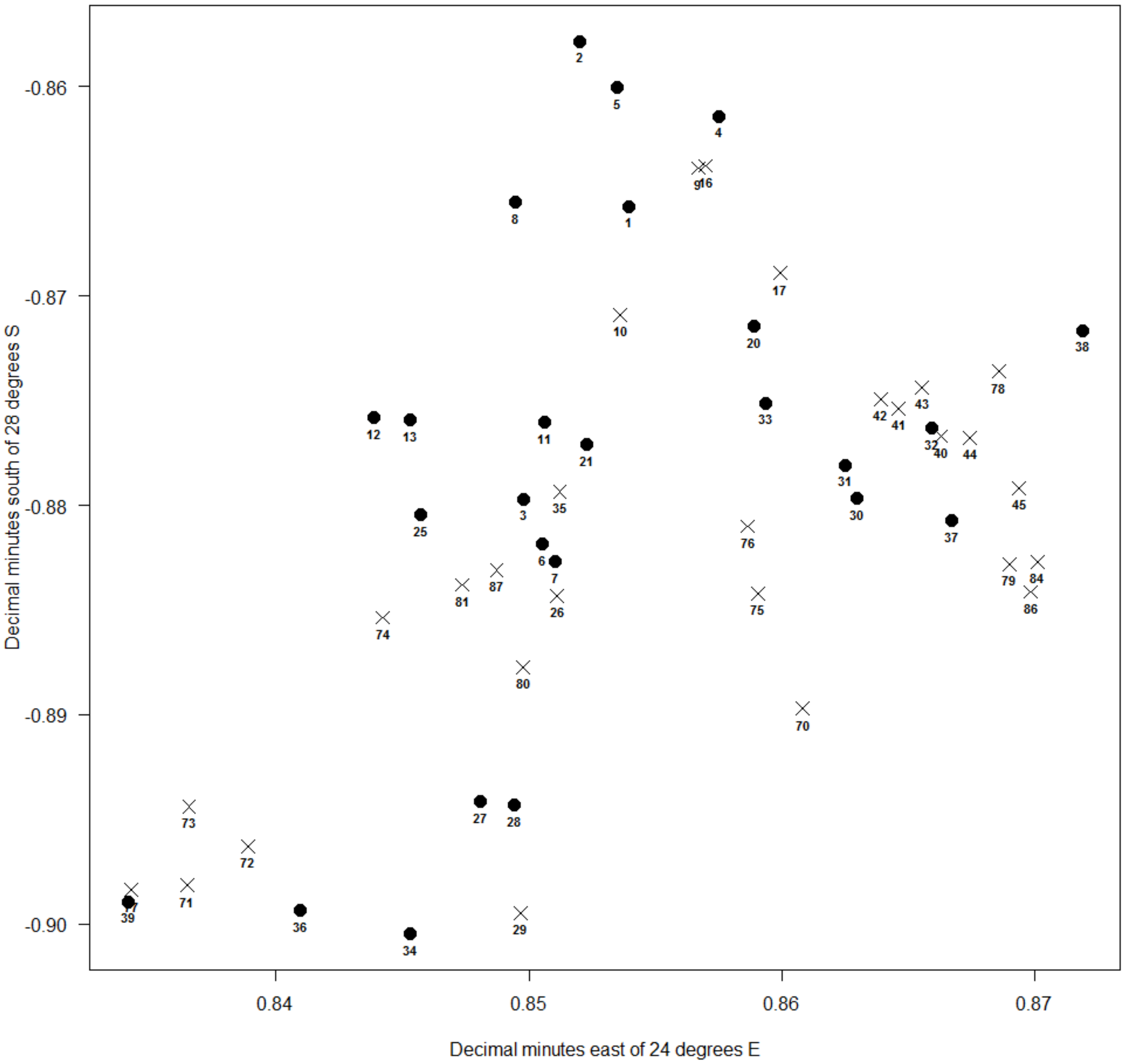


Figure 1. Map of 53 sociable weaver colonies at Benfontein near Kimberley in South Africa (1993-2014), the location is relative to 28°S, 24°E. The black circles represent the 25 colonies used in this study, crosses represent the other colonies in the study area.

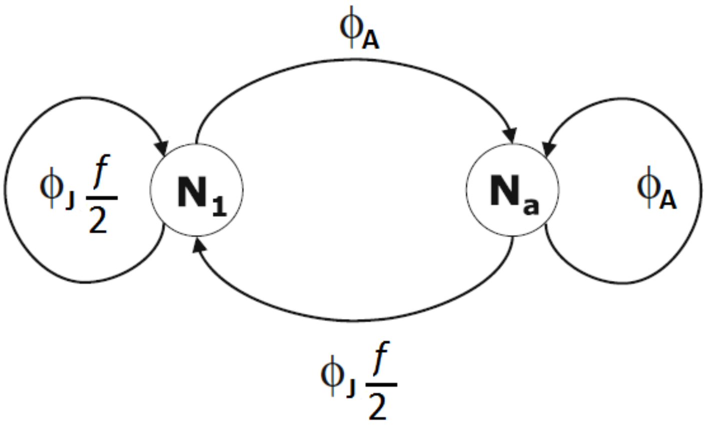


Figure 2. Life cycle graph of the sociable weaver. The population model is female-based with a pre-breeding census and two stages: 1-year-old females (N_1) and 2-year-old and older females (N_a). The demographic parameters are age-specific survival (ϕ_J, ϕ_A) and fecundity (*f*).

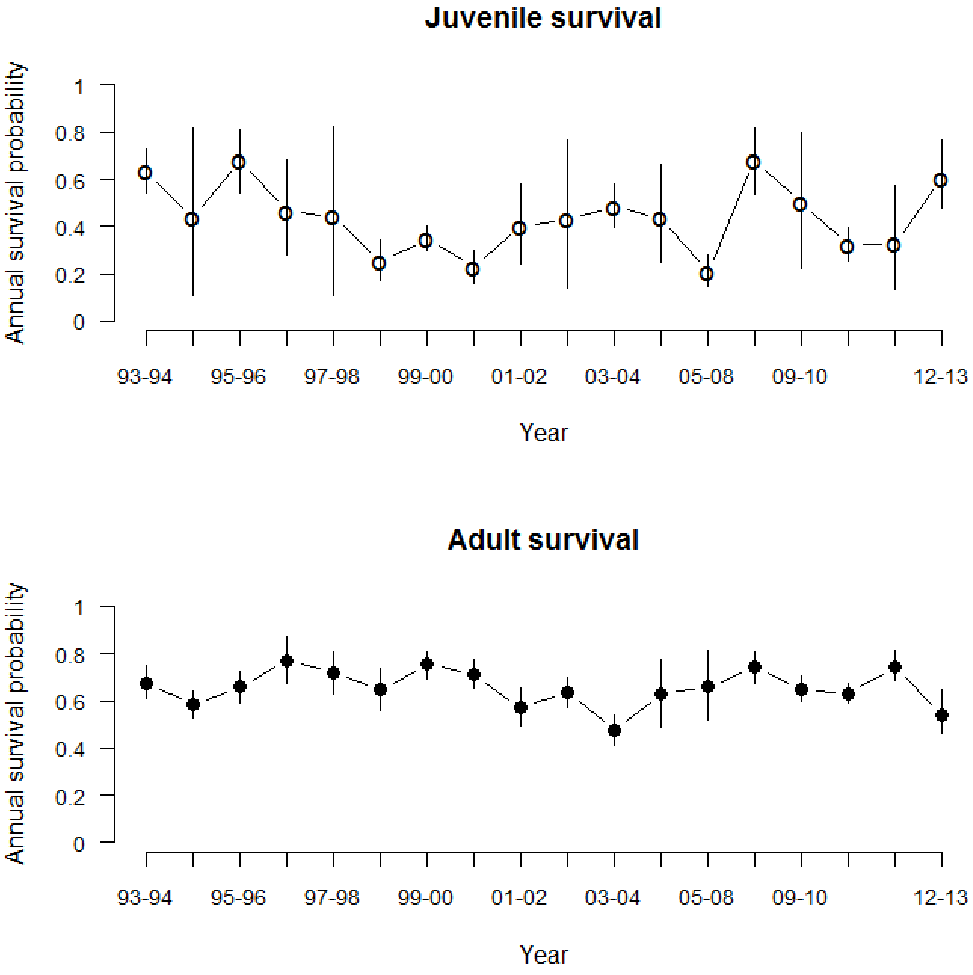


Figure 3. Annual apparent survival of juveniles (open symbols) and adults (closed symbols) of the population with 95% credible intervals (vertical lines) of the sociable weavers at Benfontein (1993-2013).

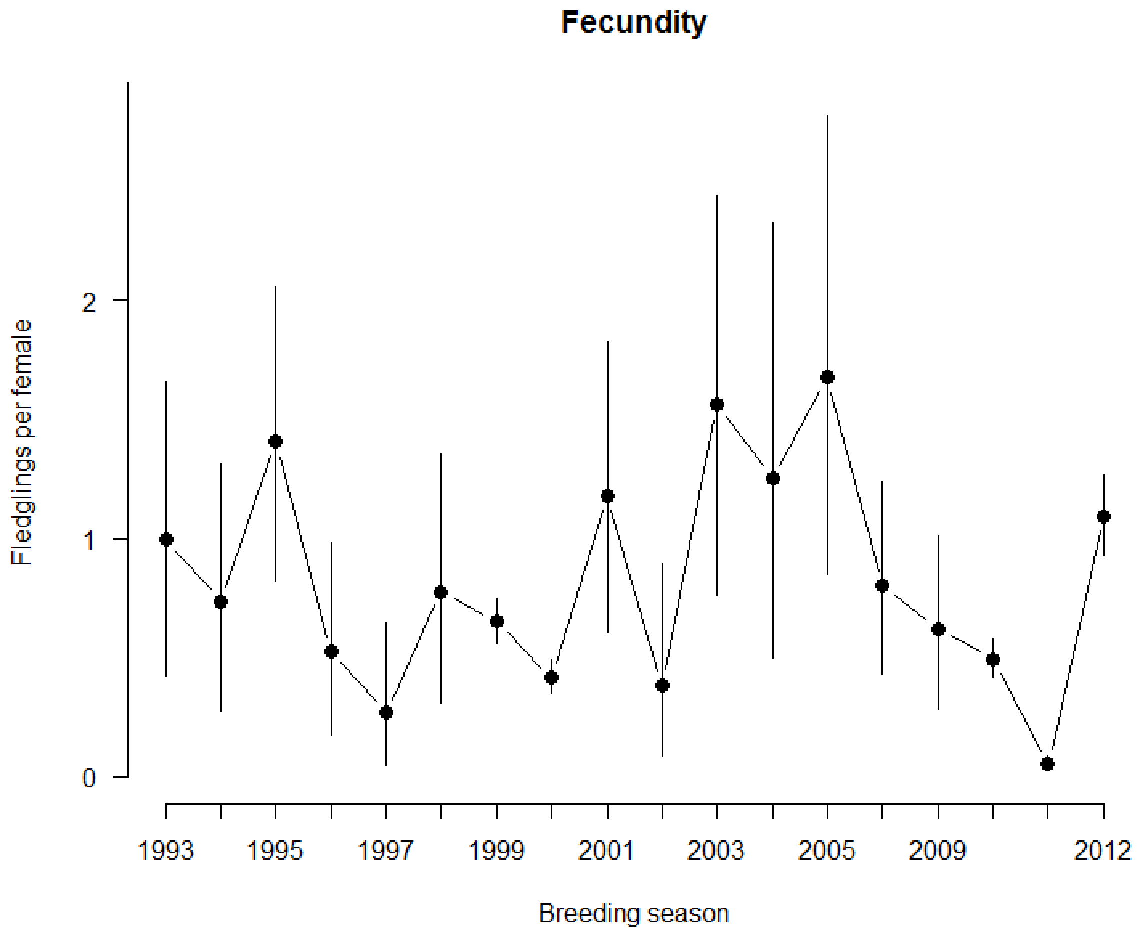


Figure 4. Fecundity (number of fledglings per adult female) of the population with 95% credible intervals (vertical lines) of sociable weavers at Benfontein (1993-2012).

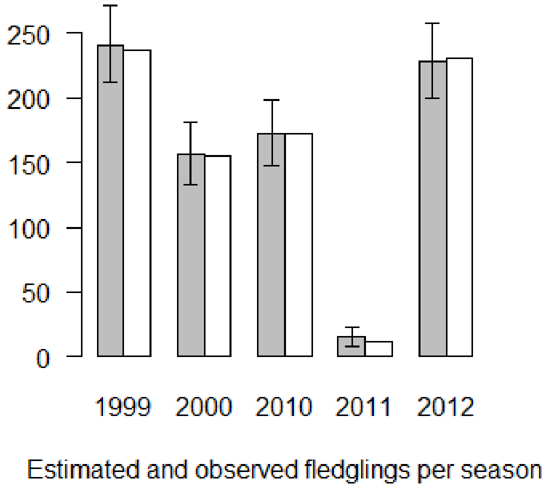
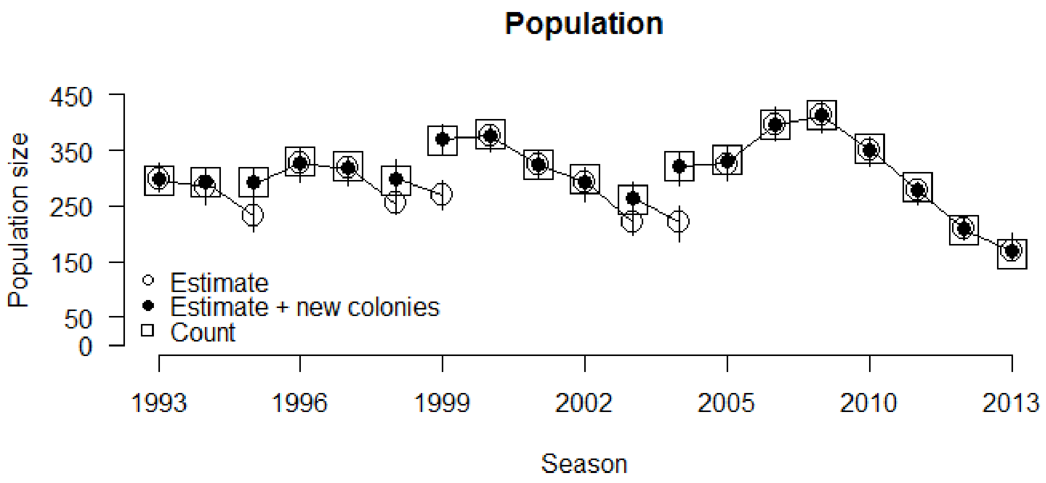


Figure 5. Comparison of the number of fledgling produced by all adult females per season estimated by the integrated population model (dark-grey bars) and observed (open bars) for the five breeding seasons with data.



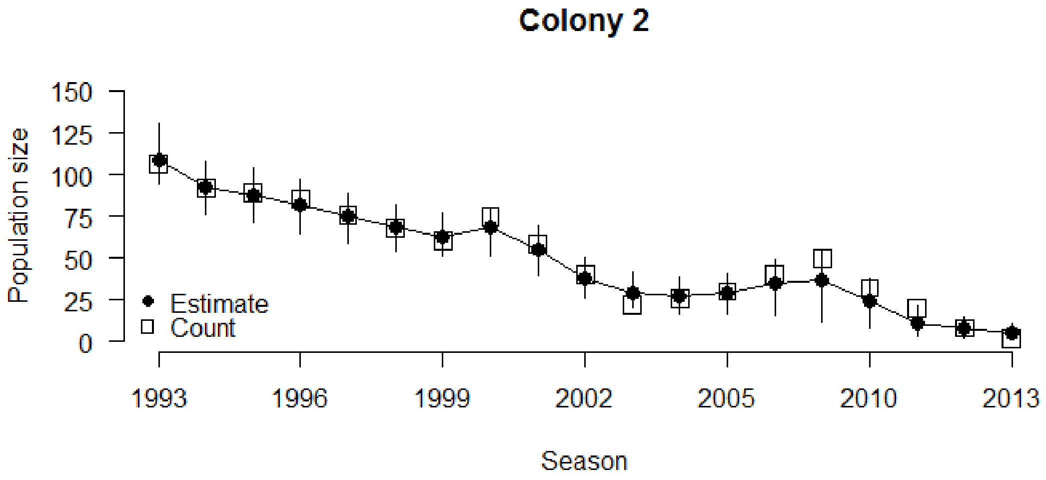


Figure 6. Observed (open squares) and estimated population sizes (open circles of the population and closed circles of colony 2) with 95% credible intervals (vertical lines) of the sociable weaver population at Benfontein (1993-2013). The closed circles in the population graph are estimated population sizes plus new colonies (study area expansion). Note the different scales of the y-axis.

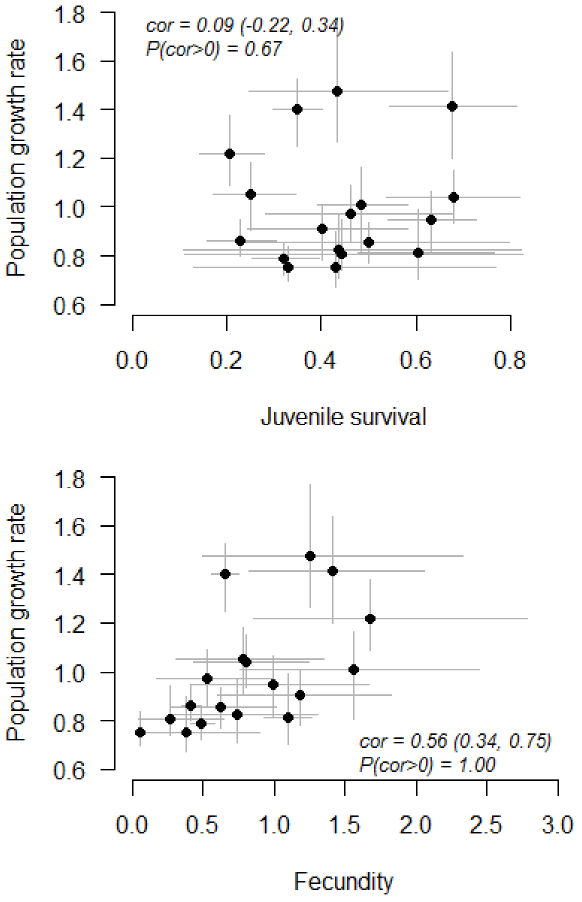
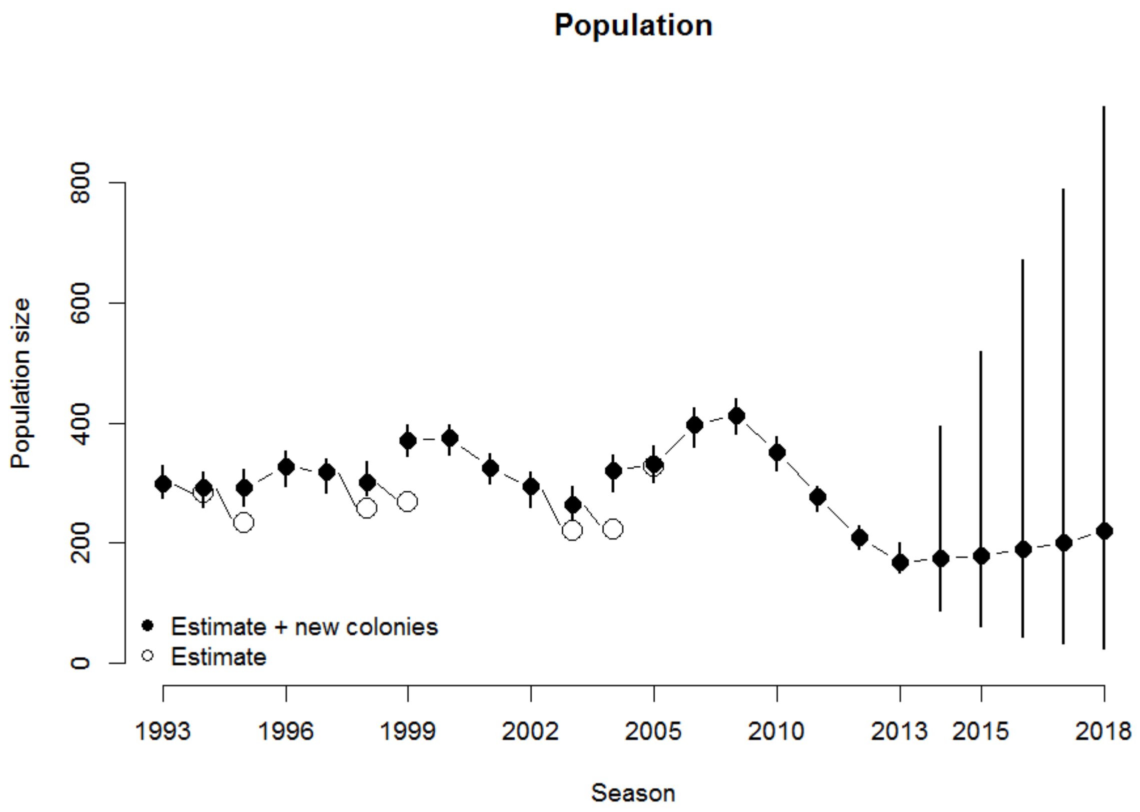


Figure 7. Estimated demographic parameters plotted against population growth rate. The legend shows the posterior mode of the correlation (cor) with 95% credible intervals and the probability of a positive correlation.



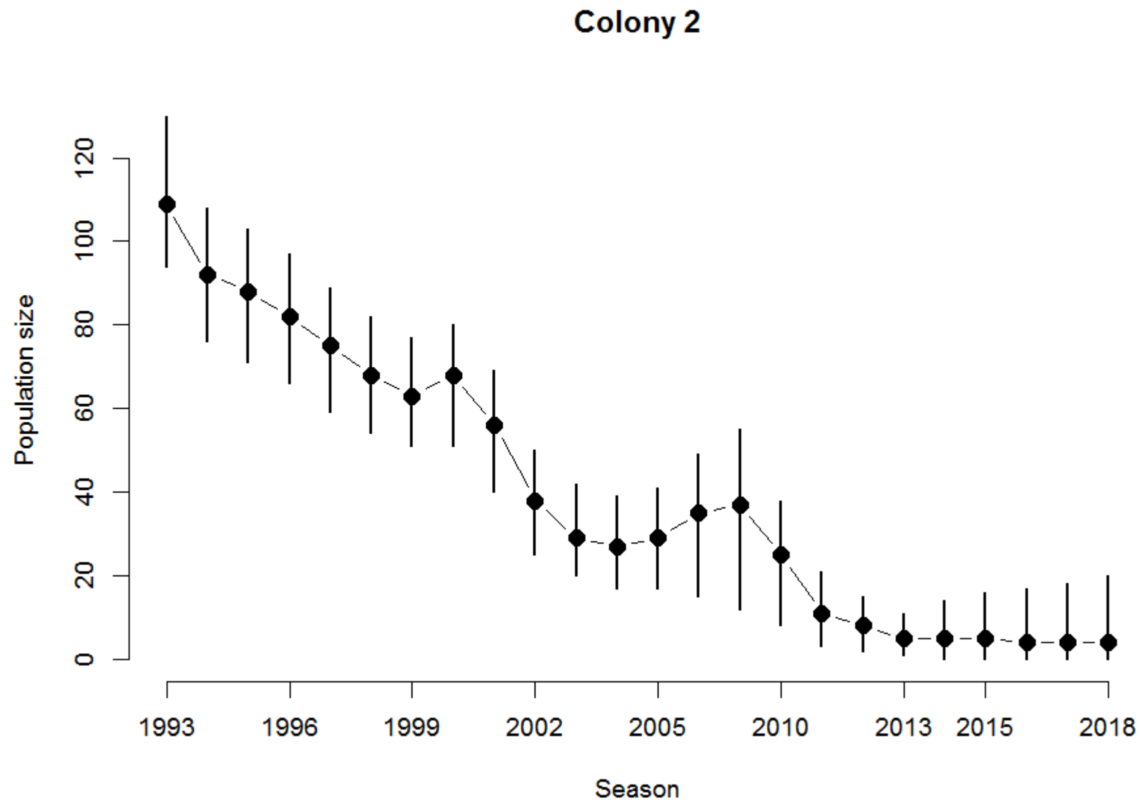


Figure 8. Estimated population sizes (1993-2013) and projected population sizes (2014-2018) with 95% credible intervals (vertical lines) of the population and colony 2.

Appendix

Table A1. Colony sizes of 25 sociable weaver colonies at Benfontein (1993-2014). Bold colony sizes were interpolated, the colony was not captured that breeding season.

	Breeding season																			
Col	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**00**	**01**	**02**	**03**	**04**	**05**	**06 07**[1]	**08**	**09**	**10**	**11**	**12**	**13**
1	42	37	22	21	30	20	15	12	**9**	6	6	0	0		0	0	0	0	0	0
2	211	185	**178**	170	**153**	**137**	120	150	**115**	80	45	53	60		**80**	100	65	40	15	5
3	58	38	17	30	17	20	25	16	13	8	8	0	0		0	0	0	0	0	0
4	77	90	70	80	**68**	56	42	44	12	0	0	0	0		0	0	0	0	0	0
5	12	40	32	24	24	14	21	24	25	10	6	0	0		0	0	0	0	0	0
6	20	20	13	33	27	22	20	25	17	25	11	11	13		12	11	10	6	5	3
7	35	30	30	39	53	32	33	30	**27**	**23**	20	**17**	13		**18**	23	15	7	6	16
8	41	43	37	36	48	30	20	26	40	70	30	22	40		53	61	45	67	40	77
11		17	19	21	**16**	**11**	6	0	**0**	0	4	8	19		**20**	21	12	22	31	40
12	27	19	5	17	19	19	24	21	20	15	4	0	0		0	0	0	0	0	0
13	71	67	43	48	41	33	30	37	**31**	25	12	17	19		15	9	0	0	0	0
20			106	118	127	91	80	72	**60**	**48**	36	22	21		18	21	21	21	25	27
21			11	22	**20**	18	20	24	20	28	23	28	17		0	0	**0**	0	0	9
25							25	28	21	25	20	31	32		32	38	28	31	23	0
27							65	70	**69**	**69**	68	52	18		54	50	36	29	15	22
28							32	35	**35**	35	27	**18**	8		15	17	20	15	0	0
30							25	22	20	23	10	9	10		0	0	0	0	0	0
31							55	**56**	**57**	**58**	**58**	**59**	60		**65**	70	75	70	50	21
32													9		51	43	46	39	25	24
33						87	**78**	**68**	**59**	**49**	**49**	30	39		**39**	**38**	38	34	32	0
34											65	**53**	40		**55**	70	62	38	29	0
36											19	18	13		36	31	20	5	11	0
37												140	116		**99**	**83**	66	57	46	44
38												27	100		**109**	**119**	128	76	53	40
39												31	18		25	23	20	9	9	0
Tot	594	586	583	659	643	590	736	760	650	597	521	646	665		796	828	707	566	415	328
/2	297	293	292	330	322	295	368	380	325	298	260	323	332		398	414	354	283	208	164

Col, colony number; 93, 1993; Tot, total; /2, total count divided by 2 (rounded) used as count in the integrated population model.

[1] No data were collected during 2006 and 2007.

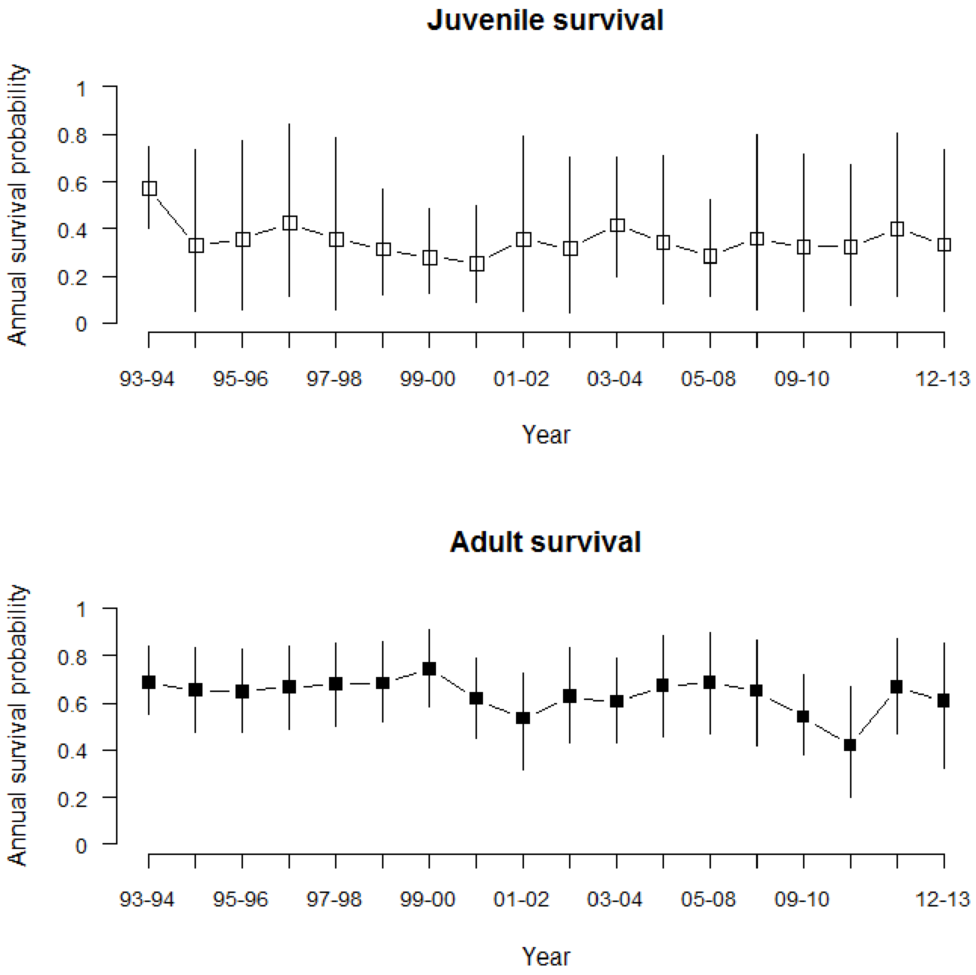


Figure A1. Annual apparent survival of juveniles (open symbols) and adults (closed symbols) of colony 2 with 95% credible intervals (vertical lines) of the sociable weavers at Benfontein (1993-2013).

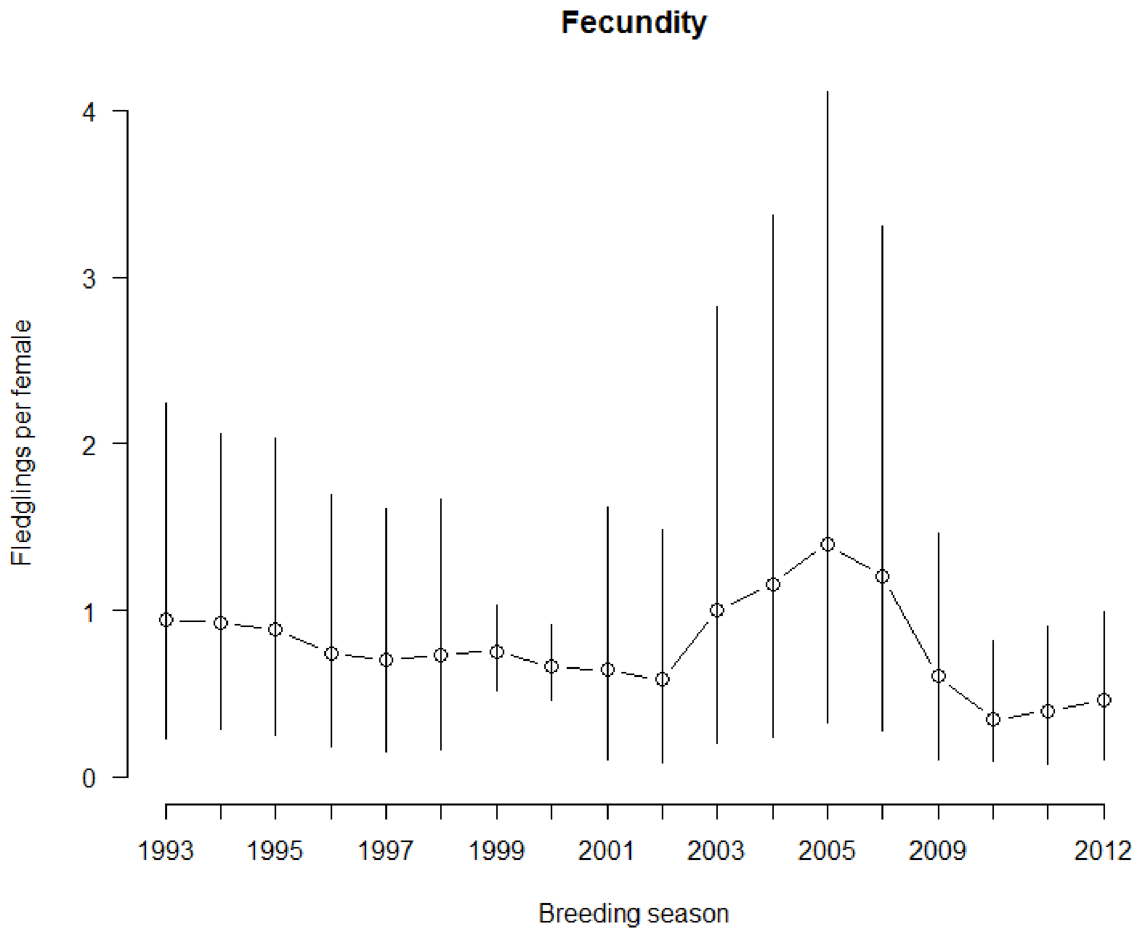


Figure A2. Fecundity (number of fledglings per adult female) of colony 2 with 95% credible intervals (vertical lines) of sociable weavers at Benfontein (1993-2012).

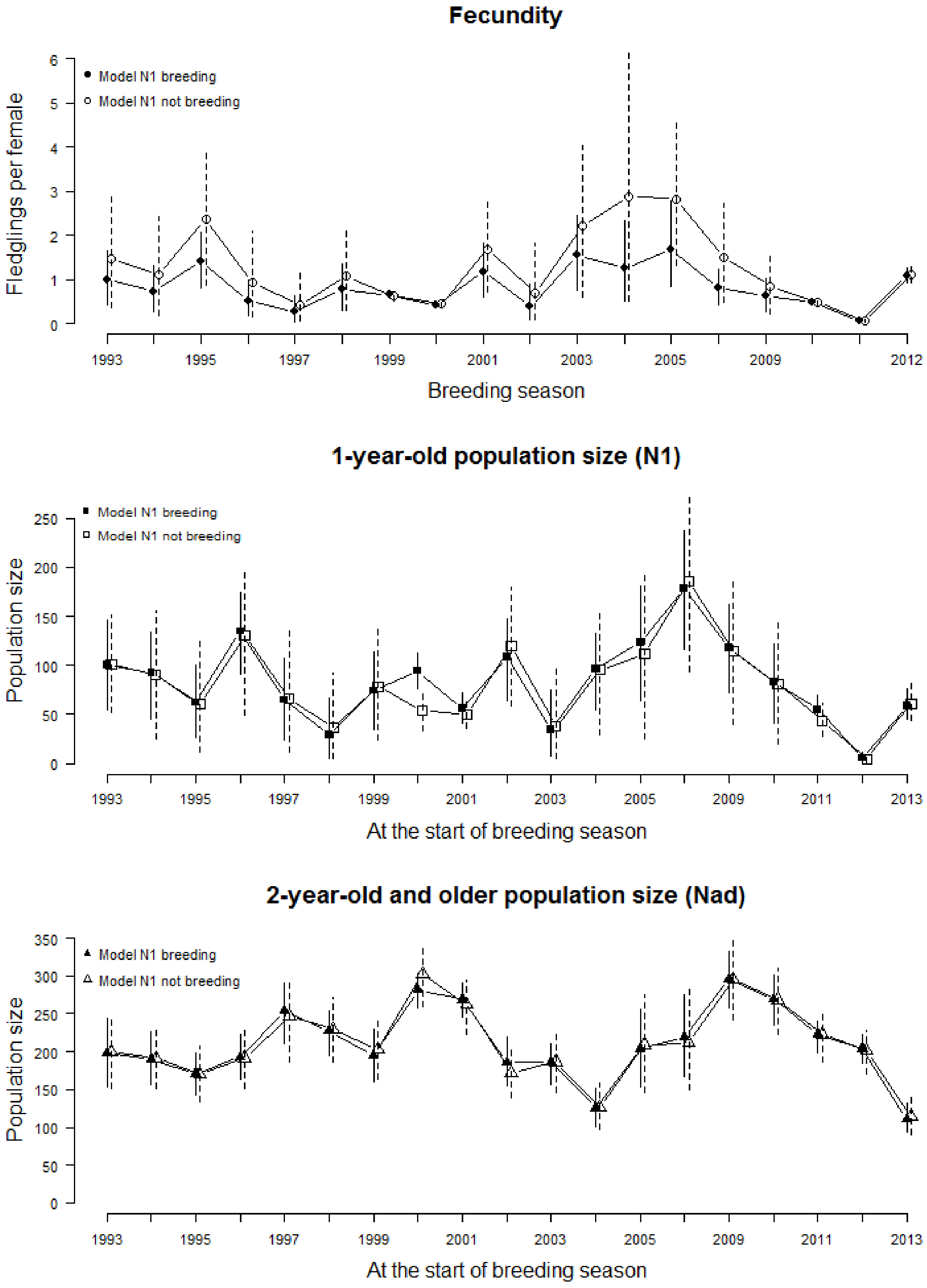
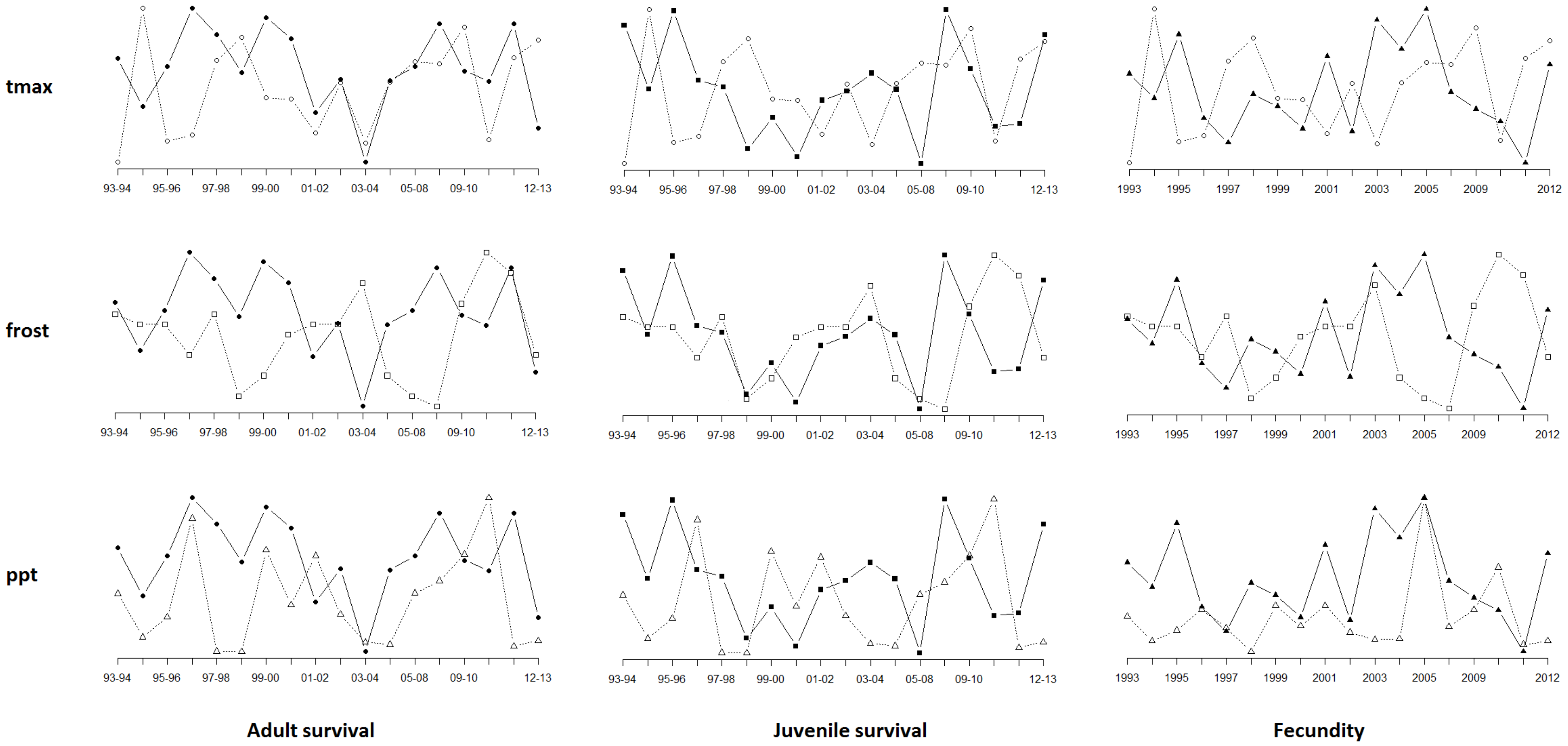


Figure A3. Estimated fecundity and population sizes of 1-year-old (N1) and 2-year-old and older (Nad) females of the sociable weaver population at Benfontein (1993-2013) of the 'full' IPM (closed symbols) and an IPM in which fecundity of 1-year-old females is set to zero (open symbols) with 95% credible intervals (vertical lines). The estimates of the two models were slightly separated to show the credible intervals.



(Closed symbols - demographic parameters; open symbols - climatic covariates)

Figure A4. Patterns of the demographic parameters of the population of sociable weavers at Benfontein and the climatic covariates (1993-2013). For details of the covariates see Table 1. Note that rainfall used in the survival models was adjusted for interval length, ie. an annual value. Rainfall in the fecundity model was aggregated over the interval.

Chapter 6

Synthesis and recommendations

"A ringing site should be trapped on a regular basis

to give meaningful results over a period of time"

SAFRING Bird Ringing Manual, 2001

This chapter synthesises the findings of the demographic analyses presented in this thesis and adds a review of current volunteer ringing in South Africa followed by recommendations to improve the value of this form of citizen science from a demographic perspective.

Synthesis of the results

Long-term ringing data of populations of 10 common species across southern Africa were analysed to investigate the influence of climatic stochasticity on vital rates and population dynamics. The data of the African reed warbler, lesser swamp-warbler, Levaillant's cisticola, tawny-flanked prinia, and spectacled weaver were collected at wetlands by licensed volunteer ringers and curated by the South African Ringing Unit (SAFRING); the data of bar-throated apalis, Karoo prinia, Karoo scrub-robin (fynbos) and sociable weaver (savanna) were collected and curated by research projects.

From 1998 to 2009 migratory African reed warblers at Paarl in the Western Cape survived better in years when the average temperature on the breeding grounds was higher: a 1.6 ^{0}C increase was associated with an increase in annual local, adult survival probability from 0.69 to 0.88. Climatic conditions in the wintering area in Central Africa (Fig. 1 in Chapter 2) - approximated by Normalized Difference vegetation Index data - could not be correlated with survival, possibly because the actual wintering grounds have never been verified by recaptures or recoveries. During the same period populations of African reed warblers across southern Africa (Fig. 1 in Chapter 3) exhibited large spatial variation in survival; mean survival ranged from 0.49 to 0.83. Survival of populations at the same latitude differed widely (Fig. 2 in Chapter 3), but could not be linked to climatic stochasticity - approximated by the seasonality of the wetland environment (vegetation types), and by rainfall regime (winter versus summer rainfall regions). Latitude 26 ^{0}S roughly separates migratory from sedentary populations of the African reed warbler. Evidence of an influence of migratory strategy on survival remained inconclusive. Migratory populations did appear to survive slightly better on average than sedentary populations (0.67 vs 0.59), but the difference was not significant.

Sympatric variation in survival of insectivorous passerines with similar life histories was larger and survival lower at a more seasonal wetland than at a climatically-stable fynbos location. At the wetland survival ranged from 0.51 to 0.66 during 1999-2013 and at the fynbos location from 0.72 to 0.79 during 2000-2007. However, the synchronous (common) and asynchronous (species-specific) components of the variation could not be correlated with actual measures of climatic stochasticity, i.e. annual temperature and rainfall and seasonal extremes. At the fynbos site this could have been due to the short study period.

For the sociable weaver data on productivity and population size, in addition to ringing data, enabled an investigation of the influence of climatic stochasticity on the population dynamics of 25 colonies in a larger meta-population (Fig. 1 in Chapter 5) in savanna habitat during 1993-2014. Neither fecundity nor age-specific survival of this population were correlated with indices of climatic extremes, but warmer years and longer or more frost intervals had a negative effect on juvenile survival, and adult survival and fecundity, respectively, in the largest colony. Previous research already suggested that colonies respond differently to climatic stochasticity.

Although only two analyses were able to correlate climatic variation to variation in annual survival, the findings do not preclude an influence of climatic stochasticity. The sparseness of most data, i.e. low recapture rates, prohibited the investigation of additive or interactive effects of climatic covariates. The field protocol of the sociable weaver research project was not formalized until the second half of the study period. As a result of the varying effort the modelling, particularly of the ringing data, was quite complex.

Constant effort ringing

When mist-netting is standardized, ringing effort is more likely to be constant/consistent, which greatly simplifies the modelling of ringing data and creates the potential for standardized modelling scripts (Robinson *et al.* 2009; Robinson *et al.* 2011). A protocol for constant-effort ringing (CE) was first used in the late 1960s in England, initiated by ringers - many of whom were volunteers - wanting to enhance the conservation value of the ringing data. An example of a survival analysis of recaptures of one of the early standardized mist-netting sites can be found in Buckland & Baillie (1987). In the 1970s the British Trust for Ornithology (BTO) formalized the CE protocol to enable pooling of the data from several sites (Robinson *et al.* 2009). A pilot CE scheme was run from 1981 to 1986 by volunteer ringer M. Boddy, starting with 17 sites in 1981, and formally adopted as a national Constant Effort Sites scheme (CES) after evaluation in 1986 (Baillie *et al.* 1986). CE ringing improves the precision of estimated juvenile and adult survival and can also provide reliable indices of juvenile and adult population sizes, fecundity and recruitment (DeSante *et al.* 1995: Peach *et al.* 1996; Peach *et al.* 1998; Saracco *et al.* 2008; review in Robinson *et al.* 2009). A recent example of the use of CES ringing data to estimate productivity is a study by Eglington *et al.* (2015) investigating the effect of spring temperature on latitudinal productivity of migrant warblers in Europe.

The CES protocol demands 12 visits on prescribed dates over the northern, temperate breeding season (May-Aug) at 10-day intervals of a fixed 6-hour period with a minimum of 4 mist-nets placed at the same location for a minimum of 4 years (Conway 2010). Constant-effort mist-netting data is seldom 'perfect'. Weather and logistics can hamper strict adherence to the protocol, but statistical analysis can account for the uncertainty in productivity and abundance indices introduced by missed visits (Peach *et al.* 1998; Miles *et al.* 2007; Cave *et al.* 2009).

Fifty years after its first conception the CES scheme has grown into a nation-wide scheme of ca. 140 sites in Britain and Ireland - all run by licensed volunteer ringers - and contributes data to the national monitoring of 120 UK breeding species (out of a total of 133 terrestrial breeding species) within the framework of the BTO's Integrated Population Monitoring Programme (Baillie 1990; Robinson *et al.* 2015a, 2015b). The CES protocol has also been adopted across Europe enabling monitoring of species on an even larger spatial scale (CES guidelines for Europe - Balmer *et al.* 2004; Robinson *et al.* 2009). The North American Monitoring Avian Productivity and Survivorship Program (MAPS) - a continent-wide network of over 500 CE mist-netting stations - was modelled after the BTO's CES Scheme (Baillie *et al.* 1986; DeSante *et al.* 1995; Saracco *et al.* 2008). MAPS provides annual regional indices of adult abundance, fecundity, and adult survival of more than 150 terrestrial species (DeSante *et al.* 2005).

Nation- or continent-wide CE ringing requires a large number of licensed volunteers and sufficient staff to curate and analyse the large amount of data gathered by the scheme. In 2014 the BTO's licensed ringers and nest-recorders contributed almost 700,000 hours (BTO 2015). In 2014 over 1 million birds were ringed, almost a quarter of a million birds were recaptured and more than 30,000 recovered by the BTO's Ringing Scheme (Robinson *et al.* 2015a). At the end of 2014 £40,000 was raised to analyse these data. At the end of 2013 there were 2,827 licensed ringers in the UK and Ireland (Walker *et al.* 2014).

Current ringing in South Africa

Piper (2000) extrapolated the number of ringers in Great Britain to southern Africa: based on its human population size southern Africa should have ca. 1200 licensed ringers. At present, as then, there are ca. 130 licensed ringers (D. Oschadleus pers. comm. 3 Dec 2015; also source of the following unless stated otherwise). Most of these ringers are volunteers: some ring alone (separate from or affiliated with a bird club), others have formed ringing groups within bird clubs (Geyser 2000), and many aid the ringing efforts of scientific projects (for example, Birdlife Plettenberg ringers contribute effort to fynbos and shorebird research of the NGO Nature's Valley Trust; Table A1). All ringing data are uploaded to the SAFRING database, including all data from research projects - an enviable situation from the BTO's perspective as they registered this on their 'wish list' (Robinson *et al.* 2011; BTO 2016). In 2013 56,709 birds of 692 species were captured, 7,732 were recaptured, and 281 recovered (Paijmans & Oschadleus 2015).

One important goal of ringing is to monitor demographics. To investigate climatic influences on demographics, long-term data are needed with sample sizes sufficient to estimate annual demographic rates (Frederiksen *et al.* 2014). In South Africa long-term, regular ringing (monthly, usually not during the austral winter (Jun-Aug)) takes place at four locations: Paarl Bird Sanctuary (Western Cape, since 1998), Helderberg NR (Western Cape, since 1986), Darvill Bird Sanctuary (Kwazulu-Natal, since 1983), and Melville Koppies NR (Gauteng, since 1974). Birds are captured and processed according to the SAFRING protocol, which describes the capture and handling protocol and the data to be recorded but does not prescribe effort (de Beer *et al.* 2001). I explored these data, apart from Melville Koppies, for the analyses presented in this dissertation. Table 1 gives an overview of all data per location to illustrate the considerable effort involved in collecting these data. For demographic analysis the recapture rates were adequate, although still sparse, for 1 species in the Paarl data, none in the Helderberg data, and for 4 species in the Darvill data. The small number of recaptures at Melville Koppies (Table 1) clearly indicates that recapture rates were too low for demographic analysis.

Tricks and wishes of ringing-data analysts

When data are sparse, current methodology provides 'tricks' to increase the precision of the survival estimates. Time-Since-Marking models (Chapter 2 in this thesis) and multi-state models (Chapter 3) are useful to account for transients, i.e. non-local individuals that are only captured once (Pradel *et al.* 1997). Random-effect models (Chapters 3 - 5) can overcome sparseness of data to a certain extent by sharing information across sites and/or years (Gelman 2005; Grosbois *et al.* 2009).

The most-fervent wish of any ringing data analyst is high recapture rates of many individuals. In general, for annual survival estimates an analyst would recommend one annual ringing session that lasts long enough to capture many birds so that the probability of annual recaptures is improved. If the aim is to estimate annual survival, most current analyses use only one recapture per year per individual. To investigate seasonal survival ringing sessions throughout the year would be needed to provide recaptures of individuals per season per year.

The use of metal rings means that birds need to be recaptured with specialized equipment by a ringer experienced in the capture and handling of birds to allow recording of the ring number. Colour rings are legible from a distance and do not require any expertise to 'recapture' as resighting. Therefore, resighting rates are often much higher than recapture rates, which increases the precision of survival estimates and the analytical scope of the data. Unravelling what makes a species' population tick, i.e. population dynamics, requires estimation of demographic rates in as much detail as possible. That implies ringing all segments of a population to enable the estimation of age-, sex-, and/or status-specific survival and data on productivity.

Recommendations

I propose a three-pronged strategy to improve the use of ringing data from a demographic perspective pertaining to existing data, future data and ringing, and the way that ringing is perceived and presented in South Africa.

Existing data

To my knowledge few data collected by individual volunteer ringers, i.e. not collected by volunteers within the context of research projects, have been analysed - either as the sole source or requested of SAFRING by researchers as augmentation of their research data - to estimate demographic parameters. These data represent considerable effort and substantial costs (purchase of ringing equipment and recurring costs of petrol and rings) donated by volunteer ringers and should be fully utilized. These are publications that estimated survival stating clearly that the data were collected independently by volunteer ringers (i.e. not for research projects): la Cock & Hänel (1987) - African Penguins *Spheniscus demersus*; Yom-Tov *et al.* (1994) - 11 southern African passerines; Peach *et al.* (2001) - 16 southern African passerines; Altwegg & Underhill (2006) - Cape Sugarbird *Promerops cafer*; Distiller *et al.* (2012) - Cape gannet *Morus capensis*; Bonnevie (2014) - Sombre Greenbul *Andropadus importunes*; Collingham *et al.* (2014) - 67 southern African species; Jansen *et al.* 2014 - African Reed Warbler (Chapter 3 in this thesis); Jansen *et al.* 2015 - African Reed Warbler (Chapter 2). Underhill *et al.* (1991) lists 3 older survival studies, 2 that estimated fecundity based on the percentage of first year birds, and 1 that estimated population size.

The SAFRING database contains more data that could be analysed from a demographic perspective, and for other studies. For example, there are several medium-term (ca. 5 years), regular ringing locations, which have not been used in survival analyses. Research projects that used ringing for other purposes than estimating demographic rates could be investigated from a demographic perspective, see chapters 4 (Koeberg data) and 5 in this thesis. Overall recruitment can be estimated based on reverse capture histories, which in combination with survival estimates can then be used to estimate population growth rate (Pradel 1996; Pradel *et al.* 2010). Sample sizes of one species that are too small for independent analysis could be combined in spatial survival analyses, see chapter 3 in this thesis. Data from one location, where regular ringing has taken place in similar-length short periods (around 1 year) interspersed by similar-length gaps, could be analysed as robust design to estimate survival (Pollock *et al.* 1990). Biometric data from individual birds that have been recaptured several times by the same ringer (to avoid heterogeneous measuring) could be explored to study how these individuals changed over time, e.g. timing and length of moult and changes in mass as an indication of condition. When birds are ringed as nestlings this could also be investigated in relation to age. Data from the South African Bird Atlas (SABAP) projects run by the Animal Demography Unit (ADU) could be used as an abundance index in combination with ringing data suitable for survival analysis in integrated population models to study population dynamics and estimate fecundity without actual productivity data (an example of bats in Schaub *et al.* 2007; examples of bird studies and a review of the methodology in Schaub & Abadi 2011). Amar *et al.* (2015) validated the use of SABAP Data as an abundance index and examples of its use can be found in Huntley *et al.* (2012) and Huntley & Barnard (2012).

Twenty-five years ago Underhill *et al.* (1991) noted a backlog in the analysis of ringing data. That situation has not changed. What has changed are the statistical methodologies and tools available (see Introduction of this thesis), which have extended the scope and greatly simplified CMR analyses. The newly formed Centre for Statistics in Ecology, Environment and Conservation (SEEC) at UCT brings together researchers interested in and capable of the statistical analysis of ecological data. A collaboration between SAFRING and SEEC could provide a platform for the full utilization of the existing ringing data recorded by southern Africa's volunteer ringers.

Future data and ringing

The information value of the data recorded per capture could be increased by a few simple additions. At present, the GPS location of captures is recorded in degrees and minutes. A minute grid at this latitude represents 17 hectares (on average). By adding the seconds to this field the precision of the location increases to ca. 48 m^2 (size of a second grid; R. Navarro pers. comm. 20 July 2015). With this increased precision the exact vegetation type can be determined using the CD-set (Mucina & Rutherford 2010) that accompanies Mucina & Rutherford (2006), which enables, for example, demographic analyses of species in particular habitats. In addition to the field 'Moult', which requires moult scores of the primary feathers which is not always recorded, a field 'Moult Y/N' could yield information on timing of primary moult. At present, the presence of a brood patch is recorded as a comment. A field 'Brood patch Y/N' would make this information available for analysis of, for example, breeding season length.

In 1964 - the year in which Cormack (1964) wrote his seminal paper that, together with Jolly (1965) and Seber (1965), formed the cornerstone of modern capture-mark-recapture analyses - Rowan analysed a large volume of ringing data collected by volunteer ringer R.A. Reed during 1954-1959 at his residence at Tonqani near Johannesburg (over 13,000 captures of 88 species and over 1300 recaptures of 44 species). Rowan concluded: "…the prime requisites seem to be repetitive trapping in a single area, consistently maintained over a period of years. This should go far towards realising the potential of ringing and recapture data and add immeasurably to the scientific value of the many hours devoted to ringing by volunteer workers throughout the country." Twenty-five years later Underhill & Oatley (1989) translated this conclusion into the Measured Effort Sites protocol, which never resulted in a MES scheme like the CES scheme in Britain. There simply are not enough volunteer ringers in southern Africa for a network of CE ringing locations. However, constant-effort ringing following a protocol as formal as the CES protocol would considerably increase the value of the current regular ringing undertaken at the above mentioned long-term ringing sites and any other regular ringing sites, e.g. Tygerberg NR. Particularly well-suited sites are those coordinated by a bird club, bird ringing unit or university, for example, since the coordination would ensure continuity. The ringing itself nor the effort would have to change much, but the data recording would include data pertaining to effort, the ringing dates would need to be formalized, and net placement would need to be as consistent as possible (Conway 2010). This would enable pooling of the data from species and from similar habitat, and yield more demographic information besides survival estimates (see Constant effort ringing). Azonal habitat like wetlands are particularly interesting in this context in a country as diverse as South Africa, e.g. Paarl is located in the winter rainfall area and Darvill in the summer rainfall area.

Regular ringing is also carried out by ringers across certain areas or in several locations. For example, a volunteer ringer from the Birdlife Port Natal bird club (Table A1) captures birds on private estates along the North Coast of Kwazulu-Natal on a monthly-basis. Such regular ringing could be enhanced by including a project following the BTO's Retrapping Birds for Survival (RAS) protocol (BTO 2016, Jan 10). RAS projects are single species projects. The aim is to catch all adults (or all of one sex) of a chosen species in a chosen study area, or at least 40-50 adults including 30 recaptures, during the breeding season. The species and the study area should be chosen with this objective in mind, e.g. species that show breeding site fidelity and that are easy to capture, areas that are large enough to support an adequate number of breeding birds. The project should run for a minimum of five years to yield sufficient data for survival estimates and the determination of trends. This type of project might also appeal to those ringers who focus their efforts mainly on certain species. As with the CES protocol effort should be consistent over the years and meticulously recorded.

SAFRING could encourage adopting a CES protocol by refunding the cost of rings used and a RAS protocol, which should, ideally, need rings only initially, by contributing towards the costs of equipment and/or petrol.

Of course, adhering to protocols that increase the effort involved in regular ringing, however little, will only become interesting/rewarding when such data are fully-utilized, i.e. analysed, and the findings communicated (see Perception and presentation of ringing below). Therefore, I recommend that the analysis stage of the process will already have been discussed and potential analysts approached for availability by SAFRING before the protocols are suggested to the volunteer ringing community. In their review of the role of ringing in southern Africa Underhill *et al.* (1991) recommended the establishment of an Avian Demography Unit to integrate research into the dynamics of bird populations. At present, a collaboration between SAFRING and SEEC would appear the most feasible option to fulfil this role.

The following are recommendations in general to enhance the value of ringing data from a demographic perspective. The proximity of a weather station to ringing sites enables investigation of climatic influences on demographic rates. Bird clubs organise regular bird watching outings, often visiting regular ringing locations. When colour rings are used in addition to the standard metal rings, these bird watchers can become citizen scientists providing resighting data. Current ringing takes place at easily accessible locations near and in urban centres and in modified habitat like the long-term ringing at Paarl and Darvill, both in bird sanctuaries that are part of waste water works. Data from unmodified habitat would provide information about the demographics of populations in their natural environment. Piper (2000) suggested enlisting farmers and those who live in natural reserves in South Africa to ring in their natural 'backyards'.

Perception and presentation of ringing

A survey of bird club websites/Facebook pages (December 2015; Table A1) revealed that, out of 25 bird clubs, 6 bird clubs mention ringing activities and 5 of those give dates and contact details of the volunteer ringers. Plettenberg Bay Facebook does report on its ringing for Nature's Valley Trust research projects, but does not do so beforehand as an activity to watch or participate in. Two of those 6 clubs explain the use of ringing data including the estimation of survival, i.e. Witwatersrand and Birdlife Northern Gauteng that also includes an explanation of its use in population monitoring and provides a link to the BTO's Population Dynamics webpage. The Cape Bird Club and Birdlife Northern Gauteng encourage participation in bird ringing. Five bird clubs provide a link to the SAFRING website. The SAFRING website itself does not explain the use of bird ringing, nor does the ADU website. The SAFRING Bird Ringing Manual (de Beer *et al.* 2001) provides a brief paragraph on the achievements of ringing. Piper (2000) states that, in his experience, most volunteer ringers understand the scientific and conservation value of ringing. Nonetheless, an explanation of the various uses of ringing data including modern-day demographic analyses - perhaps enhanced by published examples pertaining to southern Africa - on the SAFRING website would provide an easily-accessible complete picture that could serve as a starting point for those thinking of becoming licensed ringers and a source of information for those experienced ringers wanting to enhance the returns on their investment in ringing. A detailed description of the above-mentioned regular ringing protocols, including the effort involved and how it would enhance the value of ringing data should be available on this page as well.

A questionnaire directed at current volunteer ringers could elucidate how ringing is perceived in terms of the investment required (time and money), the use of the data, and the added value of ringing protocols. Such a questionnaire could also investigate the best way to communicate scientific research based on the volunteer ringers' data, i.e. dissemination of the results in the form of feedback from SAFRING. SAFRING could stipulate that when researchers request data they write an abstract of the results suitable for this type of communication. Additionally, the SAFRING ringing report, which will be published annually again (Paijmans & Oschadleus 2015), could list new research based on or including SAFRING data.

The survey of bird club websites and the SAFRING website also revealed that volunteer ringers, unlike those citizen scientists participating in the ADU projects SABAP and the many Virtual Museums (see almost daily posts on the ADU website and Facebook, which also illustrate the ADU feedback to its citizen scientists), are not lauded for their efforts. Considering the fact that ringing requires a lengthy training process and an investment in equipment and time and that the resulting data provide detailed, vital insights into the state of South Africa's avifauna and, by proxy, ecosystems this appears a large oversight.

Funding

The suggested recommendations require investments by the volunteer ringers and SAFRING, not only of time but also of funds. A potential source of those funds could be sponsoring by Birdlife South Africa (BLSA), or a collaboration between SAFRING and BLSA could be formed to raise funds. BLSA has recently adopted Birdlife International's 'Keeping common birds common' conservation project (BLSA 2015, 29 Dec). The project was established in response to findings of, among others, Voříšek *et al.* (2010) and Inger *et al.* (2015) that reported losses of more than 400 million individual birds across Europe during 1980-2009, most of which were common species.

Conclusion

We know little of the population dynamics of the common birds of southern Africa, many of which are endemic to the sub-continent. At present, ringing data collected by volunteer ringers provide the only source of data for the estimation of their vital rates, which are pivotal in understanding the causes of population trends derived from, for instance, SABAP data. Climate change is accelerating at an unprecedented rate and the extremity of El Niño and in response that of La Niña - weather phenomena that cause extreme weather around the globe - is increasing (Cai *et al.* 2015; Smith *et al.* 2015). Baselines of vital rates are essential to understand the impacts of these climatic changes on the populations of southern Africa's common species. Using available ringing data collected by volunteer ringers, supplemented by data from two research projects, the analyses in this thesis added inference to research into the impacts of climate change from the southern, temperate region - a region from which data are still sparse compared to that from the northern, temperate region (IPCC 2013). The volunteer data provided the first survival estimates of two endemic common species and the first survival estimates from southern African populations of another three common species. Small changes in volunteer ringing protocols could increase the value of the volunteer data; showcasing the results and the volunteer efforts could enhance understanding of the value of ringing and engage a wider audience of citizen scientists in this activity.

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Table 1. Details of the data collected at the four long-term, regular ringing locations in South Africa.

Location	Paarl BS	Helderberg NR	Darvill BS	Melville Koppies NR[1]
Period	Feb 1998 - May 2013	Sep 1986 - Oct 2013	Mar 1982 - Nov 2013	1974 - 2014
Coordinator	G. Scholtz until 2009 (volunteer)	Somerset West Bird Club (volunteers)	University of Kwazulu-Natal [2]	Witwatersrand Bird Club (volunteers)
Records	6,680	6,743	43,344	18,564 (including
Individual birds	6,033	6,246	39,790	578 recaptures)
Ringers	27	27	31	
Days	262	661	896	
Records/ringer[3]	1 - 4865	1 - 3872	1 - 25,121	
Species	77	92	211	135
Records/species[3]	1 - 1301	1 - 2070	1 - 7012	

NR, Nature Reserve; BS, Bird Sanctuary.

[1] Source McLuskie (2014).

[2] Birdlife KZN Midlands is actively involved with 4-6 volunteer ringers per ringing session.

[3] Range

Table A1. Bird clubs in South Africa on internet (found via Birdlife South Africa website and a Google search in December 2015).

Name (province)	Website	Ringing activities	Ringing use explained	SAFRING link
Witwatersrand (GP)	witsbirdclub.org.za	Y [1]	Y	Y [2]
Birdlife Port Natal (KZ)	blpn.org	Y [1, 3, 4]	N	N
	www.facebook.com/BirdLifePortNatal	N	N	N
Birdlife Trogons (KZ)	birdlifetrogons.blogspot.nl	N	N	Y [5]
Birdlife Polokwane (LI)	www.birdlifepolokwane.co.za	N	N	N
	www.facebook.com/birdlifepolokwane	N	N	N
Phalaborwa (LI) [6]	www.phalaborwa.birdclub.co.za	-	-	-
Birdlife Rustenburg (NW) [6]	www.birdliferustenburg.co.za	-	-	-
Birdlife Overberg (WC)	www.facebook.com/birdlifeoverberg.co.za	N	N	N
Cape (WC)	www.capebirdclub.org.za	Y [8]	N [7]	Y [8]
Tygerberg (WC)	www.tygerbergbirdclub.org	Y [9]	N	Y [5]
Birdlife Northern Gauteng (GP)	www.blng.co.za	Y [8]	Y [8]	Y [8]
Birdlife Plettenburg Bay (WC)	www.facebook.com/Birdlife-Plettenberg-Bay-551125104907923	Y	N	N
Birdlife Eastern Cape (EC)	www.facebook.com/BirdlifePortElizabeth	N	N	N
Birdlife Free State (FS)	www.facebook.com/BirdLife-Free-State-159225194134981/	N	N	N
Birdlife Vaaldam (FS)	www.facebook.com/groups/311908705529311/?fref=ts	N	N	N
Birdlife President Ridge Sanctuary (GP)	blpr.co.za	N	N	N
Birdlife Sandton (GP)	www.facebook.com/Birdlife-Sandton-403703483049429	N	N	N
Rand Barbet (GP)	barbet.web-sa.co.za	N	N	N
	www.facebook.com/Rand-Barbet-Bird-Club-145595815497807	N	N	N
Birdlife KZN Midlands (KZ)	midlandsbirdclub.blogspot.nl	Y	N	N
Birdlife Zululand (KZ)	www.birdlifezululand.co.za	N	N	N
Barberton (MP)	www.barbertonmanor.com/birding.html	N	N	N
Stanford (WC)	www.stanfordbirdclub.co.za	N	N	N
Hermanus (WC)	hermanusbirdclub.wordpress.com	N	N	N
Somerset West (WC)	www.somersetwestbirdclub.co.za	N	N	N
	www.facebook.com/SomersetWestBirdClub	N	N	N
West Coast (WC) [6]	www.sawestcoast.com/birdclub.html	-	-	-
	www.facebook.com/West-Coast-Bird-Club-629764187056868	N	N	N

GP, Gauteng Province; KZ, Kwazulu-Natal; LI, Limpopo; NW, North West; WC, Western Cape; EC, Eastern Cape; FS, Free State; MP, Mpumalanga.

[1] Advertised via newsletter.

[2] Via SAFRING logo.

[3] On Activities calendar.

[4] Activities - General information.

[5] Under 'Useful links'/'Birding links'.

[6] Website under construction or not current.

[7] The website does mention that ringing is important.

[8] On 'Bird Ringing' page.

[9] TBC Ringing Unit.