Citizen science reveals complex changes in barn swallow phenology in South Africa over three decades

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Declaration

I hereby declare that all the work presented in this thesis, titled “Citizen science reveals complex changes in barn swallow phenology in South Africa over three decades”, is my own, except where stated otherwise in the text. This thesis has not been submitted in whole or part for a degree at any other university.

Signed in Cape Town in April 2016.

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Abstract

Palearctic migrants, including barn swallows *Hirundo rustica*, responded to climate change in Europe from the mid to late 1900s with phenological changes, mostly showing earlier arrival and start of breeding. During this period, barn swallows in the Palearctic exhibited variable patterns of change in the timing of their arrival, breeding and departure from the breeding grounds. At the South African non-breeding grounds, the timing of migration shifted between the 1980s and 2000s, again with geographic variability. To explain these changes further, I examined geographic and temporal variability in the timing of flight feather ('primary') moult, and trends in body weight, in barn swallows ringed in South Africa between 1986 and 2012. Citizen science bird ringing, started in South Africa in 1948, generated all the data used in this project. All data were obtained from the South African Bird Ringing Unit (SAFRING). In the Introduction, climate change in the Palearctic, and its effects are outlined, particularly as they relate to the timing of life-cycles of long-distance migrant birds. The constraints between life-cycle stages, and how these potentially limit adaptation to climate change, are discussed. The biology and ecology of the barn swallow is described.

In the second chapter, I describe patterns of migration between five provinces in South Africa and three longitudinal Palearctic zones comprising the breeding grounds of the Palearctic barn swallow. The total numbers ringed annually in South Africa from 1952 to 2012, and totals subsequently recovered in the Palearctic, constituted the data set. To estimate the different proportions that potentially migrated to, and by inference originated in, each part of the Palearctic, I used the Kania-Busse method that accounts for spatially different probabilities of finding a ringed bird. Birds from the Western Cape were linked in almost equal proportions to all three Palearctic zones, and those from the Northern Cape and Free State mostly to the western and central zones. Those from KwaZulu-Natal migrated mostly to the central and eastern zones, and those from Gauteng mostly to the central zone.

The third and fourth chapters examine how well the assumptions of the Underhill-Zucchini moult model were supported in analysing the SAFRING barn swallow moult data set. The moult data were unevenly distributed, making it unfeasible to model a variable rate of moult. The linear moult model was thus preferred. The assumption that the primary moult start dates of individual birds are normally distributed was reasonably supported. Considering reported differences between immature and adult barn swallows in timing of migration and moult, and after identifying misclassification of the ages in the data, I concluded that the age classes should be pooled and analysed together. The expectations that immature (first year) barn swallows started moult several weeks later than adults, but did not differ in moult duration, were reasonably supported.

In Chapter Five the Underhill-Zucchini moult model was used to assess changes in the mean start of barn swallow primary moult in six zones in South Africa between 1990 and 2012, divided into two time periods divided roughly at 2003. In the Western Cape there was almost no change in mean start of moult (a two day delay) over the period, whereas in Gauteng moult started six days earlier in the second period. In southern KwaZulu-Natal, moult shifted three days earlier, and in the Free State seven days later. In the Eastern Cape moult shifted five days later and in the northern KwaZulu-Natal there was no change. These results provide further evidence of geographically variable changes in barn swallow phenology at the non-breeding grounds. The changes were generally consistent with reported changes in migratory and moult phenology for barn swallows in South Africa.

In the sixth chapter, differences in weight trends are investigated, for the period 1986 and 2012, in four South African zones divided into two time periods. The trends were described using locally weighted linear regression. Based on reports of pre-migratory weight gain at the breeding grounds, I hypothesised that there would be an increase in weight towards the end of the season before departure, and the trends supported this. The starting point of the weight gain period was estimated using break-point analysis. Start of pre-migratory weight gain shifted earlier from the first to second time periods (roughly 1990s to 2000s) in some zones, but later in others – earlier in Gauteng and the

Western Cape by 13 and two days respectively, and later in southern KwaZulu-Natal and the Free State by nine and 15 days respectively. The changes were generally consistent with reported changes in migratory and moult phenology, and with the moult phenological changes reported in Chapter Five.

In the Synthesis Chapter the reported phenological changes are integrated into a phenological calendar, and the relationships between the changes are discussed in terms of evidence for adaptation and constraints limiting it. Average phenological shifts over the second half of the twentieth century in the Palearctic for the spring phenology of plants were calculated from the literature. I then estimated the weighted averages of these shifts for each South African zone, using the proportions of birds potentially migrating from each South African zone to the three Palearctic zones (Chapter Two) as weights. These weighted averages provide hypotheses for the amount of phenological change to be expected in barn swallows in South Africa, because they describe the average changes that birds from each South African zone would have experienced at their breeding grounds. Also using the migratory connectivity results, the observed changes in the timing of mean start of moult in South Africa were used to obtain estimates of how the breeding populations in the Palearctic zones experienced the changes in moult phenology. Finally, the changes in South Africa and the Palearctic were assessed, in light of the climate changes in South Africa and at the breeding grounds. The evidence for the effects of Palearctic phenological changes on the phenology of barn swallows in South Africa was strong. The estimated shifts towards earlier start of moult and pre-migratory weight gain in some South African zones were consistent with reported advances in European spring phenology. Further, the estimated shifts towards later barn swallow phenology in other South African zones raise the possibility that the longer European breeding season has already caused non-breeding season activities (arrival, moult, pre-migratory weight gain) in certain populations to shift later. These delays, combined with the advance in European springs, could make it increasingly difficult for barn swallow populations in South Africa to survive in the long-term. There were spatially complex climate changes in South Africa over the period, and these probably contributed to the observed phenological shifts. A likely outcome is that migratory distances will be reduced through a northwards shift of the non-breeding range.

Layout of thesis

There are seven chapters, of which the first and last are the Introduction and Synthesis. Aside from the Introduction and Synthesis which have a different narrative structure, the chapters are written as papers for publication, each with its own abstract, introduction, methods, results, discussion and tables and figures sections. All acknowledgements are given at the start of the thesis. Most of the context for each chapter is provided in the general introduction, to keep the chapters brief. Where appropriate, complete technical details of methods are given once and are thereafter referred to when required in the other chapters.

Contribution of co-authors

All of the data analysis and writing were done by me. All of my supervisors commented on each chapter and on the final draft.

Les Underhill and Res Altwegg provided the general concept for the project – to analyse phenological changes in barn swallow moult phenology in South Africa. For the analysis of migratory connectivity, Les Underhill guided my choice of method. Les Underhill and Walter Zucchini developed the moult model used to analyse the moult data (Chapters Three to Five). Birgit Erni wrote the R package 'moult', which applies the method and enables one to use explanatory variables, and helped with some details of its use. Magda Remisiewicz suggested that I explore the phenology of pre-migratory weight gain (Chapter Six). Les Underhill provided code for the locally weighted linear regression method), which I adapted for use in R statistical software (Chapter Six). Les Underhill provided a novel method whereby the phenological shifts at the breeding grounds are estimated using migratory connectivity information and the phenological shifts at the non-breeding grounds (Synthesis Chapter).

Barn swallow flight feather weights used in the moult analyses were obtained from a museum specimen at the National Museum, Bloemfontein, courtesy of Rick Nuttall and Dawie de Swardt, and from specimens at the Ornithological Station, Museum and Institute of Zoology, Polish Academy of Science, in Gdańsk, courtesy of Tomasz Mokwa and Magda Remisiewicz. No birds were killed for this project and no ethics approval was required or sought. All the data were collected prior to the start of this project by citizen scientists, with the appropriate ringing permits from the relevant authorities.

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All data (ringing records) were obtained from the South African Bird Ringing Unit (SAFRING) at the University of Cape Town. Recoveries in the Northern Hemisphere of SAFRING-ringed birds that have been reported to SAFRING constitute part of the SAFRING data set. Many foreign bird ringing schemes have shared ring recovery information with SAFRING.

More than 250 bird ringers contributed the barn swallow ringing records to SAFRING. A list of known data contributors is included at the end of the thesis. I would like to acknowledge especially the

following individuals: John and David Robson, who contributed more than 25 000 records, and Jack MacLeod and H. P. Mendelsohn who each ringed over 10 000 barn swallows. The Witwatersrand Bird Club provided more than 40 000 records in the 1960s. The Natal Bird Club provided at least 4900 records, and Northern Cape Nature Conservation provided over 1000 records.

Many thanks to SAFRING, particularly Nosipho Yheyhe Mali, and to Amour McCarthy of the ADU, for being happy to help with the task of computerising thousands of historical barn swallow records. Dieter Oschadleus of SAFRING provided much help, advice and encouragement.

Andrew Pickles and Ursula Franke kindly sent me photographs of barn swallows which I have used in many presentations and in the thesis. Andrew Pickles took the photograph I have used on the cover. The barn swallow photograph by Charles J Sharp in the Introduction is reproduced under the Creative Commons Attribution-Share Alike 4.0 International license (charlesjsharp, Sharp Photography, CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=38704934). The mapping shapefiles I have used are in the public domain, downloaded from Natural Earth (www.naturalearthdata.com). Michael Brooks of the ADU provided the barn swallow SABAP range-change map. Colin Jackson discussed his experiences of ringing barn swallows and other Palearctic migrants in Kenya, and we had many conversations about the moult model and coding. David Pearson kindly provided barn swallow data for Ngulia Lodge, Kenya. Marc Herremans provided information about barn swallow body weights in Africa.

To all of my associates at UCT in Biological Sciences, Statistical Sciences and in the ACDI, I could not have done this without your friendship over the past four years, and in some cases much longer – and thank you for your valuable academic feedback and interaction during my many seminar presentations. Thank you to all of the support staff, and especially Petra Muller, for being so fast, friendly and helpful all the time. Thanks especially to the dedicated Supercare staff in Biological Sciences for maintaining a wonderfully clean environment to work in, and for your friendly smiles and welcoming greetings every day.

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Introduction

Motivation and rationale of the thesis

Unusually rapid global climate change, characterised largely by increasing temperatures, occurred in the second half of the twentieth century (Vose *et al.* 2005). This had widespread ecological effects for many plant and animal species, including changes in the timing of life-cycles (phenological changes), mostly reported for species in the Northern Hemisphere (Walther *et al.* 2002, Parmesan & Yohe 2003, Parmesan 2006). At the broadest level, the objective of this thesis was to add to the understanding of phenological responses to changes in the timing and conditions of seasons ('seasonality') caused by climate change. Further, relatively few studies have addressed phenological changes in the Southern Hemisphere, although progress has been made (see Chambers *et al.* 2005, Møller *et al.* 2011, Altwegg *et al.* 2012, Chambers *et al.* 2013, Bussière *et al.* 2015). This thesis aims to address this particular knowledge gap, focusing on the phenology of a long-distance migratory species in South Africa.

The focus of this thesis is phenological change in a long-distance Palearctic-African migrant species, the barn swallow *Hirundo rustica*. Many species of long-distance migrants – up to a third of those analysed – declined in numbers between the 1970s and 1990s, whereas only half as many increased in numbers over this period (Sanderson *et al.* 2006, Walther *et al.* 2011), raising widespread concern about these species. Over the same period, long-distance migrant species tended to arrive at the Palearctic breeding grounds earlier each year; this general trend has been correlated with a tendency for springs to become warmer and hence start earlier each year, at least in the western and central Palearctic (Mason 1995, Huin & Sparks 1998, Ahas 1999, Sparks & Menzel 2002, Walther *et al.* 2002, Cotton 2003, Parmesan & Yohe 2003, Crick 2004, Menzel *et al.* 2006, Parmesan 2006, Pulido 2007, Rubolini *et al.* 2007, Sparks & Tryjanowski 2007, Knudsen *et al.* 2011). In many parts of the Palearctic the start of breeding shifted earlier, consistent with earlier arrival and earlier start of spring (Crick *et al.* 1997, Crick & Sparks 2006). However, the patterns have not been the same throughout the

Palearctic. In Norway, for example, earlier arrival was associated with warmer springs for some, but not all species, from 1980–2000 (Barrett 2002), but there was no general trend towards earlier arrival, because springs did not get consistently warmer over time (Barrett 2002). The overall combination of observations – uneven rates and directions of climate change, and declining populations, with some in severe decline – suggested climate change might have compounded other environmental threats, leading to worse declines. Further, the population declines were generally more severe for long-distance than short-distance migrant or resident species, suggesting that long-distance migrants might be particularly at risk from climate change (Sanderson *et al.* 2006).

The abundant and widespread Palearctic subspecies of the barn swallow (*H. r. rustica*), however, showed on average no decline (Sanderson *et al.* 2006), or small to moderate declines, from 1970–2000 (Walther *et al.* 2011). Based on these and similar reports, and its large population size, the species was categorised 'Least Concern' (BirdLife International 2012). The fact that barn swallows did not decline on average, whereas many other species did, raises intriguing questions about why some species are more resilient to climate change than others. Unlike the Palearctic barn swallow, the North American barn swallow (*H. r. erythrogaster*), decreased severely from 1970–2000, a pattern reported for most long-distance migrant Nearctic passerines (Hobson *et al.* 2015). These comparisons suggested that the Palearctic barn swallow might have particular life-history traits that make it more resilient than other species to environmental threats and global change, keeping the global population relatively healthy.

A general aim of this thesis was to provide an integrated description, or model, of the population-level changes in barn swallow phenology at the non-breeding grounds. An integrated model is essential in explaining the estimated changes, because the stages of the life-cycle are intricately related and cannot be examined in isolation. This particular study of barn swallow life-history of was prompted largely by the unexpected geographical variability in migratory phenology between the 1980s and 2000s in barn swallows in South Africa (Altwegg et al. 2012). Another study reported changes in moult phenology in the Free State, and in migratory phenology in KwaZulu-Natal (Møller *et al.* 2011). These two studies provided a set of results against which to compare the patterns of change in moult (Chapter Five) and pre-migratory weight gain phenology (Chapter Six) presented in this thesis.

Palearctic barn swallows encounter diverse conditions, with breeding grounds that span 100° of longitude in Europe and Asia (Rowan 1968, Moreau 1972) and non-breeding grounds that stretch from the west African northern tropics to the southern-most parts of Africa, except in the most arid zones (Moreau 1972, Earlé 1997). Barn swallows migrate to South Africa from the entire west-east range of the Palearctic into central Siberia (up to about 90°E) (Rowan 1968, Oatley 2000). Across this vast breeding range climatic patterns vary, and climate change has occurred differently in the west than in the east, and in the north than in the south (Ahas *et al.* 2002). Barn swallows in South Africa thus comprise groups that have been exposed to massive geographic differences in Northern Hemisphere climate and in twentieth century climate change. Differences in phenology in South Africa are thus likely to reflect the variability of responses to the patterns at the breeding grounds.

A final practical motivation for choosing the barn swallow was the availability in the SAFRING data base of an unparalleled data set of moult and body mass records, and ringing and recovery records, for barn swallows in South Africa over several decades and in many places. This data was essentially donated to SAFRING by hundreds of qualified 'citizen scientist' bird ringers. Barn swallows are a popular species to ring – they form dense flocks above their roosts in Africa in the evenings (Turner 2006), when they are often trapped en-masse using mist nets. Ringing and processing can continue all night, and the birds are released in the morning. As a result, barn swallows have been ringed in greater numbers than any other passerine species in South Africa, making a study of this scope possible.

Layout of the remainder of the Introduction

Climatic conditions differ substantially between the Northern Hemisphere, where most long-distance migrant birds breed, and the Southern Hemisphere, where some migrant species spend their non-breeding season. One climatic difference that has important implications in the light of climate change is that seasonality is more pronounced in the Northern Hemisphere (Alerstam 1990). The first section below, entitled ‘Climate, seasonality and phenology’, addresses the causes of this phenomenon, and its implications for ecological responses to climate change. The focus then shifts to a discussion of Northern Hemisphere climate change, and its causes and ecological effects. Palearctic migration is then briefly introduced, and the risks posed by climate change – as they relate specifically to phenology – are discussed. Some factors that enable species to respond to climate change, or that constrain responses, are then discussed. The discussion then briefly considers other factors that might affect the phenological patterns discussed in this thesis.

The life-history of the barn swallow s introduced, focusing on aspects dealt with in the thesis. Changes in barn swallow phenology are summarised, providing a framework against which to assess the results of this study. Finally, the analytical rationale of each chapter is introduced, as are the data and methods.

Climate, seasonality and phenology

The timing of the seasons is fundamentally important to life on earth because it affects the timing of plant and animal life-cycles (‘phenology’) (Walther *et al.* 2002). The earth’s climate – that is, average long-term broad-scale weather patterns – changes constantly at a slower or faster rate everywhere on earth, causing variability in the timing of seasonal events, and the life-cycles, or phenological schedules, of plants and animals have evolved to cope with a certain degree of variability in climate and seasonal timing. Northern Hemisphere climatic conditions, north of the sub-tropics, are characterized by large seasonal differences in temperature and precipitation, with dry and often freezing winters; most growth and reproduction occurs in spring and summer – this pattern is in contrast to that of the Southern Hemisphere, where the difference between summer and winter conditions is less pronounced (Alerstam 1990). In the Nearctic and Palearctic zones where winters are too cold for growth and summers are mostly warm, the “start of spring” occurs when temperatures reach a threshold above which plants begin to produce leaves and insects emerge to feed on the new growth. The food provided by the abundance of new plant growth and insects, together with the increasing temperatures, supports the start of breeding in the higher tropic levels; there is thus a time-lag in start of spring activities, with the primary producers starting earliest and the highest trophic levels starting latest (Alerstam 1990).

Since the 1950s, rapidly increasing greenhouse gas emissions (mostly of CO_2) have led to directional climate change, with many places becoming consistently hotter and drier over time (Vose *et al.* 2005). The effect of increasing spring temperatures between the 1950s and 2000s in the boreal regions of the Northern Hemisphere, in contrast to in temperate regions with mild winters, has caused spring activities to begin earlier, especially during the last decades of the 20th century (Walther *et al.* 2002, Lemoine & Böhning-Gaese 2003, Root *et al.* 2003, Menzel *et al.* 2006, Parmesan 2006, Knudsen *et al.* 2011). Warmer conditions have been moving northwards in Europe at an average rate of 2–14km per year from the 1950s to the 2000s – for example, the summer mean temperature for the city of Toulouse in the south of France was 3°C warmer and drier in the 2000s than during the 1950s, and Geneva in Switzerland was warmer and drier in the 2000s than in the 1950s (Beniston 2014). The northward shift of warm weather has been slower in the west and faster in the east of Europe (as far east as 24°E) (Beniston 2014).

Many ecological changes have occurred because of these climate changes (Parmesan & Yohe 2003, Knudsen *et al.* 2011, Chambers *et al.* 2013). The ranges of many species in Europe have shifted northwards under pressure from the northward shift of warm spring and summer weather, but at a rate five times slower than the shift in climate (Chen *et al.* 2011, Beniston 2014). Population declines in long-distance migrants in Eurasia and North America have been linked to an inability to respond fast enough to phenological changes at the breeding grounds (Jonzén *et al.* 2006, Møller *et al.* 2008). There is now a sense of urgency to explore why particular species are able to adapt fast enough to phenological changes, while others are not.

At the same time that populations are faced with climate changes, they might also be under pressure from other factors, such as hunting, the use of pesticides and pollutants (Sanderson *et al.* 2006), and land-use change and loss of habitat associated with increased agricultural activity (Lemoine *et al.* 2007). Further, droughts can reduce populations, as occurred for Palearctic long-distance migrant populations during the severe three decade drought from 1968–1997 in the Sahel, a region on which many of these species depend (Walther *et al.* 2011). There is still much to discover about the mechanisms and effects of climate change and constraints to change, particularly in the Southern Hemisphere and at population, community, and ecosystem levels (Knudsen *et al.* 2011, Chambers *et al.* 2013). Further, there is value in cross-validating findings using different methods and data sets (Knudsen *et al.* 2011).

Geographic differences in Palearctic climate patterns and climate changes

Geographic variability in responses to climate change is related to geographic differences in long-term average climate and short-term climate change. The temperate conditions of western Europe are the result of warm air flowing into Europe from the Atlantic – these winds have a moderating effect on the climate, generating warmer winters and cooler summers, and the warming effect decreases inland and to the east, causing harsher winters and summers (Seager *et al.* 2002, Seager 2006). From the west of Russia eastwards, the Palearctic climate is generally hotter in summer and colder in winter than further west in Europe, where temperatures are moderated by the onshore westerly winds that bring maritime conditions and milder weather (Beniston 2014). At the eastern edge of Siberia (54–55°N 109–110°E) in the Yenisei River Basin, climate is moderated by the influence of Lake Baikal, which brings warmer winters and cooler summers than in most of Siberia to the west (Ananin & Sokolov 2009).

Climate changes since the 1950s in European Russia and Siberia have been different to those in the UK, mainland Europe and Scandinavia – springs have generally started earlier (‘advanced’ in phenological terminology) by 10 to 20 days in western, central and northern Europe; however, springs have started later (‘been delayed’) by 14 days in far western Siberia, east of and close to the Ural mountains (55.5°N 60.5°E) (Ahas *et al.* 2002). Similarly, in southeastern Europe (Slovak Republic) the timing of arrival of migratory birds (Sparks & Braslavská 2001), and in the Balkans start of the growing season (Menzel & Fabian 1999) have shifted later. The far south east of Siberia near Lake Baikal became warmer and drier from the 1970s to 1990s; from the mid- and late-twentieth century, springs shifted earlier (mid-spring by 9 days) while all other seasons shifted later (mid-winter by 12 days) (Ananin & Sokolov 2009). In other parts of the Palearctic spring phenology has not changed, for example in northern Norway, between 1980 and 2000 (Barrett 2002). Generally, the warming that occurs during the Northern Hemisphere spring begins earlier in the west and later in the east; warm summer conditions, however, occur earlier in the south and later in the north (Ahas *et al.* 2002). The Baltic, northern European regions and Ukraine generally have more variable spring phenology than western Europe (Ahas et al. 2002). The Tibetan Plateau is a major migratory barrier in the south for most of the long-distance migrant passerines that breed in Siberia, and most migrants circumvent it (Irwin & Irwin 2005). On the Tibetan Plateau the start of spring plant growth shifted earlier more than twice as fast (about four days per decade) as boreal and Mediterranean regions (about 1–2 days per decade) from 1982–2011; the onset of plant growth in spring shifted later in the west, and earlier in the east, both by 5–10 days (Shen *et al.* 2015). There is still much to discover about the mechanisms and effects of climate change and constraints to change, particularly in the Southern Hemisphere and at population, community, and ecosystem levels (Knudsen *et al.* 2011, Chambers *et al.* 2013). Further, new studies using different methods and data sets are valuable for cross-validating existing results (Knudsen *et al.* 2011).

Palearctic long-distance migration

Bird migration is an adaptation to large-scale spatial seasonal differences in weather (particularly temperature) and food availability, and it enables migratory birds to live for most of the year in places where conditions are optimal for breeding and survival (Alerstam 1990, Berthold 1996). As a result of the climatic patterns that arise ultimately from the tilt of the earth's axis and its spin, most migrant birds breed in the Northern Hemisphere and migrate southwards during the northern winter, although relatively few species make the longest migrations across the equator into the Southern Hemisphere (Moreau 1972, Alerstam 1990, Walther *et al.* 2010).

Climate change could pose a greater risk to migratory species than to residents (Lehikoinen *et al.* 2004, Sanderson *et al.* 2006), and to long-distance migrants than short-distance migrants (Both & Visser 2001). Timing of breeding is influenced by when food is available at the breeding grounds (Martin 1987). When the timing of insect prey abundance changes at the breeding grounds, birds are generally at a disadvantage, because insect phenology responds to changes in temperature faster than bird phenology (Crick & Sparks 2006). However, because they are either present or nearer to the breeding grounds, resident species or short-distance migrants are potentially able to respond much faster than long-distance migrants to shifts in food abundance (Alerstam & Högstedt 1980, Lehikoinen *et al.* 2004). Selective pressure on some species to benefit from an earlier start of spring at the breeding grounds could cause mistiming between the main stages of the life-cycle, breeding, migration and moult, and the optimal conditions for each stage (Both & Visser 2001, Both et al. 2010). Further, ecological mistiming caused by different rates of climate change at the breeding and non-breeding grounds can cause population declines in long-distance migrants – this has been demonstrated for the Nearctic, but not the Palearctic (Jones & Cresswell 2010).

Migrant species leave their non-breeding grounds at dates determined by a combination of factors, including changes in day length, temperature, and the internal 'circannual' rhythms of the body clock, and they have evolved to arrive at an optimal time for breeding (Berthold 1996). External factors, such as intensity and timing of weather events, rainfall, prey and habitat condition can also affect the timing of migration (Berthold & Terrill 1991, Visser & Both 2005, Pulido 2007). These factors, and how they interact, can all contribute to constraining responses to climate change. Variable relationships between temperature and arrival have been demonstrated – for example, an increase of 1°C in spring temperature in Britain was associated with an advance of 5.4 days (Sparks & Tryjanowski 2007) or 1.6–1.8 days in mean arrival date (Sparks 1999); the same temperature increase in Finland and Slovakia was associated with an advance of 1.2 and 2.1 days respectively (Sparks 1999). And for several species in Norway, a 1°C increase in spring temperature caused arrival to advance by 1–3 days (Barrett 2002). Further, a 1°C increase specifically in spring temperature in Europe resulted in earlier spring phenology of both wild and agricultural plants of nearly 5 days; conversely, a 1°C increase in autumn temperature resulted in 2.4 day later autumn phenology (Menzel *et al.* 2006). The latter meta-analysis (Menzel *et al.* 2006) specifically tested whether these trends were biased by selective reporting of significant findings, and found that there was no bias, thus strengthening the evidence that there has been an advance in spring activities in Europe, and that this advance is related to increased temperatures.

It is not clear how behavioural (phenotypic) changes could occur at the non-breeding grounds in response to shifts in the timing of spring (and hence of food supply) at the breeding grounds. Responses to phenological changes at the breeding grounds would occur through microevolution, in response to the selective pressure to arrive and breed earlier (Jonzén *et al.* 2006). Even though adaptive responses have been demonstrated, for instance in barn swallows *Hirundo rustica* (Møller 2001), responses in one life-history trait do not necessarily solve the problem of mistiming (Winkler *et al.* 2002). For instance, pied flycatcher *Ficedula hypoleuca* populations in the Netherlands laid clutches earlier, but did not arrive earlier, over the period 1980–2000; earlier laying was in response to changes at the breeding grounds, namely increasing spring temperatures and earlier food supply (Both & Visser 2001). The birds were prevented from arriving earlier, however, because arrival date is constrained by the date of departure from the non-breeding grounds (and by other factors) (Both & Visser 2001). If the trends towards earlier food supply and earlier egg-laying continued, laying date would eventually be prevented from shifting any earlier by the lack of response in the arrival date; this constraint could lead to reduced fitness and population declines (Both & Visser 2001).

Phenological changes in long-distance migrants can result from climate changes encountered anywhere during their annual journey, and the evidence reflects this diversity of causes: they have been ascribed to conditions at the breeding grounds (Bussière *et al.* 2015) and during migration or at the non-breeding grounds (Saino *et al.* 2004, Balbontín *et al.* 2009, Robson & Barriocanal 2011, Ockendon *et al.* 2012, McKellar *et al.* 2013). Changes in rainfall variability and increasing average temperatures in the Southern Hemisphere have caused phenological responses in some Southern Hemisphere species (Chambers et al. 2013). However, temperatures at the breeding grounds at the start of breeding appear to be the overwhelming cause of changes in reproductive phenology for long-distance migrant passerines (including barn swallows) (Ockendon *et al.* 2013).

The barn swallow

The subject of this thesis is the nominate subspecies of the barn swallow, *Hirundo rustica rustica*, which breeds throughout the Palearctic as far east as the Yenisei Basin in Central Siberia (at about 92°E), and migrates mostly to southern Africa during its non-breeding season (Moreau 1972). For this reason, when I refer to the Palearctic in the context of barn swallows, I mean those regions west of 92°E. However, 'Palearctic migrants' in general refers to species from the entire Eurasian region.

The swallows and martins together comprise the family Hirundinidae (Turner 2004), and barn swallows belong to the genus *Hirundo* which is genetically closest to several other genera that build mud nests (Dor *et al.* 2010). There are 14 species in the genus Hirundo, and 10 of these are found only in Africa (Dor et al. 2010). Of the remaining four *Hirundo* species, *H. rustica* is cosmopolitan – its six subspecies breed, and some are resident, throughout much of Eurasia, parts of the Middle East and North Africa, and North America (Dor et al. 2010). The non-breeding ranges of the migratory *H. rustica* subspecies are located mostly in Africa or South America (Turner 2004). The second *Hirundo* species not restricted to Africa is *H. smithii*, which is found in Asia and Africa; the remaining two *Hirundo* species not restricted to Africa are found in Australia, New Zealand and the Pacific Islands (Dor et al. 2010).

The barn swallow *H. rustica* has six recognized subspecies – four are long-distance migrants (although the migration distances vary widely) and two are non-migratory (Moreau 1972, Cramp 1988, Turner 2006, Dor *et al.* 2010). Of the long-distance migrants, the nominate subspecies *H. r. rustica* breeds in the Palearctic (Figure 1), *H. r. erythrogaster* breeds in the Nearctic, *H. r. gutturalis* breeds in south-east Asia, and *H. r. tytleri* in north-west Asia (Moreau 1972, Cramp 1988, Turner 2006, Dor *et al.* 2010). Of the non-migratory subspecies, *H. r. savignii* is found in Egypt and *H. r. transitiva* in the Middle East (Moreau 1972, Cramp 1988, Turner 2006, Dor *et al.* 2010). The species *H. rustica* breeds at elevations up to about 3000m (BirdLife International 2012).

H. r. rustica spends the boreal winter in Africa south of approximately 10°N, but mostly south of the equator (Moreau 1972, Turner 2006, Walther *et al.* 2010), and possibly in wetlands in the south west of Madagascar (Gardner & Jasper 2011). *H. r. erythrogaster* spends the boreal winter mostly in South America (Cramp 1988, Turner 2006), with a breeding population that has become established in Buenos Aires, Argentina (Martinez 1983 *cited in* García-Pérez *et al.* 2013). The Argentinean breeding range has since expanded (Morici 2012, García-Pérez *et al.* 2013, Grande *et al.* 2015). The species is monophyletic (Dor et al. 2010), meaning that all the subspecies evolved from the same ancestral species. In this thesis the data, analysis and discussion are henceforth restricted to the nominate subspecies of the barn swallow, *H. r. rustica*, specifically to those individuals (comprising the vast majority) that spend the non-breeding season in Africa.

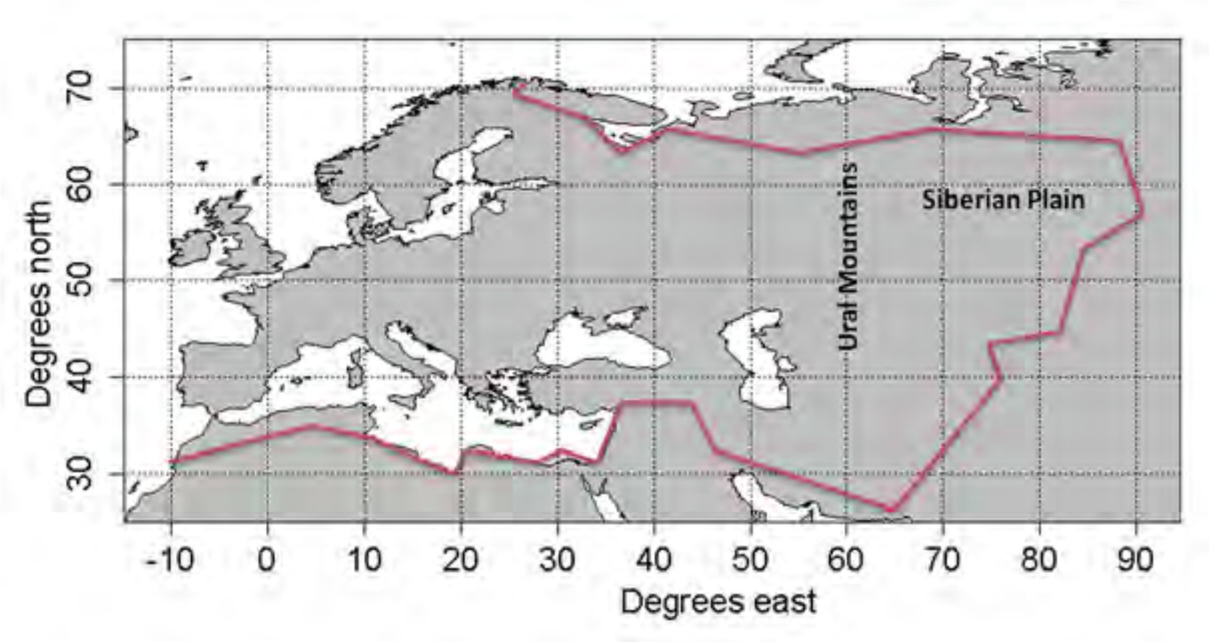

Figure 1. Map of the Palearctic, with the breeding range of the Palearctic barn swallow enclosed in the north, east and south by red line. The range extends in the west of the Palearctic throughout the British Isles. Range is based on Turner (2004) and Møller (1994). Coastline graphics obtained from www.naturalearthdata.com.

Figure 2. Photograph of a barn swallow *Hirundo rustica rustica* in song, by Charles J Sharp (Sharp Photography CC BY-SA 4.0). https://commons.wikimedia.org/w/index.php?curid=38704934.

Habitat and distribution

During migration and at their non-breeding grounds, barn swallows congregate in the evening in flocks and form communal roosts at night, typically in reed-beds (for example, *Phragmites australis* or *Cyperus papyrus*) (Turner 2004), or stands of tall grass such as *Pennisetum spp.* (Bijlsma & van den Brink 2005). Where reed beds or grass are unavailable, they sometimes roost communally in other vegetation types near water sources (Turner 2006). The number of birds using a particular roost can vary from several hundred to over a million from year to year, and is partly influenced by the size of the reed-bed and the timing and amount of rainfall at the roost (van den Brink et al. 1997).

Barn swallows arrive in South Africa from September to November, and depart mostly in April (Earlé 1997). The birds depend on a supply of fresh water to drink, and on enough moisture in the environment to provide breeding habitat for their insect prey (Cramp 1988). Every province in South

Africa has regions where some fresh water, such as wetlands, rivers or farm dams, is available in summer. The birds are thus capable of inhabiting any part of the country, as long as roosts and water are available. Conditions of drought or extreme temperature can cause high mortality among barn swallows in Africa, and this is thought to reduce population sizes in the Palearctic (van den Brink *et al.* 1995, van den Brink *et al.* 2000, Walther *et al.* 2011) – mortality results because fresh drinking water and insect prey become unavailable during drought (Cramp 1988; Turner 2006).

South African Bird Atlas Project reporting rates of barn swallows are greater in the eastern and northern parts than in the south western parts of the country (Animal Demography Unit 2016). There are regions within every province of South Africa where conditions and habitat during summer are ideal for barn swallows, so they are found throughout the country. The Western Cape has a Mediterranean winter-rainfall climate (Harrison et al. 1997), much like that at their breeding grounds in southern Europe. The rest of the South Africa is mostly summer-rainfall, with sub-tropical conditions on the east coast; conditions are generally drier and cooler on the Highveld, which is the eastern portion of South Africa with an altitude of 1500–2100m above sea level (Harrison et al. 1997). The Highveld region includes Gauteng, the Free State, the eastern parts of the Eastern and Northern Cape, Limpopo in the north, Mpumalanga in the east, and the North West province. The climatic differences become particularly relevant for barn swallows in the light of climate change in South Africa, which has affected the different regions differently (Cunningham et al. 2015). These changes will be discussed in the Synthesis Chapter.

Description

Barn swallows have for decades been the most abundant long-distance migrant songbird, but this situation is thought to have developed during the 1900s because of the global increase in human-built structures (mostly barns) that provide nesting spaces (Moreau 1972, Zink *et al.* 2006). Barn swallows are adapted to a temperate climate and are generally found wherever flying insects are abundant, and hence near water sources (Turner 2004). Their diet includes insects of 80 families, but they eat mostly

Diptera (flies) at the breeding grounds and mostly Hymenoptera (bees, ants, wasps and sawflies), Isoptera (termites and flying ants) and Coleoptera (beetles), and sometimes the seeds of African species of *Acacia* (renamed *Senegalia* or *Vachellia* (Kyalangalilwa *et al.* 2013)) at their non-breeding grounds (Turner 2004). Barn swallows are small, weighing 16–24g, with the long pointed wings that are typical of long-distance migrants (Mönkkönen 1995). They have a forked tail with long tail-streamers; the crown and upper parts of the back are glossy and dark-blue, the throat and forehead are chestnut-red with a distinctive dark blue breast-band, and the breast is cream or off-white; males are larger, glossier and have longer tail streamers than females (Turner 2004).

Life history – breeding, dispersal, migration, moult and aging

Barn Swallows arrive in the Northern Hemisphere at the start of spring and breed in the Mediterranean and boreal zones throughout spring and summer (Moreau 1972). Females returning for their first breeding season disperse further than males from their natal site, usually within 10km but sometimes much further (Cramp 1988; Turner 2006; Balbontín et al. 2009). Breeding begins shortly after arrival at the breeding grounds – earlier in the south (in February to April in North Africa and southern Europe), and later in the north (in June, in Finland and Siberia; Turner 2004). Barn swallows lay on average five eggs per clutch over five days, and the clutch is incubated for on average 15 days; nestlings then take three weeks to fledge, and parents provide care for a week after fledging (Møller 1991). A brood thus takes on average about 45 days to produce, with on average 47 days separating clutches (Møller 1991). They lay on average two (up to three) clutches each breeding season, with the proportion of second and third clutches greatest in the south of the breeding grounds where summer is longest, and decreasing to the north (and possibly decreasing from west to east) (Møller 1984). The first brood typically consists of four to five nestlings and the second of three to four; fledging success remains high at 80–90% throughout the season (Cramp 1988, Møller 1989, Turner 2004, Turner 2006). Pairs produce on average six or seven fledglings in a season, with the average ranging from three in northern Europe to eight in southern Europe (Cramp 1988, Møller 1989, Table 9.1 in Turner 2006).

Southward migration after breeding takes an individual barn swallow up to four months (Cramp 1988), and northward migration between five and ten weeks (Mead 1970, Huin & Sparks 1998). This difference is in accord with the theory that northward migrations should be faster than the southward migration, because migrating faster and arriving earlier as a result improves breeding success (Kokko 1999). During migration barn swallows can fly at 40–50kph, slowing down to forage (Park et al. 2001, Turner 2006, Bruderer & Boldt 2008). At such speeds they can relatively easily cover the reported distances of 350km per day (Rowan 1968) required for the fast northwards migration.

Adults typically return each year to the previous year's breeding and non-breeding sites, or to nearby sites (Rowan 1968, Moreau 1972, Oatley 2000). A third to a half of first year birds ('juveniles') survive both migrations to return to breed (Turner 2006). Of surviving adults, the average lifespan is one to two years, with few surviving to seven or eight years (Turner 2006). About one third of adults survive each year (Møller 1989).

Barn Swallows in their first year of life are considered immature, and from the 2rd year adult (D. Oschadleus, pers. comm.). However, as immature barn swallows moult into adult plumage during their first non-breeding season they become difficult to distinguish from adults, which makes aging difficult (Turner 2006). The Barn Swallow undergoes a complete moult, including body and flight feathers, mostly at the non-breeding grounds (Broekhuysen & Brown 1963, Ginn & Melville 1983). Some start to moult their body feathers at the breeding grounds, juveniles before adults (Jenni & Winkler 1994, Pérez-Tris et al. 2001). In southern Europe, about 9% of adults (but almost no juveniles) moult the first one to three flight feathers, and suspend moult during migration (Ginn & Melville 1983, Pilastro *et al.* 1998). Some barn swallows from southern Asia begin primary moult at the breeding grounds (Moreau 1972). Adults arrive first at the non-breeding grounds, and begin moult or resume if suspended, several weeks earlier than juveniles (Herroelen 1960, Broekhuysen & Brown 1963, Møller *et al.* 2011).

Changes in barn swallow phenology in the Palearctic

In the United Kingdom barn swallow arrival shifted earlier by 9 days from 1950 to 2005 (Sparks & Tryjanowski 2007), although the trend shown in Figure 2 of that study suggests that the advance occurred only from 1985 onwards. In Denmark there was no apparent change in mean first arrival date from 1984 to 2003 (Møller 2004). Barn swallows in the Slovak Republic spent a progressively shorter time at the breeding grounds from 1960 to 2000, with arrival shifting later by 2.5 days per decade, and departure earlier by 1.5 days per decade (Sparks & Braslavská 2001). In northern Europe, on the Baltic, barn swallows arrived earlier by 5 days per decade between 1973 and 1990 (Sokolov *et al.* 1998). In eastern Siberia near Lake Baikal, the breeding range of the north-west Asian subspecies, *H. r. tytleri* (Dor *et al.* 2010), mean first arrival of *H. r. tytleri* shifted earlier by 4 days between 1938–1962 and 1984–2002 (Ananin & Sokolov 2009). A direct link between ecological conditions at the non-breeding grounds, and arrival date at the breeding grounds, has been demonstrated for barn swallows – better conditions at the non-breeding grounds result in faster moulting, enabling earlier departure and thus earlier arrival at the breeding grounds (Saino *et al.* 2004).

For the barn swallow, arrival date at the breeding grounds is at least partially genetically controlled (Møller 2001, Saino *et al.* 2013). In species such as the barn swallow that usually raise one or two broods per season, a longer European summer could enable more birds to raise an extra brood (Jenni & Kéry 2003). This response could arise through phenotypic plasticity or microevolution. The relative importance of phenotypic plasticity and microevolution as adaptive responses to climate change was assessed among North American species – although adaptive responses were ascribed to both of these mechanisms, phenotypic plasticity alone was regarded as insufficient (Buskirk et al. 2012).

Analytical objectives

In contrast to the large amount of research into barn swallow phenology in the Palearctic, only two studies (Møller *et al.* 2011, Altwegg *et al.* 2012) have been published on barn swallow phenological changes at the non-breeding grounds. The analyses presented in this thesis aim to address this imbalance. There were three analytical objectives of this thesis. The first objective was to quantify the migratory connections of barn swallows between the breeding and non-breeding grounds (Chapter Two). The second objective was to estimate changes in the timing of primary feather moult in South Africa, from 1990 to 2012 (Chapters Three to Five). The third objective was to assess whether pre-migratory weight gain occurs in South African barn swallows in South Africa , and to estimate changes in the start of pre-migratory weight gain (Chapter Six). Using the estimates of chapters two to six, the objective of the Synthesis Chapter was to present a geographically integrated assessment of the relationships between the phenological shifts in South Africa, and phenological shifts and climate changes Palearctic.

Context and background relevant to each chapter

Migratory connections

Migratory connectivity (Webster *et al.* 2002) describes the connections created between regions by the populations that migrate between them. Mixing occurs when individuals from a breeding population migrate to two or more non-breeding regions and mix with other breeding populations at their destination. For example, tracking using light-level geolocators has shown that European hoopoes (*Upupa epops epops*) from the same breeding location used different migration routes and different non-breeding sites in north Africa (Bächler et al. 2010). Barn swallows breeding in Switzerland and northern Italy were tracked (also using light-level geolocators) to non-breeding sites mostly in Cameroon, but some migrated much further south, to South Africa (Liechti *et al.* 2015). Migratory connectivity can be estimated in many ways, for example, using ringing and recovery data (e.g. Perdeck 1977, Clark *et al.* 2009), single-capture methods involving the collection of samples and analysis of stable isotopes (e.g. Marra *et al.* 1998, Evans *et al.* 2003, Hobson *et al.* 2004, Møller & Hobson 2004, García-Pérez & Hobson 2014), trace elements (e.g. Szép *et al.* 2009) and genetic analysis (Webster et al. 2002). Tracking of individuals, for example radio telemetry (e.g. Iverson *et al.* 1996) or light-level geolocators (Bächler *et al.* 2010) provides insight into actual migratory routes as well as revealing destinations. Aside from bird ringing, most methods for estimating connectivity use costly devices or laboratory equipment and require more specialised training, making them suitable only for relatively small studies (Greenwood 2007). If the devices must be recovered, there is the added risk of non-recovery. For instance, to assess the suitability of geolocators for tracking hoopoes *Upopa epops epops* in Switzerland, 19 birds were fitted with geolocators; only five geolocators (26.3%) were recovered.

Bird ringing data is, however, abundantly available thanks to large ringing schemes and the work of thousands of citizen scientists over many decades, and much can still be learnt from it, particularly about patterns at population and species levels (e.g. Underhill *et al.* 1991, Spina 1999, Baillie *et al.* 2007, Greenwood 2007).

Aside from technological advances already mentioned, new ways to process ringing data are actively being developed to assess migratory connectivity. For example, correlating survival at the breeding grounds to primary productivity at the non-breeding grounds can provide estimates of potential destinations at the non-breeding grounds (Szép *et al.* 2006). Connectivity can be estimated by cluster analysis of the distances between capture and recapture sites – this method makes no assumptions about population structure(Ambrosini *et al.* 2009). And when the number of ringed birds is unknown, connectivity has been estimated from sparse recovery data (Korner-Nievergelt *et al.* 2012).

The migratory connections of barn swallows have been partially described in terms of the spatial distribution of ringing recoveries (Rowan 1968, Mead 1970, Zink 1970, Loske 1986, Oatley 2000), cluster analysis (Ambrosini *et al.* 2009), and stable-isotope analysis (Evans *et al.* 2003, García-Pérez & Hobson 2014). The early estimates of barn swallow migratory connectivity were that British barn swallows migrated to the eastern parts of South Africa, whereas those from Germany spent the boreal winter at least 1600km north of South Africa (Davis 1965, Moreau 1972). It soon became apparent, however, that there were exceptions. By 1968 it was clear that barn swallow populations in South

Africa came from breeding regions widely distributed throughout the Palearctic breeding range, as far east as the eastern limits of this subspecies, and that within different parts of South Africa there were variable mixtures of birds from different breeding areas (Rowan 1968). The subsequent review of all barn swallow recoveries of South African-ringed birds supported this finding (Oatley 2000). At a broader scale, cluster analysis of ringing recoveries suggests that populations from further north at the breeding grounds tend to migrate further south (Ambrosini *et al.* 2009), illustrating 'leap-frog' migration in barn swallows (Alerstam & Högstedt 1980, in Nearctic barn swallows, Hobson *et al.* 2015).

Ringing recoveries provide proof of migratory connections, but they nonetheless pose some difficulties: first, they are often rare, and they depend on human density in an area and awareness about finding bird rings, so they require intensive (or long-term) ringing effort to obtain; and second, recovery rates can vary by orders of magnitude over time, making comparison between periods difficult (Perdeck 1977). Further, distributions of ringing recoveries provide a biased estimate of connectivity because they do not take into account geographic differences in the probability of finding a ringed bird at the destination (Perdeck 1977). The 'division coefficient' method (Kania & Busse 1987) overcomes this bias by simultaneously estimating the ring re-encounter probabilities and proportions potentially migrating to each destination (division coefficients, or migration rates). Using the division coefficient analysis, I estimated the unbiased distributions of barn swallows from South Africa at their breeding grounds.

Estimating moult phenology

Moult is an essential process for birds because the plumage must be kept in good condition for breeding, migration and survival in general (Ginn & Melville 1983). The main activities in the avian life-cycle - breeding, migration and moult – usually comprise separate stages in long-distance migrants because of the energetic, physical and time constraints imposed by each process (Jenni & Winkler 1994). Because of these constraints, climate changes during one process can affect the entire life-cycle. To understand how the life-cycle of a species responds to climate change one therefore needs to consider the full life-cycle, including moult.

The timing of moult can change through two mechanisms: first, a change in the duration of moult through a change in the rate of feather material production in each follicle, which is closely linked to the metabolic rate (Lindström *et al.* 1993), and thus to prey availability and foraging efficiency. However, changes in moult duration are more likely to occur through a change in the number of primaries growing simultaneously (Rohwer & Rohwer 2013). Second, moult season timing can change through the entire moult period shifting earlier or later, with an unchanged duration.

The stage of moult of an individual bird caught just once can be directly observed and quantified quite accurately, hence moult phenology can be readily estimated (Ginn & Melville 1983, Underhill & Zucchini 1988). Early methods that were used to analyse moult data applied ordinary least-squares linear regression of moult score against date, or moult date against moult score (Pimm 1976). However, linear regression assumes that the residuals of the dependent variable are normally distributed, and that the variance is uniformly distributed throughout the range of the dependent variable, and these assumptions do not hold for moult data (Underhill 1985). Further, the progress of moult is a result of underlying physiological processes, not time, and the observation dates which make up the time series are biased by the ringing-timetables of the bird ringers – people go ringing when birds are likely to be seen, during good weather, and when they have time available – generally on weekends and holidays (the same bias applies to any volunteer-based sampling – Knudsen 2011). For these reasons, linear regression is statistically inappropriate for estimating population-level moult parameters from moult scores and observation dates (Summers *et al.* 1980, Summers *et al.* 1983, Underhill 1985).

A maximum-likelihood method (Underhill 1985, Underhill & Zucchini 1988) was subsequently developed specifically to analyse moult data. The model was then expanded to cater for species in which some parts of the population (those not yet moulting, or those finished moulting) are not represented in the sample (Underhill *et al.* 1990). The method has been reviewed analytically (Newton & Rothery 2000), and extensively used – a Google Scholar search for 'Underhill & Zucchini 1988' on 19 January 2016 indicated that this paper has been cited in 148 studies, and Web of Science lists 99 citing papers (eg. Cooper *et al.* 1991, Barshep *et al.* 2013, Dietz *et al.* 2015).

The original Underhill & Zucchini (1988) method assumed linear growth for the full tract of flight feathers. Moult progress is mostly linear in passerines (Ginn & Melville 1983), but not in all waders (Summers *et al.* 1980, Summers *et al.* 1983). Using the moult parameters estimated separately for each primary feather (Serra 2002, Underhill 2003), a method was then developed to estimate a flexible moult curve (Remisiewicz *et al.* 2009) – the flexible (and more complex) approach makes it possible, first, to accurately model moult progress when it is non-linear; and second, to check whether the assumption of linear moult progress (Underhill & Zucchini 1988) is supported. In the third chapter I apply this approach to the barn swallow moult data set, and assess whether the linear or flexible model is better supported by the data.

The second key assumption of the Underhill & Zucchini (1988) moult model is that all individuals have the same duration of moult. The moult model can estimate different mean durations and start dates of moult for different groups (Erni *et al.* 2013) – this provides a way to handle exceptions to this assumption, by estimating different durations for different groups. This capacity makes it possible to avoid over- or under-fitting the model unintentionally, which can occur when many groups are modelled separately and then the results compared. In the fourth chapter, I explore differences in the timing of moult in first year and adult barn swallows – if they have different moult durations, they should be analysed separately to obtain unbiased results. To inform this decision, I take into account the confounding factor of the risk that age is misclassified by ringers – young birds that have moulted into adult plumage are often classified as adults (Turner 2006). Widespread misclassification would make it impossible to analyse the age classes separately.

The focus of this thesis is changes in the timing of events, and in the fifth chapter I explore whether moult phenology changed over time in South Africa, and whether there were geographic differences. If it did, were the changes in the same direction as, and as large as, the reported changes in migration (Altwegg et al. 2012)? If changes were not detected, this would suggest that the moult period (the start or end of moult, or both) was unable to shift correspondingly to keep track with the changes in migration. This would indicate that one important physiological process (moult) was capable of limiting a phenological response in another process (earlier or later departure). I will discuss this in more detail in the synthesis.

Seasonal and geographic weight and body patterns

Whereas migration and moult are discrete stages in the life-cycle, body weight increases or decreases all the time, and by different magnitudes over various time-frames. Changes in body weight reflect mostly changes in fat content, and most energy is obtained through the breakdown of fat (Lindström & Piersma 1993). Hence, variability in body weight reflects variability in energetic resources and demands. Body weight fluctuates over short periods in response to weather (Ormerod 1989), food availability, and the risk of predation (Rogers & Smith 1993, McLeod *et al.* 2008). There are also clear seasonal patterns, most prominently winter fattening in resident birds (Nolan Jr. & Ketterson 1983) and pre-migratory weight gain in migratory birds (Biebach 1996). Further, there are daily weight fluctuations which can be large – for example, female barn swallows incubating eggs have been observed to increase in weight by nearly 15% and decrease by 9% in a day (Jones 1987). These daily fluctuations associated with the high costs of breeding are similar to the amount of fuel carried during migration in the Britain (Coiffait *et al.* 2011). For this thesis, barn swallows were observed during feather moult, which is an energetically demanding processes (Jenni & Winkler 1994). One might thus expect to see average weight decrease during moulting in some places, or at least not to increase during moulting. Analysing the change in body weight over time provides a window into the deposition and catabolism of fat which continues throughout the life-cycle. This can provide insight into preparation for, and competing requirements, of each activity (Jenni-Eiermann *et al.* 2002). Unlike moult scores, weight can take on a range of values and it reflects local environmental conditions, as well as phenotype; it can increase or decrease daily, and is not linear (Clark 1979). As a result, body weight is potentially a sensitive indicator of spatial, temporal and phenotypic variability, and a seasonal weight trend contains much useful information.

'Pre-migratory weight gain' is a rapid deposition of fat reserves in the weeks before migration, and is found in nearly all migratory birds (Berthold 1996), including barn swallows at their breeding grounds (Pilastro & Spina 1997, Rubolini *et al.* 2002, Coiffait *et al.* 2011). The main objective of this analysis was to assess the evidence of a period of pre-migratory weight gain in barn swallows at their non-breeding grounds, and to determine whether this stage showed any phenological change over time. Observing changes in pre-migratory weight gain phenology could help to clarify precisely how the phenological changes in barn swallows are mediated at the non-breeding grounds. I describe the synchronised seasonal weight patterns using a locally weighted linear regression (Mullers *et al.* 2009), and the date of start of pre-migratory weight gain was estimated directly using a maximum likelihood break-point detection method (Muggeo 2008), and used bootstrapping to generate non-parametric confidence limits for the estimated start of pre-migratory weight gain.

Summary of findings and synthesis

The changes in barn swallow phenology that were observed at the Palearctic breeding grounds presumably required compensatory phenological changes at the non-breeding grounds. Møller et al. (2011) described changes in barn swallow moult phenology, and Altwegg et al (2012) in migratory phenology in South Africa. The unexpected geographic patterns of these changes hinted at the effects of migratory mixing in South Africa. In the synthesis I present an integrated calendar of the pattern in barn swallow phenology, and consider whether migratory phenology is constrained by limitations related to moulting and the process of pre-migratory weight gain. Further, I present some predictions of phenological shifts at a broad geographic scale, in Siberia, the UK and western Europe, and the central part of the breeding range. I relate these predictions to climatic differences between these regions and discuss the implications for phenological constraints. The cumulative effects of climate changes at the breeding and non-breeding grounds are considered.

Bird ringing data used in this thesis

I obtained all data from the South African Bird Ringing Unit (SAFRING; Underhill & Oatley 1994) – the variables used were capture date and location, body mass, wing length (for fully moulted birds) and the moult score. Ringing is assumed not to cause any changes in the bird, particularly in migratory behaviour (Clark *et al.* 2009). Although a fraction of birds caught in mist nets may be injured or die as a result, an analysis of data from many ringing stations over many years has found that more than 99% typically survive without injury, and even injured birds generally have good survival prospects (Spotswood *et al.* 2012). Ringing can sometimes cause injury if it is done incorrectly. For example, infections can result from rings being fitted too tightly or incorrectly, and the injury frequency can depend on the type of ring used (Griesser *et al.* 2012). However, the vast majority of birds that are ringed are unscathed, if ringing is done by qualified ringers (de Beer *et al.* 2001). Mist netting and ringing are thus widely regarded as ethically acceptable sampling and marking methods

Compared to many other passerines, barn swallows can be removed from mist nests quickly and easily (S. Hofmeyr, pers. comm.). Most barn swallows are caught during targeted ringing, which often begins in the evening and goes on late into the night. Very few barn swallows are captured in the course of general passerine ringing activities. To capture barn swallows, mist-nets are placed at the edges of the reed-beds where they roost, and birds returning to the roost for the night after feeding are caught. The birds are placed in separate ringing bags for storage and returned to the bags after handling, and are released in the morning; many hundreds of birds can be ringed in a night by a group of experienced ringers (C. Jackson, pers. comm.).

More than seventy thousand barn swallows were ringed in South Africa between 1963 and 1968 in an effort to discover migratory connections (Elliott 1974). In line with this objective, birds were simply ringed, aged and sexed when possible, and released. Since the 1990s there has been growing recognition of the value of taking a full suite of observations, including at least the body mass, wing length, tail length, presence of brood patch, and moult score, for every bird – this approach to data collection makes possible range-wide and long-term analyses such as those in this thesis. This research highlights the value of citizen science data, and sets the stage for further long-term monitoring of the ongoing effects of climate and global change.

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Chapter Two

Migratory connections of barn swallows in South Africa to their Palearctic breeding grounds

Abstract

The timing of barn swallow migration in South Africa changed between 1987 and 2011, but with geographic variability. A possible explanation for this is that individuals from breeding populations separated and migrated to non-breeding quarters that were unevenly distributed across South Africa, and further that climate change had regionally variable impacts at the breeding grounds over the period. Recovery distributions reflect migratory connections, but they can be biased by geographic differences in the chance that a ring is recovered. I analysed barn swallow ringing records, obtained between 1952 and 2011, for five provinces in South Africa – Northern Cape, Western Cape, Free State, Gauteng, and KwaZulu-Natal (the source areas) and recoveries made north of the equator in three zones of the Palearctic – west of 10°E, including the United Kingdom (‘western’), between 10°E and 60°E (‘central’), including much of Europe and all of western Russia, and east of 60°E (‘eastern’), which includes Siberia as far as the Ural Mountains (the destination areas). For each source area, I calculated the proportions of ringed birds recovered in each destination area (the recovery distribution). I then estimated the ring re-encounter probability in each Palearctic zone and the ‘division coefficients’ (the proportions of ringed birds that potentially migrated) from each non-breeding zone to the breeding zones. Ring re-encounter probability declined from 40 birds per 1000 ringed in the western zone to 28 in the central zone, and 18 in the eastern zone. Birds from two or three Palearctic zones mixed in each South African zone, in varying proportions. Eastern South Africa (KwaZulu-Natal) contained birds mostly from the eastern zone, as well as the central zone. The vast majority of birds in north eastern South Africa (Gauteng) were estimated to be from the central zone. The central western part of South

Africa, the Free State and east border of the Northern Cape, contained birds mostly from the western zone. In the Western Cape in the south west of South Africa, the estimates reflected an almost equal mixture of birds from each Palearctic zone, with slightly more from the eastern zone. These results provide the geographic framework for explaining the changes in phenology described in the following chapters, and understanding their relationship to conditions in the Palearctic.

Introduction

The timing of barn swallow *Hirundo rustica* migration in South Africa changed between 1987 and 2011 (Møller *et al.* 2011, Altwegg *et al.* 2012), and there were puzzling differences in the changes between the geographic regions – in the north east, the midpoint of departure shifted earlier, and in the south west, departure shifted later; in the east (KwaZulu-Natal), arrival was earlier and departure was unchanged or later. This pattern could be the effect of climate change differences in different parts of the breeding grounds (Altwegg *et al.* 2012). This hypothesis assumes, first, that breeding barn swallow populations in these zones were unevenly distributed and to some extent separated in South Africa, making differences in the northern hemisphere climate change effects discernible in South Africa; and second, that climate changes were not uniform across the Palearctic. The first step in exploring this was therefore to quantify the migratory connections of barn swallows to their breeding grounds. The second part of the hypothesis, relating to uneven effects of climate change at the Palearctic, will be discussed further in the synthesis chapter.

Migratory connectivity researchers based in Europe or Britain have mostly reported on the destinations of birds ringed at their Palearctic breeding grounds and recovered elsewhere. Conversely, migratory connectivity research in southern Africa has mostly considered birds ringed in South Africa and recovered or caught alive in the Palearctic. In some parts of their range, barn swallows illustrate what is known as ‘leap frog’ migration, with those from furthest north at the breeding grounds migrating furthest south at the non-breeding grounds (Alerstam & Högstedt 1980, Ambrosini *et al.* 2009, Hobson *et al.* 2015). Some studies of barn swallows ringed in Europe and recovered in Africa suggest that birds from different breeding regions have distinct and separate territories at the non-breeding grounds: most western European (but not British) barn swallows spend the boreal winter near the equator generally in West Africa, whereas eastern European and Siberian barn swallows migrate to east Africa, and along the east coast of South Africa as far as Cape Town (Moreau 1952, de Bont 1970, Mead 1970, Zink 1970). There was also confusing evidence, even in the 1960s, that several small breeding populations divided and spent the non-breeding season in widely separated parts of Africa (Moreau 1972). Further, British barn swallows, which the early evidence suggested were restricted to the north eastern part of South Africa (Zink 1970, Moreau 1972), seemed to undergo a range expansion in the early 1960s into the former Cape Province (Mead 1970). Studies by researchers based in Africa have shown that barn swallows from throughout western and eastern Europe, and from Eurasia as far as 91°E, migrate south as far as South Africa, and mix at the non-breeding grounds (Rowan 1968, Oatley 2000): those ringed in the Western Cape have been recovered in Britain, eastern Europe and Siberia; those in the north east of South Africa migrate to all parts of the Palearctic; and those on the east coast migrate mostly to eastern Europe and Siberia. Further, barn swallows in Namibia and Botswana constitute a mixture of birds from England and from northern Europe (Loske 1986, van den Brink *et al.* 1997).

A useful way to describe the migratory connections between a group and the areas that the group migrates to, is to calculate the proportions of individuals in the group that migrate to each different place; these proportions add up to 100%, and describe the geographic distribution of a group of birds at their destinations (Webster *et al.* 2002). Ringing recoveries (in this study, rings found and reported from dead or live birds), or electronic tracking devices, provide information about the destinations of migrating birds, but recoveries are rare and tracking is expensive. A distribution of the recoveries of the ringed birds from a group tells one how many of the birds were recovered in each destination. Ringing recoveries are thus useful because they provide an estimate of the geographic distribution of the group. However, ringing recovery distributions are biased, because it is not equally likely throughout a species' range that a ring will be encountered and reported; in other words, for a given species migrating to a region, the species will have a particular 'ring re-encounter probability' or 'finding probability' (Perdeck 1977). Most studies of barn swallow migratory connectivity have mentioned this bias (Rowan 1968, Oatley 2000, Møller & Hobson 2004, Ambrosini *et al.* 2009). A method to account for this bias when using ringing recoveries to estimate migratory connectivity has been developed (Busse & Kania 1977, Busse 1981, Kania & Busse 1987).

The objective of this study was to estimate the proportions of birds that migrated northward from parts of South Africa to parts of the Palearctic, taking into account the different finding probabilities in different parts of the breeding grounds. These proportions are also called 'division coefficients' because they describe quantitatively how a group of birds is divided up over several destination areas (Busse & Kania 1977).

Methods

From the South African Bird Ringing Unit (SAFRING) data base (Underhill & Oatley 1994), I obtained all barn swallow ringing records and calculated the number of birds ringed annually in each province. Provinces are referred to using the provincial names and borders as in 2015, and were allocated based on the coordinates of each ringing location: Western Cape (WC), Northern Cape (NC), Free State (FS), Gauteng (GP), KwaZulu-Natal (KZN) (Figure 1a). The other four provinces of South Africa were excluded because they had either too few birds ringed or recovered to analyse.

Also from the SAFRING data base, all recoveries north of 36°N of birds ringed in South Africa were extracted. I consider recoveries to include all recovery sources – live recaptures and rings found on dead or hunted birds. In South Africa, barn swallows were mostly trapped on arrival in the evening at roosts using mist nets, according to methods described in the SAFRING Bird Ringing Manual (de Beer *et al.* 2001). These were grouped into three Palearctic longitudinal sections ('zones'): west of 10°E ('western'), between 10°E and 60°E ('central'), and east of 60°E ('eastern') (Figure 1b). The western zone includes the British Isles and part of western Europe and Scandinavia, and the central zone covers the rest of southern, western, eastern Europe and Scandinavia as well as the Eastern European Plan (from 35°E to 45°E) as far east as the Ural Mountains. The eastern zone covers the Siberian region east of the Ural Mountains. These zones cover the full extent of the breeding range of Palearctic barn swallows that migrate to Africa (Cramp 1988). I took into account the longitudinal distribution of recoveries when deciding on the divisions. Further, I chose these divisions for three reasons: first, the

Kania & Busse (1987) method limits the number of destination groups (in this case Palearctic zones) to at most the number of source areas; second, the distribution of recoveries suggested that different proportions of birds from each province would migrate to each Palearctic zone; and third, creating further divisions would have created zones with too few recoveries from some of the provinces. Each geographic zone – provinces in South Africa, or longitudinally separated regions in the Palearctic – is taken to reflect all the non-breeding birds, or breeding populations, living in that area.

I used the 'division coefficient' method (Busse & Kania 1977, Kania & Busse 1987) to estimate the different 'ring re-encounter probabilities' for each Palearctic zone, and for each province, the proportion of birds that migrated to each zone ('division coefficients'). The Kania & Busse (1987) method calculates the division coefficients by solving simultaneous equations, one for each source area, to obtain the 'ringing-recovery ratio' for each destination: the number of birds migrating to a destination that must have been ringed (throughout all source areas) to produce one recovery at the destination area (e.g. a ratio of 300:1 implies that 300 birds must be ringed to obtain 1 recovery). If there are two source areas (A, B) with ringing totals $\mathrm{N_A}$ and $\mathrm{N_B}$ and two destinations $(1, 2)$ with recoveries (r) at each destination from each source $(\mathrm{r_{1A}}, \mathrm{r_{2A}}, \mathrm{r_{1B}}, \mathrm{r_{2B}})$, the ringing-recovery ratios $(\mathrm{x_1}$, $\mathrm{x_2})$ can be obtained by solving this set of two equations (Kania & Busse 1987):

$$\mathrm{N_A} = \mathrm{x_1 r_{1A}} + \mathrm{x_2 r_{2A}} \qquad \mathrm{N_B} = \mathrm{x_1 r_{1B}} + \mathrm{x_2 r_{2B}}$$

The ringing-recovery ratio (x) multiplied by the number of recoveries (r) at a destination from a source area gives the total number of birds potentially migrating to that destination from that source area. The total potentially migrating to the destination divided by the total ringed at the source gives the division coefficients (D). For the two source and two destination example, the four division coefficients are given by

$$D_{A1} = (x_1 * r_{1A})/N_A \qquad D_{B1} = (x_1 * r_{1B})/N_B$$

$$D_{A2} = (x_2 * r_{2A})/N_A \qquad D_{B2} = (x_2 * r_{2B})/N_B$$

For each source area, the total number of the birds potentially migrating to each destination from one source equals the total number of birds ringed at the source; hence the division coefficients add up to one for each source. The inverse of the ringing-recovery ratio is the ring re-encounter probability for that destination.

I obtained 95% confidence limits for the ring re-encounter probabilities and division coefficients using the non–parametric bootstrap method of (Korner-Nievergelt *et al.* 2010). This method generates a new set of simultaneous equations for each resampled data set, and from the distribution of the estimates, the 2.5th and 97.5th percentile are taken as confidence limits . I used 1000 bootstrap samples (iterations) to obtain the confidence limits. The 'birdring' package (Korner-Nievergelt & Robinson 2014) for R version 3.1.2 (R Core Team 2015) was used for all calculations. I made a modification to the 'birdring' package so that, for each province, the division coefficients for each source area always added up to 100% of birds ringed, even when more than two source areas are analysed (approved by F. Korner-Nievergelt, pers. comm., 18 November 2014).

To illustrate the potential corrective effect of the Kania & Busse (1987) method, I also calculated the uncorrected recovery distribution for each province, dividing the total number of recoveries from each province by the number of recoveries made in each Palearctic zone. The recovery distribution thus ignores both the number of birds ringed at the source and any differences between destinations in ring re-encounter probability.

Migratory distances

An understanding of the average migratory distances covered by barn swallows from each South African zone will be useful in the Synthesis chapter. For this purpose, the mean great-circle distances (shortest distance over the earth's surface between two points) between the geographic coordinates of the ringed and recovered (or found) birds were calculated separately for each Palearctic zone and South African province. Records include barn swallows ringed in South Africa and recovered in the Palearctic, or vice versa. The results are presented as supplementary information.

Results

Data

The data set consisted of all SAFRING barn swallow ringing records collected between October and April from 1952 to 2011 in South Africa. Five provinces had enough records and Palearctic recoveries for analysis: Western Cape, Northern Cape, Free State, Gauteng, and KwaZulu-Natal. The final data set comprised 201195 records; from 1952 to 1986 there were 128048 barn swallows ringed, of which 87% were ringed between 1962 and 1971. A further 73148 were ringed after 1987 (Table 1, Figure 2). This ringing effort generated 552 recoveries in the Palearctic, giving an overall recovery rate of 0.27% (27 per 10 000; Table 1). The recovery rate from 1952 to 1986 was 0.38% (38 per 10 000), and from 1987 to 2011 it was 0.08% (8 per 10 000; Table 1). The distribution of the ringing and recovery dates was such that I could not divide the data set into two periods to analyse separately so as to compare ringing-recovery ratios between periods. As a result, the migratory connectivity estimates are for the entire period.

The central Palearctic zone, in which 61% of the recoveries were made, had the highest recovery rate at 0.17% (17 per 10 000) of all barn swallows ringed (Table 1). The eastern zone, in which 11% of the recoveries were made, had the lowest recovery rate, at 0.03% of those ringed (3 per 10 000; Table 1). The former USSR/Russia contributed the most recoveries (327) followed by Great Britain with 113 (Table 2).

Migratory connectivity estimates

Ring re-encounter ('finding') probability was highest for the western zone at 0.40% (95% CL 0.24% – 0.85%), lower for the central zone at 0.28% (0.23% – 0.34%) and lowest for the eastern zone at 0.18% (0.12% – 0.27%) – for each 10 000 birds ringed, 40, 28 and 18 recoveries are expected in each zone respectively (Table 3; Figure 3). The 95% confidence intervals of the finding probabilities for the western and eastern Palearctic zones did not overlap, whereas the limits for the central zone overlapped those of the western and eastern zones.

The estimated division coefficients (Table 3, Figure 3) reveal that barn swallows from different parts of the breeding grounds were widely mixed in South Africa, rather than being segregated. The mixture was structured rather than homogenous (Figure 3). Those from the western provinces of South Africa (Northern Cape and Free State, but not the Western Cape) were distributed across the western and central Palearctic zones (Northern Cape: 55% to the western zone; Free State: 76% to the western zone). The Western Cape birds were distributed roughly evenly across the three zones (28%, 31% and 40% to the western, central and eastern zones respectively). Those from furthest east (KwaZulu-Natal) in the central (39%) and eastern (56%) Palearctic zones. Birds from the north east (Gauteng) were distributed mostly (79%) in the central Palearctic zone. There was one recovery in the eastern zone of a bird ringed in the Northern Cape in 1967, but this was excluded from the analysis because of its uniqueness. The almost complete absence of recoveries from the Northern Cape and the Free State in the eastern Palearctic zone suggests that almost no birds from western half of South Africa breed east of the Ural Mountains, except those found furthest south (in the Western Cape). The Kania & Busse

(1987) method has several assumptions and requirements, discussed below, which were satisfied by the data.

Migration distances

The mean great-circle distance between ringing and recovery or finding ranged from 8882km between Gauteng and the central Palearctic zone, to 11175km (26% further) between the Western Cape and the eastern Palearctic zone (Table S1). Overall, mean distances ranged from 9009km between Gauteng and the Palearctic to 10043km (11% further) between the Western Cape and the Palearctic.

Discussion

The results of this study indicate that barn swallows from widely separated parts of the breeding grounds met and mixed in different parts of South Africa, and that the mixture was not homogenous. The results quantify and confirm the migratory connections described by Rowan (1968) and Oatley (2000), whose presentation of the recoveries of South African ringed birds in the Palearctic revealed widespread mixing of birds from different parts of the Palearctic.

In the 1950s and early 1960s barn swallow ringing was only just beginning in South Africa, and there were few recoveries in the Palearctic of birds ringed in South Africa (Elliott & Jarvis 1970). Based on the early work in the 1950s and 1960s, the distributions of recoveries of birds ringed at the breeding grounds suggested that barn swallows from Germany remained close to the equator during the non-breeding season. In the late 1960s, Rowan (1968) reported that barn swallows from South Africa had been recovered throughout the western and central Palearctic (in southern and northern countries, including those in Scandinavia), and as far east as Siberia. Even after this, reports from Europe still suggested that north western European barn swallows spent the non-breeding season nearer the equator in Africa, while British barn swallows reached South Africa, although acknowledging that there was some evidence to the contrary (Zink 1970; Mead 1970; de Bont 1970; Moreau 1972). However, the idea of full segregation of breeding populations at the non-breeding grounds was no longer tenable after Rowan's (1968) publication.

Migratory connectivity patterns estimated using groups of ringed and recovered birds depend largely on the researcher's choice of groups at the ringing area and divisions at the destination, and are thus not as objective as, for example, statistically determined clustering of recoveries (Ambrosini *et al.* 2009). In this study, however, I believe this subjectivity was justified by the hypothesis-based approach of this thesis: there was prior evidence of geographic differences (in barn swallow phenology) between the South African zones (Møller *et al.* 2011, Altwegg *et al.* 2012), and variability in migratory connectivity between areas is a possible factor explaining these differences. Further, I chose the longitudinal destination divisions because of the potential of range-wide differences in the effects of climate change at the breeding grounds. There are also important latitudinal differences in Palearctic climate and climate changes (Ahas *et al.* 2002), and it would be interesting to explore the relationships between climate change in northern and southern parts of the breeding grounds to barn swallow phenology at the non-breeding grounds. However, the Kania & Busse (1987) division coefficient method would not permit a latitudinal division in this case - this is because it has the requirement that each bird must be able to arrive at any destination without crossing over other destinations. A latitudinal division would violate this. I was further guided by the distribution of ring recoveries across the breeding range.

The reciprocal pattern of connectivity, that is, where in Africa barn swallows migrate to when they leave their Palearctic breeding grounds, has been partially described from distributions of birds ringed in the Palearctic and recovered in Africa (Zink 1970), and using a cluster detection method (Ambrosini *et al.* 2009). The reciprocal pattern is yet to be fully described. Progress has been made by comparing stable-isotope profiles and phenotypic and demographic characteristics in breeding populations – Møller & Hobson (2004) reported that a Danish barn swallow population comprised birds that used different parts of the non-breeding grounds in Africa, providing evidence for migratory mixing at the breeding grounds. Cluster analysis of ringed and recovered birds provided evidence at a broader scale – barn swallows from most of the Palearctic breeding range except the southern Palearctic were linked to South Africa, with birds from Eastern Europe and Russia were linked to eastern parts of Southern Africa, and those from Western Europe and the British Isles migrating to the western parts of Southern Africa (Ambrosini *et al.* 2009). My results are thus largely consistent with the findings of Ambrosini *et al*. (2009) as far as they relate to South Africa. Ambrosini *et al.* (2009) further showed that birds from south western Europe migrate to western central Africa, but noted that these birds might still have been migrating when encountered. Aside from the obvious differences in method, the protocol in this study differed from that of Ambrosini *et al.* (2009) in two ways: first, I showed the potential proportions migrating to the breeding grounds east of 60°E from southern and eastern parts of South Africa, whereas they excluded birds east of 60°E; and second, I assessed connectivity only from South Africa to the Palearctic, whereas they assessed connectivity in both directions, using records of birds ringed at the breeding grounds recovered in Africa or vice versa.

The patterns of migration revealed from my results reflect substantial mixing of widely separated breeding populations. My findings confirm the patterns of migratory connectivity which Rowan (1969) and Oatley (2000) reported from the uncorrected recovery distributions. The most noteworthy differences between the recovery distribution and the division coefficients were in the Western Cape and KwaZulu-Natal – more birds from these provinces migrated to the eastern zone than the uncorrected recovery distribution suggested. This reflects the importance of the vast land mass of eastern Eurasia for barn swallows (Moreau 1972).

Barn swallows are known to exhibit site-fidelity in their breeding area: dispersal takes place by returning first year birds (Turner 2006), which generally select a breeding site within 10 km from of their original nest. Adult barn swallows mostly return to the same breeding site (Cramp 1988, Turner 2006). Site-fidelity in returning adults has also been reported at the non-breeding grounds (Rowan 1968, Moreau 1972, Oatley 2000). The migratory connections I describe therefore apply in both directions: from the Free State, for example, an estimated 76.0% of ringed birds migrated to the western zone; I thus infer that the same proportion of birds found in the Free State potentially came from the western zone.

It is worth noting that the confidence intervals reflect the variability of the entire result set comprising the ring re-encounter probabilities and division coefficients, and that these cannot vary independently of one another. Most models do not estimate mutually-constrained sets of ratios, so this constitutes an unusual situation. Hence, to avoid misinterpreting the confidence limits, one must remember that the coefficients always change simultaneously if the data change, and the division coefficients for each province must always add up to one.

One of the requirements of the Kania & Busse (1987) method is that the finding probability should not vary during the study period. Unfortunately it was not possible to calculate the finding probability for the period from 1987 to 2011 because there were too few recoveries during this period. The sharp decline in recovery rate in the late 1980s was probably caused by a drop in ringing activity and reduced public awareness of bird-rings, related to the political and socio-economic changes in Europe and the USSR (Oatley 2000; M. Remisiewicz pers. comm.). Further, the recovery rate appears to be independent of the number of birds ringed; this is what one would expect if the probability of a Palearctic recovery was influenced by factors in the Palearctic. In spite of this difference in recovery rate, the potential proportions migrating to each Palearctic zone for the entire period were qualitatively the same as those for the earlier period (1952 to 1986). The actual proportions that migrated to each Palearctic zone in the period 1987 to 2011 might have been different to those before 1987, but there was not enough data to test this.

The Kania & Busse (1987) method could be used estimate the proportions potentially migrating southward to the non-breeding grounds. To do so, ringing totals in several separate Palearctic zones, and all recoveries of these ringed birds from the non-breeding range, must be included. Palearctic ringing totals would have to be obtained from the individual ringing centres or national ringing schemes (Korner-Nievergelt *et al.* 2012). There is a potential problem, however, with using the Kania & Busse (1987) method to estimate the southward pattern: non-breeding barn swallows are distributed throughout much of Southern Africa, and a large proportion of birds recovered in Africa, north of South Africa, might not yet have reached their southern destination. Hence, the assumption that the birds have arrived at their final destination might often be violated (Ambrosini *et al.* 2009). A method which does not require ringing totals (such as that developed by Korner-Nievergelt t al. 2012), might be appropriate to estimate the reciprocal range-wide migratory connectivity pattern, although the problem of birds captured while on migration would still need to be solved. Ultimately, a combination of methods, including those which do not require recapture, is necessary to provide a comprehensive understanding of connectivity patterns (Kania & Busse 1987).

The longitudinal zones that I defined at the breeding grounds do not correspond to western, central and eastern Europe, which all fall within the ‘western’ and ‘central’ zones used here. Hence, these findings are not directly geographically comparable with those of other studies which defined separate non-breeding territories for western, central and eastern European barn swallows (Moreau 1952; Zink 1970; Moreau 1972; Ambrosini *et al.* 2009). However, such a comparison was not my objective. The divisions were chosen rather to maximise the difference in climate between the zones, for the purpose of using these proportions at a later stage to relate differences in climate change at the breeding grounds and non-breeding grounds.

The division coefficient method (Kania & Busse 1987) has several assumptions, as well as requirements that enable the set of simultaneous equations to be solved. First, there must be at least two groups and two destination areas. All possible destination areas must be included, so that the proportions potentially migrating can reflect the migration of all birds from the source area (if some areas are omitted, the proportions potentially migrating will be biased; Kania & Busse 1987). The requirements of the simultaneous equations method are that there must be at least as many source groups as there are destination areas, and that if there are as many groups as destination areas, the equations must all differ. The barn swallow data satisfied these requirements.

The remaining requirements determine the accuracy and reliability of the results: first, the ringing-recovery ratio should not differ between areas within a destination zone (alternatively, the groups of ringed birds should be distributed similarly within each destination zone). The Palearctic breeding range includes regions such as deserts and ocean where the chances of encountering a ring are very low, so this requirement was probably not fully satisfied by the data (however, it is almost never fully satisfied; Kania & Busse 1987). Second, birds from each source area must be equally likely to survive migration, so that they are then equally available to be found and reported later. There was no reason to suspect that this assumption was violated in the barn swallow data. Third, each destination area can be reached without crossing another destination area (in other words, rings were not recovered from migrating birds). As barn swallows have the capacity to cross substantial barriers in a single flight (Moreau 1952, 1972, Cramp 1988, Rubolini *et al.* 2002), those breeding furthest east could cross the south eastern Palearctic deserts rather than choose a more temperate but longer route, hence this assumption is probably reasonable. Finally, the ring re-encounter rate for each destination area should not change during the sampling period, unless equal proportions of birds were ringed before and after the change in each source area. In the barn swallow data, the recovery rate dropped during the 1980s and the data in each zone were not equally divided between the two periods, so this assumption was violated – however, this did not bias the results because the vast majority of the recoveries were made before then.

To obtain these migratory connectivity estimates I used a non-statistical method that applies a basic algebraic method, solving a set of simultaneous equations, to estimate the key unknowns. The problem of unequal ring re-encounter probabilities at the migratory destinations had been identified at least a decade earlier in the 1960s, and it was solved by Busse & Kania (1977). The simplicity of the division coefficient method arises directly out of the constraints of the original data set – a single set of ratios of recovery totals to ringing totals for each zone and destination, from which one can estimate one set of division coefficients. Bootstrap sampling provides a way to estimate the uncertainty. The bootstrapped confidence limits provide the range of possible migratory connectivity scenarios that can be obtained from the single observation of ringing and recovery totals. These limits must however be interpreted carefully, because the division coefficients are mutually constrained (they must to add up to 100% for each source area).

Much could be learnt about the effects of climate through long-term surveillance to detect changes in migratory connectivity at a range-wide scale, and this would be impossible without citizen scientist bird ringers (Underhill *et al.* 1991, Greenwood 2007). The Kania & Busse (1987) method requires a relatively large number of recoveries, and the recovery rate of long-distance migratory passerines is low, hence it would require either many years of ringing at current rates, or several years of much more intensive ringing activity, before enough recoveries were available to determine a change in connectivity over time. Very intensive ringing efforts would be required to reveal short-term changes in connectivity, which might well result from rapid global change. A coordinated citizen science barn swallow ringing programme could provide the levels of ringing necessary to monitor changes in migratory connectivity, and the South African Bird Ringing Unit is the logical organisation to set up and coordinate a programme like this. However, if the recovery rate for barn swallows in the Palearctic continues to be as low as it has been since the early 1980s, such a project could take many years to generate sufficient recoveries for analysis of connectivity patterns after 1981. This situation would need to be addressed and possibly other analytical methods used to estimate barn swallow connectivity for periods after 1981.

The pattern of migratory connectivity presented here estimates at a broad scale how barn swallows populations from South Africa were distributed at the breeding grounds. Because recoveries from the entire breeding range of Palearctic barn swallows were available, this description provides a complete geographic framework in which to begin to interpret the changes in phenology that have been observed in South Africa. This context is key to explaining the complex relationships between changes in one part of the world and phenological responses that occur elsewhere and which then affect future events. Within this geographic context one can then begin to explore differences in the capacity of populations from different breeding and non-breeding zones to cope with global change. This is the subject of the rest of this thesis.

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Tables and Figures

Table 1. Numbers of barn swallows ringed in South Africa with SAFRING rings, and recovered in the Northern Hemisphere, by province and time period. Palearctic zones: western = W; central = C; eastern = E. For description of Palearctic zones see Figure 1b.

Province	Period	Ringed	Recovered				Recovery rate (%)			
			W	C	E	Total	W	C	E	Total
Free State	1952-1986	731	0	1	0	1	0.00	0.14	0.00	0.14
	1987-2011	15563	23	4	0	27	0.15	0.03	0.00	0.17
Northern Cape	1952-1986	6168	18	10	0	28	0.29	0.16	0.00	0.45
	1987-2011	9	0	0	0	0	0.00	0.00	0.00	0.00
Western Cape	1952-1986	21163	36	27	21	84	0.17	0.13	0.10	0.40
	1987-2011	6140	1	1	2	4	0.02	0.02	0.03	0.07
KwaZulu-Natal	1952-1986	11355	0	19	20	39	0.00	0.17	0.18	0.34
	1987-2011	17199	5	6	3	14	0.03	0.03	0.02	0.08
Gauteng	1952-1986	88631	70	258	11	339	0.08	0.29	0.01	0.38
	1987-2011	34236	2	12	2	16	0.01	0.04	0.01	0.05
All	1952-1986	128048	124	315	52	491	0.10	0.25	0.04	0.38
	1987-2011	73147	31	23	7	61	0.04	0.03	0.01	0.08
Total		201195	155	338	59	552	0.08	0.17	0.03	0.27
Recovery Total (%)			28	61	11	100				

Table 2. Numbers and percentages of South African ringed barn swallow recoveries in the Palearctic.

Country	1952–1986	1987–2011	Total	Percentage
USSR / Russia	314	13	327	59.2
Great Britain	89	24	113	20.5
Finland	17	4	21	3.8
Denmark	17	1	18	3.3
Ireland	12	1	13	2.4
Poland	10	2	12	2.2
Germany	6	2	8	1.4
Norway	6	1	7	1.3
France	4	0	4	0.7
Other	16	13	29	5.3
Total	491	61	552	100.0
Percentage	88.9	11.1	100.0	

Table 3. Division coefficients (proportions potentially migrating to each zone, reported here as percentages) estimated using the method of Kania & Busse (1987) for barn swallows ringed in South Africa and recovered in the Palearctic. Brackets enclose 95% confidence intervals. The division coefficients for each province add up to 100%. For description of Palearctic zones see Figure 1b.

		Western (W10E)	Central (E10_W60E)	Eastern (E60E)
	Ring re-encounter probability	0.40 (0.24–0.85)	0.28 (0.23–0.34)	0.18 (0.12–0.27)
Division coefficients	WC	28.4 (14.2–43.2)	31.2 (19.7–45.8)	40.4 (26.8–53.2)
	NC	55.4 (26.8–79.3)	44.6 (20.7–73.2)	(no recoveries)
	FS	76.0 (42.9–95.1)	24.0 (4.9–57.1)	(no recoveries)
	GP	14.6 (6.4–25.7)	79.4 (66.6–88.4)	6.0 (2.5–11.4)
	KZN	5.3 (1.0–13.9)	38.6 (23.5–55.8)	56.1 (38.0–72.0)

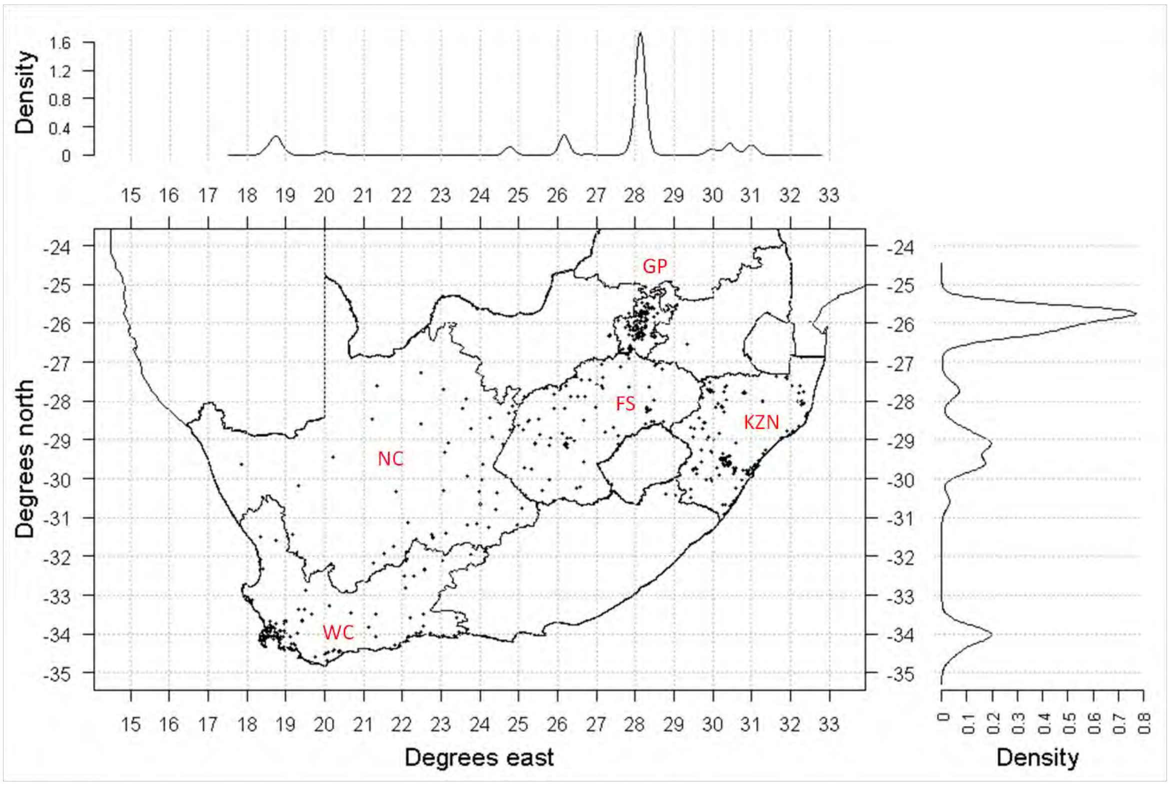

Figure 1a. Map of all barn swallows ringed between October 1952 and April 2012 in South Africa and submitted to SAFRING. The kernel density curves indicate the distributions of the number of birds ringed. Provinces: WC: Western Cape, NC: Northern Cape, FS: Free State, GP: Gauteng, KZN: KwaZulu-Natal.

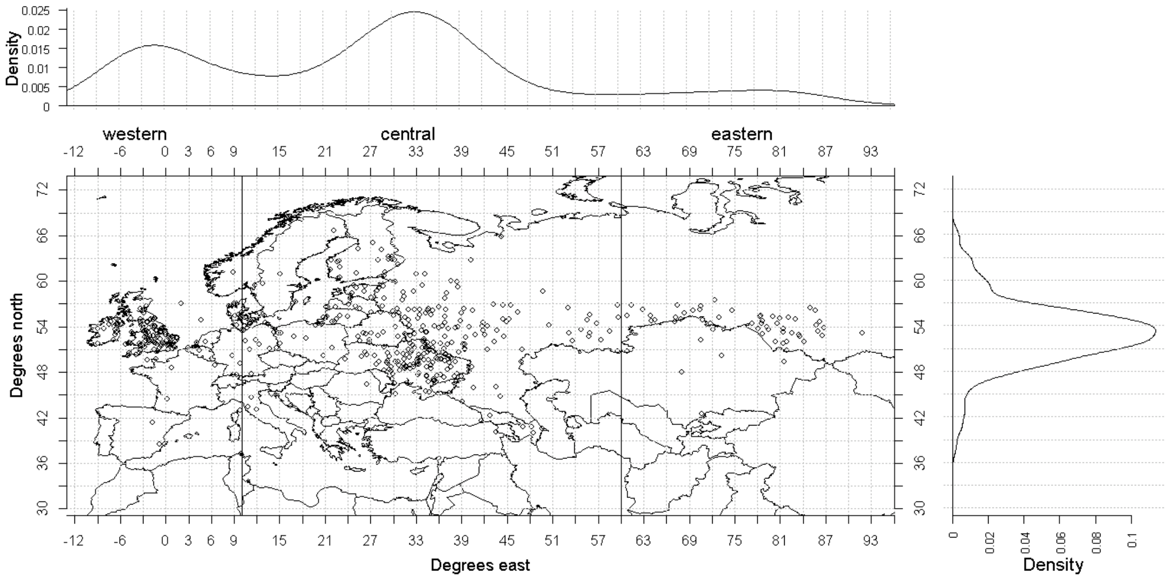

Figure 1b. Map of barn swallow recoveries in the Palearctic, for barn swallows ringed with SAFRING rings in South Africa between 1952 and 2011. Western zone: West of 10° E; central zone: 10°E to 60°E; eastern zone: east of 60°E.

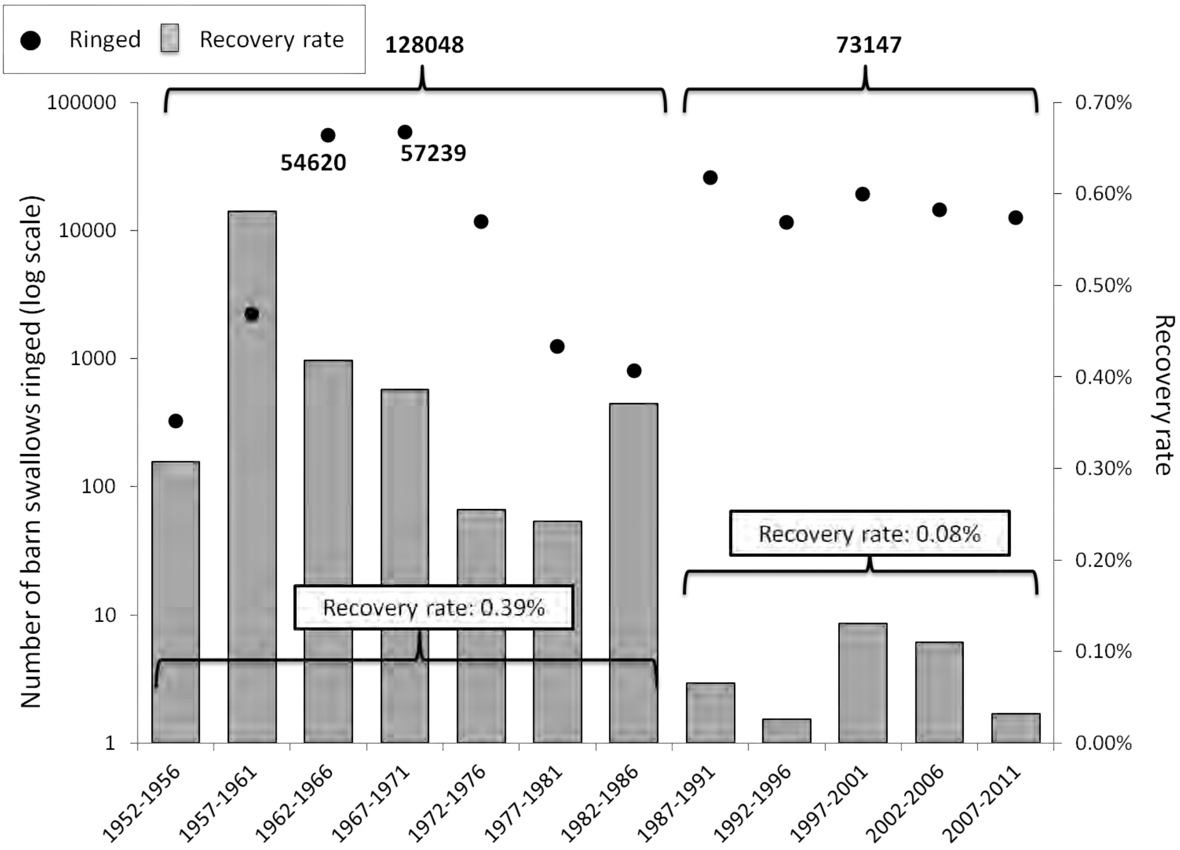

Figure 2. Numbers of barn swallows ringed in South Africa and the percentage recovered in the Palearctic, by five year period between 1952 and 2011. The totals ringed up to and after 1986 are highlighted above the graph. The totals ringed in the periods 1962-1966 and 1967-1971 are included as reference values.

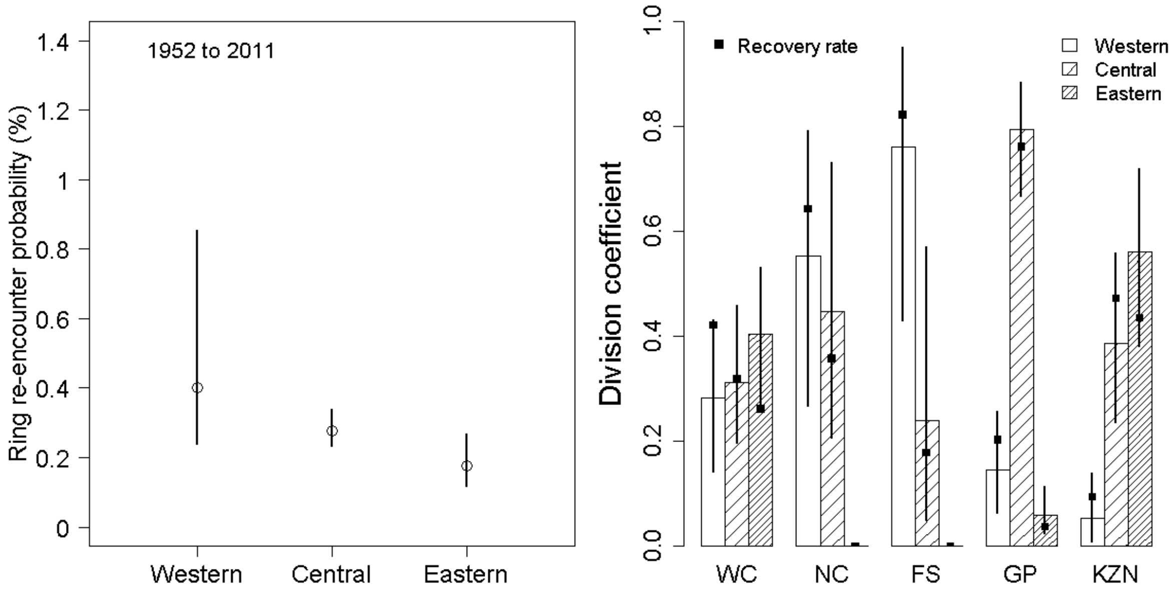

Figure 3. Ring re-encounter probabilities and division coefficients (proportions of birds that migrated to each zone) of barn swallows ringed in South Africa for the period 1952 to 2011, recovered in three Palearctic zones comprising the entire breeding grounds (see text). South African provinces: FS: Free State; NC: Northern Cape; WC: Western Cape; KZN: KwaZulu–Natal; GP: Gauteng. Vertical error lines are non-parametric 95% confidence intervals for the estimates. The division coefficients for each province add up to 1, and the coefficients do not vary independently of one another.

Appendix

Table S1. Great-circle distances of migration (km) (mean, sample standard deviation, sample size) between capture and recovery for barn swallows ringed in South Africa and recaptured or found in the Palearctic, or vice versa. For description of Palearctic zones see Figure 1b.

		Palearctic zone		
	western	central	eastern	All
Free State	9525 (368, 83)	9377 (824, 16)	9039 (n/a, 1)	9496 (469, 100)
Western Cape	9852 (311, 122)	9880 (487, 31)	11175 (427, 25)	10043 (585, 178)
KwaZulu-Natal	9697 (328, 34)	9278 (662, 31)	10163 (450, 23)	9671 (602, 88)
Gauteng	9180 (306, 146)	8882 (557, 293)	9955 (597, 13)	9009 (535, 452)

Chapter Three

Methods of modelling the phenology of flight feather moult in barn swallows ringed in South Africa

Abstract

Moult is an essential process for birds, because the plumage must be kept in good condition by the replacement of worn feathers. Estimates of the timing of moult in a population can be derived from observations of retrapped individuals, or from observations of birds caught only once. I used the Underhill-Zucchini moult model to estimate moult phenology in barn swallows *Hirundo rustica* for 19007 birds captured once in South Africa between 1990 and 2012. The Underhill-Zucchini model makes four statistical assumptions: moult progress increases linearly, the duration of moult is the same for all individuals in the population, the start dates of individuals are normally distributed, and moult stage does not affect an individual's chance of being captured. Accounting for the uneven distributions of the moult data, I tested whether the assumption of linearity was reasonable for the barn swallow data set by comparing the progress of moult modelled for the full primary tract against the cumulative feather growth curve (per-feather model), accounting for spatial and temporal variability. Records were first analysed together, and the analyses was repeated after dividing the data by province (Western Cape, Gauteng, southern KwaZulu-Natal) and time period (1990–2005 and 2006–2011). The duration of moult for the entire data set was 123 days (95% confidence interval (CI): 122–125) for the full tract model, and 134 days (127–141) for the per-feather model. The mean start and end of moult were 29 November (95% CI: 28 November–30 November) and 1 April (1 April–2 April) respectively, for the full-tract model. For the per-feather model, the mean start and end of moult were 3 November (29 October–9 November) and 17 March (16 March–19 March), significantly earlier than the full-tract model. The uneven distributions of the moult data, and of the moult scores

of primary feathers, had a greater impact on the per-feather model than on the full-tract model: using the per-feather model, the beginning and end of moult were estimated most inaccurately when the moult data distributions were most uneven. For some groups (Gauteng and southern KwaZulu-Natal, second period), the per-feather and full-tract models were consistent. I therefore chose the simpler full-tract model as the more parsimonious model for later analyses of the barn swallow data set. To test the validity of the Underhill-Zucchini barn swallow moult estimates, I compared the full-tract model estimates with estimates derived from a small data set of 34 same-season recaptures; the results were consistent. Finally, the mean moult start dates of individuals were normally distributed. These findings form the basis for the moult model specifications used later in this thesis.

Introduction

The Underhill-Zucchini moult model (Underhill 1985, Underhill & Zucchini 1988) is a maximum-likelihood approach that was developed specifically to estimate moult phenology within an appropriate statistical framework. The Underhill-Zucchini (1988) model has three statistical assumptions about the sampled population, on which the accuracy of the estimates depends: first, moult progress is linear from start to end; second, the duration of moult is the same for all individuals; and third, the moult start dates of individuals are normally distributed (Underhill & Zucchini 1988). In this chapter I test whether the barn swallow moult data set, collected in South Africa by citizen scientist bird ringers, reasonably supports the first and third of these statistical assumptions. In the next chapter the second assumption, relating to duration of moult, is addressed. These assumptions will not all be perfectly satisfied, but they do not need to be for the model to be trusted – the extent to which they are violated will determine the accuracy and reliability of the estimates; however, it is better to describe how the assumptions are violated, and to choose the most appropriate model specification accordingly.

Most methods for estimating moult phenology, including the Underhill-Zucchini (1988) model, have the statistical requirement that the rate of moult (to be more precise, the rate of feather material production over the entire period) is constant, so there is a linear relationship between date and moult index (Pimm 1976, Summers *et al.* 1980, Summers *et al.* 1983, Underhill 1985, Underhill & Zucchini 1988). The constant rate of moult can be at any scale, ranging from the linear growth of the individual primary feathers (Underhill 2003) to the linear growth of the full tract. In other words, the model in its original form cannot estimate a non-linear rate of moult. The Underhill-Zucchini model requires a constant moult rate because it estimates only three parameters – the mean start date, the duration (of which constant moult rate is the inverse), and an estimate of variability in start date (Underhill & Zucchini 1988); from these parameters it is only possible to model a straight line between the start and end of moult. One can model a non-linear moult rate by deriving a cumulative growth curve from separate per-feather models (Remisiewicz *et al.* 2009).

The moult model has the further underlying requirement that the moult must be ascending and continuous from start to finish (Underhill & Zucchini 1988). This means that the innermost primary must begin to moult first, and each subsequent feather must start moulting after the previous one (which is usually not yet finished when the next one starts moulting). Therefore, non-ascending moult or interrupted moult cannot be modelled using the Underhill-Zucchini (1988) moult model. Barn swallows have ten primary feathers on each wing; the tenth, the outermost, is vestigial and is not included in the scoring system (Ginn & Melville 1983). The primaries are moulted sequentially and continuously, starting with the innermost primary (Ginn & Melville 1983).

The first objective of this chapter was to determine whether the moult rate of the entire primary tract was in fact linear in barn swallows, and could thus be appropriately modelled using the Underhill-Zucchini model. I assessed consistency between the results of the two methods – a close match between the cumulative growth curve (Remisiewicz *et al.* 2009) and the constant rate full-tract model would provide evidence of real constant growth rate, and would justify using the simpler full-tract model in future. Where there were differences between the two methods, I tried to differentiate between real variability in moult rate and variability resulting from data quality.

The second objective of this chapter was to verify the assumption that the start dates of the individual birds are normally distributed. A final aim of this chapter was to verify the Underhill-Zucchini (1988) model estimates by assessing inconsistencies between them and moult estimates derived from barn swallows captured and recaptured within the same non-breeding season (Newton & Rothery 2000).

Methods

Barn swallow ringing records from 1990 to 2011 with primary moult and age-class data were extracted from the SAFRING data base (Underhill & Oatley 1994) on 5 June 2012. Years refer to non-breeding seasons – hence, 1990 refers to October 1990 to April 1991. Barn swallows were mostly trapped on arrival at roosts in the evenings using mist nets, according to methods described in the SAFRING Bird Ringing Manual (de Beer *et al.* 2001). I included recaptures in the full data set only if the recapture event took place in a subsequent non-breeding season to the first ringing event. The full data, consisting almost entirely of independent single observations, but containing second observations for a few birds recaptured in a later year, was used to model moult phenology according to the Underhill-Zucchini (1988) moult model, using the 'full-tract' and 'per-feather' models described below.

Guided by reported geographic differences in barn swallow phenology in South Africa (Altwegg *et al.* 2012), to which I refer later in this thesis, I divided the data into geographic zones and time periods, and estimated separate durations, mean start dates, and standard deviation on mean start date for these groups. In this chapter the three the zones which had the most data (Western Cape, Gauteng and southern KwaZulu-Natal) were used (Figure 1). The borders used here are similar to those used in Altwegg et al. (2012), but expanded to include more records. Potential age-class differences are dealt with in the next chapter. I did not group by sex because fewer than 20% of the barn swallows were sexed (SAFRING, unpublished).

To model moult phenology based on the progress of moult of individuals recaptured during the same moult, I obtained from the SAFRING data base a different set of records, for all barn swallows which were ringed and recaptured within the same non-breeding season, and which were moulting on both occasions ('same-season recaptures'). All SAFRING barn swallow data from 1990 to 2012 were queried to obtain the recaptures.

Moult was scored in the hand by qualified ringers using the British Trust for Ornithology technique (Ginn & Melville 1983) in which a worn feather is scored as 0, a growing feather from 1–4, and a fully grown replaced feather as 5. Birds with an entirely worn primary feather tract were classified as 'pre-moult', with an entirely replaced primary feather tract as 'post-moult', and with a tract showing active moult as 'in-moult'. Feather weights (Table 1) were obtained from a barn swallow skin in the collection of the National Museum in Bloemfontein (R. Nuttall pers. comm.) according to the recommended protocol (Underhill & Joubert 1995). For comparison with the feather weights used, feather weights from three more barn swallow specimens were subsequently obtained from Poland (M. Remisiewicz, pers. comm.). For one of the Polish specimens, only the left wing was available, and this specimen was included to increase the sample size.

The raw moult scores were transformed into proportion feather mass grown using the feather weights (Summers *et al.* 1983, Underhill & Joubert 1995), and this was used as the moult index in analysis. For convenience, this moult index was multiplied by 100 and reported as percentage feather mass grown ("PFMG"). The proportions of feather mass assigned to each moult score have been revised over time from thirds (Ashmole 1962) to fifths (Ginn & Melville 1983, Summers *et al.* 1983). The values used in this thesis were multiples of eighths (Underhill 2003): a moult score of zero is equivalent to zero feather mass and a moult score of one is equivalent to one eighth of feather mass. For moult scores two, three and four, the proportions of feather mass are 3/8, 5/8 and 7/8 respectively. A moult score of five is equivalent to 100% of feather mass.

Modelling moult phenology

I used the Underhill & Zucchini (1988) moult model, which uses maximum likelihood estimation, to estimate the key moult parameters – the estimated duration of moult (in days), and the mean start date of moult and standard deviation in start date for the population. The mean end date of moult is estimated as the sum of start date and duration (Underhill & Zucchini 1988). Standard deviation (SD) in start date is an estimate of the synchronicity of moult timing in the population around the mean start of moult (Underhill & Zucchini 1988). If PFMG does not increase linearly (which can only be revealed using a method that does not enforce linearity), one can sometimes improve linearity by applying an exponential transformation (Underhill *et al.* 1990, Barshep 2011). I did not apply this transformation, but I explored the reasons for any non-linearity. The moult model was fitted first for the entire primary tract ('full-tract model'), then for each primary separately ('per-feather model')

(Underhill 2003). The moult parameter estimates (duration, mean start and end of moult, and standard deviation in start dates) have been rounded off to the nearest whole day. Where required, the differences between estimates are calculated from these whole numbers. Standard errors on the differences between estimates are based on pooled variances.

Choosing the data type

The moult model requires that one specifies which stages of moult were present in the population during sampling, and this is achieved by choosing one of five possible "data types". This choice is made once for all the data that is used to run the moult model. I was guided in the choice of data type by the proportions of birds in various stages of moult in the data set. The five possible data types are as follows: type one is used if the stages of moult are only categorised (e.g. 'pre-moult', 'in-moult, 'post-moult'); type two is used for populations of birds in all stages of moult (pre-moult, moulting, and post-moult), and moult scores can be used; type three is used when only moulting birds are present; type four is used when only moulting and post-moult birds are present; type five is used when only pre-moult and moulting birds are present. Types one and two assume that all birds are available for sampling throughout the period. Data types one, two and three were made available in the original model (Underhill & Zucchini 1988), and types four and five were made available later (Underhill *et al.* 1990).

If the start and end of the period of residence are not adequately sampled, there will be insufficient information in the data set about moult during these periods. When a primary feather has insufficient information about the early or late stages of moult, estimates for that primary will be inaccurate. For instance, 10 000 birds might have been ringed (a large sample) but if they were ringed after all birds had reached moult stages 3 of the first primary, the effective sample size for moult stages 1 and 2 of the first primary would be zero. Further, inadequate sampling early or late in the season will make it difficult to determine whether pre- or post-moult birds were actually present in the population in meaningful numbers (which would justify data types two, four or five), or whether only moulting birds were actually present (requiring data type three). Hence, data types two, four or five should not be chosen without first assessing the distributions of moult scores.

Testing the assumption of linearity

As well as comparing the full-tract model and the cumulative growth curve, I calculated moult estimates for each third of proportion feather mass grown (‘per-thirds models’), to determine whether the rate of moult varied between the thirds of moult. To do this, the PFMG scores within each third were first rescaled to range from just above zero to just below one, using the following procedure. Scores of zero were discarded. To obtain a new variable containing the rescaled PFMG scores for the first third, scores from just over zero to just below 0.33 were divided by 0.33, and scores greater than or equal to 0.33 then changed to 1 (because for these scores the first third of moult was complete). Two more new variables were added, containing the rescaled PFMG scores for the second, and third, thirds of moult respectively. For the second third, scores between 0.33 and just below 0.66 first had 0.33 subtracted, then the remainder was divided by 0.33; for this third, scores below 0.33 were set to zero (because the first third of moult was not yet started) and scores of 0.66 or more were set to 1 (because these scores had completed moult of the middle third). For the final third, 0.66 was subtracted from scores between 0.66 and just below 1.00, and the remainder divided by 0.33. Scores below 0.66 were set to zero, because these had not yet started moulting the final third. The first group was thus composed of in-moult and post-moult birds (data type 4), the second group of pre-moult, in-moult, and post-moult birds (data type 2), and the final group of pre-moult and in-moult birds (data type 5). Using the three resulting new variables, ‘PFMG 1st third’, ‘PFMG 2nd third’, ’PFMG 3rd third’, moult was then modelled separately for each third as it would be for the full tract, specifying the appropriate data type.

Data types per primary

Every time the moult model is used one must specify the type of data used, in terms of which moult stages were present when sampling. When the full tract is considered, this involves specifying whether pre-moult or post-moult birds were present in the population and were sampled along with the moulting. To estimate moult for each primary feather individually, I used the same moult data set that was used to model moult for the full-tract. I divided the full data set by primary feather, to make up nine separate data sets.

Whereas the full-tract data set contains full-tract (nine digit) moult scores, in the data set for each primary feather contains only the moult scores assigned respectively to each primary feather. An appropriate moult data type must then be specified for each of the nine ‘per-primary’ data sets. If the data set contains birds that are pre-moult, moulting and post-moult (data type two, as described earlier), the data sets for every primary can contain values ranging from zero (pre-moult) to five (post-moult). However, if pre-moult and post-moult birds are excluded from the full data set (as in data type three), for the remaining moulting birds, the data set for the first primary feather will not include moult scores of zero (pre-moult), and the data set for the ninth primary feather will not include moult scores of five (post-moult). However, for the data sets for primaries two to eight, moult scores could range from zero to five, so data type two should be appropriate. Therefore, if a ‘type three’ full data set is used, although they come from the same full data set, the data type can differ between the primaries.

Comparing the cumulative growth curve and the full-tract model, to test linearity of moult

Using the method of Remisiewicz et al. (2009), I estimated cumulative growth curves. From the per-feather models, the number of feathers growing at any one time was calculated, and using these values, the total amount of feather growth produced on each day was estimated – this step accounts for the overlap of growth of adjacent primaries (Remisiewicz *et al.* 2009). Accumulating the total daily feather growth over the growth period of all the primaries generates an estimate of the cumulative growth curve for all primaries.

To estimate the duration for the entire primary tract from the per-feather models, I calculated the difference between the start day and end day of the cumulative growth curve (Remisiewicz *et al.* 2009). For this duration, I added approximate confidence intervals: for the upper limit, the difference between the lower 95% confidence limit for mean start date of primary one and the upper 95% confidence limit for mean end date of primary nine. I derived the lower limit in a similar fashion. I compared the cumulative growth curve, the per-thirds model, and the full-tract model by visually assessing the overlap between the confidence limits of the models.

The purpose of this analysis was to assess visually the differences between the flexible and inflexible moult models; it was not to assess geographic and temporal variation in moult phenology. Hence, I present detailed parameter estimates in a table only for the entire data set; for the data separated by zone as well as by time period, I present only the graphs showing the difference between the three models. I report all of the estimates for the zones and time periods in Chapter Five, which relates specifically to geographic and temporal variation in moult phenology.

Test of the assumption that individual moult start dates are normally distributed

I tested the assumption that the start dates of moult are normally distributed. I used the Underhill-Zucchini (1988) model for the full-tract (using data type 3) to obtain an estimate of moult duration for the entire data set. For each bird, multiplying each PFMG score by the estimated duration of moult yielded the number of days since the start of moult. The projected start day was estimated as the observation day minus the estimated number of days into moult. I then standardised the projected start days using the formula $(X - x)/s$ where X is each projected start day, x is the mean of the projected start dates, and s is the standard deviation of the projected start day. To test the normality of the projected start dates, I plotted the histogram of the standardised projected start dates, overlaid by the standard normal curve. I describe the distribution in terms of its kurtosis and skewness, using the package ‘e107’ (Meyer *et al.* 2012) for R (R Core Team 2015).

Moult phenology derived from same-season recaptures, for comparison with the moult model estimates

From the ‘same-season recaptures’ data set, I selected and analysed those records for which the difference between PFMG scores at the first and second capture was more than 0.10 (10%). From birds captured twice, assuming a constant rate of moult, the start and end dates of moult for each bird were estimated by extending the individual growth line (the progress of moult from capture to recapture in that bird) back to the start of moult (where PFMG = 0) and forward to the end of moult (PFMG = 1) and obtaining the dates at which these values fell. The progress of moult from the mean of the extrapolated start dates, to the mean of the extrapolated end dates, was then plotted and compared to the Underhill-Zucchini (1988) moult model estimates for this data set. For use in the Underhill-Zucchini (1988) moult model, the recaptures data set was randomly divided in half. From the birds in the first randomly selected half, the first capture event was used, and from the second randomly selected half, the second capture event was used. A new data set was then constructed from this random selection of first and second capture events, and the Underhill-Zucchini (1988) moult model applied to it.

Some further notes about the methods

Moult models were fitted using the R (v. 3.2.2) (R Core Team 2015) package ‘moult’ (v. 1.4) (Erni *et al.* 2013). The asymptotic standard errors for mean moult duration and start date were calculated using the covariance matrices generated by the moult package, which in turn are based on numerical derivatives of the likelihood function. Kernel density plots were used to illustrate the distribution of sampling dates and PFMG scores. Because the densities were used only to provide a visual illustration of the distributions and not for statistical purposes, I ignored the slight inaccuracy of the density distributions caused by the fact that PFMG scores are constrained to fall between 0 and 1, whereas density plots are not constrained.

This chapter and the next were completed when only feather weights from a single specimen were available. Using feather weights from a single specimen to obtain percentage feather mass grown could theoretically lead to inaccurate PFMG values and moult phenology estimates, although the risk is probably negligible, for three important reasons. First, the Bloemfontein specimen used was of a normal healthy bird with primary feathers in good condition. Second, much variability is introduced by the fact that moult scores are estimated visually for each primary feather – this variability probably far outweighs the slight differences in primary feather weights between individuals. Third, even inter-species differences in primary feather weights (for species with similar wing-shapes) do not lead to important differences in moult estimates (Bonnevie 2010), and therefore the much smaller differences between individuals of the same species are not likely to cause errors. Finally, to verify that no error was introduced by using a single specimen, feather weights of two more barn swallows were obtained (M. Remisiewicz, pers. comm.). To quantify the effect of using only the Bloemfontein specimen, I generated a second moult data set, using the same records as the full-tract data set. In the second data set, the PFMG scores were based on the means of the primary feather weights of all four specimens. Using the second data set, I obtained new Underhill-Zucchini (1988) moult model estimates. These were then compared with the original estimates obtained using the single specimen feather weights. Differences of several days between the estimates obtained from these two data sets would suggest that the single specimen feather weights were unrepresentative and hence unreliable. Conversely, if the single specimen feather weights were representative and reliable, I would expect the differences between the estimates to be negligible. I did not compare the estimates statistically.

Results

The data set contained 20141 records collected between 1990 and 2012 in South Africa (Table 2, Figure 1); of these, 591 (5.6%) were either pre-moult (2.9%) or post-moult (2.7%) (Table 2, Figure 2a). The distribution of sampling during the non-breeding season was uneven, with November, December and January contributing 37.9% of the records and February and March contributing 60.6% (Table 2, Figure 2a). A total of 84.8% of pre-moult birds were recorded before January (pre-moult birds recorded after January were probably post-moult birds that were miscategorised, but they made no difference to the results so this possibility was unimportant). Of the birds in the first third of PFMG, 61.5% were recorded in November and December; of those in the second third, 88.0% were recorded in January and February; of those in the final third, 93.7% were recorded in February and March, with more in March; and of post-moult birds, 89.1% were recorded in February and March (Table 2). Because of low proportions of pre- and post-moult birds in the data set (Table 2), I excluded these non-moulting birds from the final data set. All the proceeding analyses and results thus included only moulting birds (n = 19007; moult data type three). Considering only moulting birds, 57.6% had PFMG scores showing more than 50% feather mass growth (Figure 2b).

Without dividing the data into time periods or zones, the first and second primary feathers were fully moulted at the time of capture for more than 90% of the birds; more than 80% had the third and fourth primaries fully moulted at the time of capture; and for the ninth primary, only 22.6% of the birds recorded had begun to moult (Table 3a). Similar patterns occurred when the data were divided into zones and time periods (Tables 3a & b): for the WC zone in both periods and GP zone in the first period, more than 97.9% of the birds had completed moulting the first and second primary feathers at the time of capture.

Moult phenology estimates, used in testing the assumption of linearity

Moult duration for the full-tract model, for the countrywide data set, was 123 days, slightly shorter than the total moult duration of 134 days derived from the per-feather models (Table 4, Figure 3). Moult durations of the separate primaries ranged from 16 days for primary nine to 32 days for primary two, with an average duration of 24 days. Mean start of moult for the full-tract model was 25 days (SE 0.02) later than the mean start of moult for the first primary modelled separately. The mean end of moult for the full-tract model was 14 days (SE 0.01) later than for the mean end of moult of the ninth primary (Table 5). Moult progress for the full-tract model was generally consistent with the per-feather and per-third models from primary five up to the start of growth of primary nine (Table 4; Figure 3). When the separate zones and time periods were analysed, the full-tract, per-thirds and per-feather models were less consistent in those groups in which most birds were sampled after moulting their first four primaries (Table 3b), namely Gauteng and the Western Cape in the first period (Figure 4). In the remaining groups, in which more birds were sampled after moulting their first four primaries (Table 3b), the consistency between the full-tract, per-thirds and per-feather models was generally greater (Figure 4). For the second period, the models for southern KwaZulu-Natal and Gauteng were almost completely consistent up to the start of growth of the ninth primary (Figure 4). The differences in moult phenology between the zones and time periods are secondary to the objectives of this chapter. They are the subject of Chapter Five.

The kernel density plots of ringing date illustrate the fact that most of the ringing took place from January onwards, after the completion of the moult of the first four primary feathers (Figures 3 & 4). For the WC zone, period 1, the kernel density plots reflect the fact that most of the data were collected from January to April; this uneven distribution of moult information is likewise reflected in the extremely large confidence limits of the first four primaries for this zone and period (Figure 4).

The estimated order of moult for the first and second primaries was switched in some cases (for the southern KwaZulu-Natal zone in both periods, for the GP zone in the second period, and the WC zone in the first period); similarly, the ninth primary appeared before the eighth primary for the WC zone in period 1 (Figure 4).

Normality of the distribution of individual start dates of moult

The distribution of projected start dates in the full-data set was approximately normal, as indicated by visual inspection of the distribution, and by comparison of the normal curve with the standardised projected start dates (Figures 5a & b). For the estimated moult duration of 123 days, the kurtosis and skewness were close to the expected values for a normal distribution, and using duration of 20 days more or less did not change this result (Table 6).

Moult phenology derived from same-season recoveries

There were 59 same-season recaptures at the non-breeding grounds between 1952 and 2012, for which moult data were recorded; of these, 36 had an increase in PFMG of more than 10%, and of these two had unusually slow moult progress and were excluded, leaving 34 birds to analyse. All were captured between 1999 and 2010 (Figure 5).

The difference between the moult model and the extrapolated estimates was slight: the extrapolated estimates were five days later for the mean start date, and three days later for the mean end date, respectively. The difference in duration between the methods was two days (Table 7, Figure 6).

Effect of using feather weights from a single specimen

The differences in barn swallow moult phenology obtained using the single specimen feather weights and those obtained using the averages for the four birds (Table S1) were negligible: there was no difference in duration, −0.3 days in mean start date and −0.07 days in standard deviation in start date. In other words, no bias was introduced by using the feather weights from the single bird.

Discussion

The first objective of this study was to test whether the SAFRING barn swallow moult data supported the assumption of the Underhill-Zucchini (1988) moult model that flight feather moult progresses linearly. To test this assumption one must compare the full-tract model with the cumulative growth curve. The Underhill-Zucchini (1988) moult model comes with the recommendation that, to obtain reliable estimates, the records should be distributed over a longer portion of the non-breeding season. In other words, if the data (moult scores, ringing dates, and moult stages per primary feather) are too unevenly distributed, the results will be less accurate. Because it is flexible, the cumulative growth curve is more sensitive to this problem.

There was evidence in the literature of a constant moult rate in barn swallows – for barn swallows ringed in the Congo in the late 1950s, there was no evidence that moult rate changed during the moult period, or during the moult of one primary feather (de Bont 1962, 1970). To test the assumption of constant moult rate for barn swallows I compared the inflexible full tract model against two flexible models (per-feather, and per-thirds of PFMG) and looked for discrepancies. If one ignores the observed distributions of moult score and of sampling date (and especially the distribution of moult scores by primary feather), the plots from the flexible models suggest that the rate of moult begins slowly, then accelerates to a constant rate, and finally increases near the end during the growth of the ninth primary feather. However, taking into account the distributions of the data and of the moult information contained in the primary feather scores, there is good reason to doubt these ‘accelerating moult’ models.

The full-tract, per-thirds, and per-feather models were most consistent around the middle of the moult period, where the most support in the data was available. Based on this consistency, the date at which 50% feather mass growth is reached seems to provide the most accurate estimate of moult phenology possible, using this data set. In both directions away from the centre of the moult period the quantity of data declined, as did the amount of information (or variability) contained in the moult scores.

At the level of the primary feather, the same principle applies – the records should more evenly represent the stages of the growth of each primary. A model of any kind depends on their being sufficient information (that is, variability) in the data. The uneven distribution of moult stages by primary feather translates into an uneven distribution of information about moult, and therefore insufficient variability. In all cases, primaries five to eight had better quality information, because they had more evenly distributed moult stages. This explains why the estimates for the first four and the ninth primaries had large standard errors, making them potentially unreliable. The unreliability of the estimates for these primaries was most apparent for the smaller data sets (groups), where the greater uncertainty was not masked by large sample size. I therefore found that there was insufficient evidence to justify using the more complex cumulative growth curve over the simpler full-tract model.

Assuming that records are evenly distributed (which was not the case for all the primaries in the barn swallow data set), there are two main reasons why the rate of moult might vary over the moult period (Newton 1966), and which could thus violate the assumption of constant rate: the first reason is related to how moult progress is measured and scored; the second reason is when there is real change (flexibility) in the rate of feather material production during the moult period. The first reason was ruled out because I standardised the raw moult scores relative to the weight of each feather and of the feather tract (Summers *et al.* 1980, Summers *et al.* 1983, Underhill 2003). Hence, most the remaining flexibility is either real, or is caused by unexplained variability between groups (that is, when there are groups with differing moult phenology which have not been separated).

The results reflected in several ways the inappropriateness of the cumulative growth curve for the barn swallow data set. First, in the Western Cape and Gauteng zones, the inaccuracy (and hence over-fitting) was indicated by the wide confidence intervals for the first four and the ninth primaries, relative to the estimates in the middle of the non-breeding season. In these zones virtually all birds had completed moult of the first two primaries at the time of capture. Second, if barn swallow moult really did follow an accelerating trend, I would expect the size of the difference between the cumulative growth curve and the full-tract model to be fairly similar amongst the groups; however, the differences ranged from slight (in Gauteng in both periods, and Southern KwaZulu-Natal in the second period) to extreme (in Gauteng and Southern KwaZulu-Natal in the first period). Third, the flexible models extended well beyond the limits of the data in some groups (Western Cape, and Gauteng first period); and fourth, the paucity of information in the moult scores of the first primary caused this primary to be placed after the second primary in the sequence of mean start dates in most groups, even though in reality barn swallows moult their feathers in sequence (Ginn & Melville 1983). For the same reason, the order of the eighth and ninth primaries was switched for the Western Cape zone in the first period. This inaccuracy does not stem from an incorrect choice of data type: when there is so little information in a moult score, no change of data type can resolve the problem. Further, my choice of data type was based on prior knowledge and assumptions about the biology of the species; hence, within the framework I used to test the assumption of linearity, it would have been inappropriate to use different data types in order to obtain a better fit.

Having found that the cumulative growth curve was poorly supported near the start and end of moult, I now explore the evidence in favour of the full-tract model. For some of the groups – the Gauteng zone in the second period in particular – the flexible model was consistent with the full-tract model from the first to the eighth primaries. And in the southern KwaZulu-Natal zone in the second period, the discrepancy was slight from the second primary onwards. In Gauteng and southern KwaZulu-Natal, although the density distributions of moult scores were similar in the first and second periods, there were relatively more records earlier in the non-breeding season in the second period, thereby improving the accuracy (and linearity) of the cumulative growth curve, particularly over the first four primaries.

For the ninth primary, for the entire data set and for Gauteng in particular, the rate of moult was much faster than for the other primaries. However, in the Western Cape zone (in both periods) and the southern KwaZulu-Natal zone (in the second period), the rate was relatively close to that of the central primaries, although the ninth primary (cumulative growth curve) still ended moult earlier than the full tract model. The ninth primary might in reality moult faster than the others, as an adaptation to complete moult quickly before departure. However, it is known that many immature barn swallows begin their northward migration before completing the ninth primary (de Bont 1970, Jenni & Winkler 1994, Turner 2006), so there seems to be little evidence of pressure to moult the ninth primary faster. This also suggests that one of the assumptions of the Underhill & Zucchini (1988) moult model – that moult stage does not affect capture probability – is not necessarily well supported for barn swallows. Rather, if many birds depart before completing moult, this would cause the observed lack of information about the later-stages of moult for the ninth primary, and in turn bias the estimates towards the apparently faster moult which was observed for the ninth primary. In conclusion, for the barn swallow data set, the full-tract model seems to be fairly insensitive to the shortage of information for the first few and the ninth primaries. In other words, the partial violation of the assumption that moult stage does not affect capture probability has little effect on the full-tract model in this case, because there is so much data to support the estimates around for the central primaries.

Based on the partial consistency of the flexible model and the full-tract model in certain groups, and the generally insufficient support for the cumulative growth curve, and taking into account that the full-tract model is simpler, I decided to use only the full-tract model in the analyses later in this thesis. By assessing the moult data distributions in the light of the model's assumptions I was able to choose an appropriate model specification for the barn swallow data set. The results strongly suggest barn swallows have linear primary moult, although to verify this would require a more evenly distributed data set, with regular sampling from the very beginning of arrival of barn swallows to their final departure.

Normality of distribution of individual start dates of moult

The second objective of this study was to assess whether the barn swallow data set supported the assumption that the individual start dates of moult were normally distributed. There was no reason to reject the hypothesis that the data supported this assumption. Derived from the duration estimated for the full tract, the standardised distribution of start dates was closely matched by a standard normal curve, and the skewness and kurtosis were almost the same as expected for a standard normal distribution. This finding is interesting because there is no *a priori* reason why the start (or end) dates of moult should be normally distributed. In fact, one can make a reasonable case for normally distributed, or skewed or peaked distributions of these parameters, and it is possible to modify the model to assume other distributions (Underhill & Zucchini 1988). It seems likely that the start (and end) of moult for an individual (or group of similar individuals) would depend largely on when the individual or group arrives or must depart, and on local conditions, so the distributions of these parameters for a particular group of similar birds, even those arriving on the same day, might well not be normal. However, for any data set consisting of a number of birds with different schedules, the chance that the start and end of moult are normally distributed increases because of the effect of averaging the schedules. An alternative method exists for testing normality of start dates: if the distribution of start dates were normally distributed, the cumulative proportion of birds in moult should increase at a rate described by the standard normal curve (Newton & Rothery 2000). The same method could be applied to the barn swallow data, and I expect that it would support the normality of barn swallow start dates.

Questioning the Underhill-Zucchini estimates

The third objective of this study was to assess whether the results of the Underhill-Zucchini (1988) moult model were consistent with estimates obtained using a different and yet also appropriate method. A model that is inconsistent with some other source of trusted information raises doubts, and consistency is encouraging. I tested whether the Underhill-Zucchini (1988) model generated accurate estimates for the ‘recaptures’ data set. As shown in the previous section, the individual start dates of barn swallows in South Africa were normally distributed. Based on this, one can assume that the means of the extrapolated start and end dates were accurate, assuming that the progress of moult was linear, as the earlier results suggest. The consistency between the Underhill-Zucchini (1988) moult model estimates for the recaptures data set and the averages based on the extrapolated start and end dates provide evidence that the moult model estimates are an accurate representation of reality, even when there are relatively few records.

Conclusions

The analyses used here provided insufficient evidence to justify using the more complex and flexible cumulative growth curve for this data set. Rather, the full-tract model which assumes linear progress of moult during the season was more appropriate for the barn swallow data set. In the next chapter I deal with the assumption that moult duration is the same for all individuals. To test this, one needs to separate the data into relatively homogeneous groups: with this aim, I explore the difficulty of separating the adults from immatures, given the risk of age misclassification. This chapter and the next form the basis for further fine-grained phenological analyses of barn swallow primary moult.

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Tables and Figures

Table 1. Barn swallow primary feather masses, relative feather mass, and cumulative relative mass, obtained from a skin in the collection of the National Museum in Bloemfontein, South Africa (R. Nuttall, pers. comm.).

Primary	Mass (g)	Relative mass	Cumulative relative mass
1	0.0101	4.9%	4.9%
2	0.0131	6.4%	11.3%
3	0.0156	7.6%	18.9%
4	0.0181	8.8%	27.7%
5	0.0223	10.9%	38.6%
6	0.0253	12.3%	50.9%
7	0.0287	14.0%	64.9%
8	0.0341	16.6%	81.5%
9	0.0380	18.5%	100.0%
Full tract	0.2053	100.0%	100.0%

Table 2. Seasonal distribution of South African barn swallow moult records, categorised into pre-moult birds, moulting birds grouped by thirds of PFMG (see text), and post-moult birds. Values in italics show percentages of records per month (rounding errors are present in the percentages).

Month	Pre-moult	First 3rd	Second 3rd	Third 3rd	Post-moult	Total
Oct	24	3	0	0	0	27
Nov	408	772	16	0	0	1196
Dec	69	1667	177	3	12	1928
Jan	54	1341	2951	149	11	4506
Feb	16	183	4705	2145	70	7119
Mar	20	3	848	3798	414	5083
Apr	0	0	0	246	36	282
Total	591	3969	8697	6341	543	20141
Oct	*4.1*	*0.1*	*0.0*	*0.0*	*0.0*	*0.1*
Nov	*69.0*	*19.5*	*0.2*	*0.0*	*0.0*	*5.9*
Dec	*11.7*	*42.0*	*2.0*	*0.0*	*2.2*	*9.6*
Jan	*9.1*	*33.8*	*33.9*	*2.3*	*2.0*	*22.4*
Feb	*2.7*	*4.6*	*54.1*	*33.8*	*12.9*	*35.3*
Mar	*3.4*	*0.1*	*9.8*	*59.9*	*76.2*	*25.2*
Apr	*0.0*	*0.0*	*0.0*	*3.9*	*6.6*	*1.4*
Total	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*	*100.0*

Table 3a. For moulting barn swallows, distribution of moult stages for each primary feather (P1–P9), first using the undivided data set, and second for the GP zone, divided by time period (period 1: 1990–2005, period 2: 2006–2011). Values are the percentages for each primary feather of records with each moult score. Greyed-out values reflect data that were excluded from the data set so that only moulting birds were analysed. Rounding errors are present in the percentages.

	Moult stage	Percentage of records by primary feather in each moult stage								
All data (n=19007)		P1	P2	P3	P4	P5	P6	P7	P8	P9
	0	0.0	0.5	3.8	8.4	14.8	24.5	42.1	58.9	77.4
	1	1	1.5	2.2	2.8	3.9	6.4	8.5	8.1	6.3
	2	0.8	0.9	1.2	1.5	2.2	4.1	5	5.4	4
	3	0.7	0.8	1.1	1.6	2.7	4.7	5.3	5.2	4.7
	4	1.3	1.5	2.4	3.6	5.7	8.9	9.6	8.9	7.5
	5	96.2	94.8	89.4	82.2	70.7	51.4	29.4	13.5	0.0
	Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
GP, period 1 (n=4476)		P1	P2	P3	P4	P5	P6	P7	P8	P9
	0	0.0	0.1	1.1	3.8	8.9	20.2	43.4	63.5	79.8
	1	0.1	0.3	0.9	1.6	3.8	7.6	8.7	5.9	6.0
	2	0.2	0.5	0.8	1.1	2.5	5.8	5.9	5.2	4.0
	3	0.3	0.6	1.0	1.7	3.4	5.9	5.0	4.7	3.2
	4	0.5	0.6	1.1	2.5	5.3	8.5	8.3	8.3	6.9
	5	98.9	97.9	95.0	89.4	76.3	52.0	28.6	12.3	0.0
	Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
GP, period 2 (n=582)		P1	P2	P3	P4	P5	P6	P7	P8	P9
	0	0.0	0.3	3.1	8.9	20.1	37.6	55.5	66.8	81.6
	1	0.7	1.4	2.6	4.3	6.2	5.7	4.5	5.5	4.6
	2	0.7	0.9	1.0	2.6	3.3	5.2	5.5	5.2	3.4
	3	0.7	0.3	1.7	2.2	4.0	5.2	4.6	4.1	4.6
	4	1.0	1.7	3.8	7.2	9.5	6.7	7.4	6.0	5.7
	5	96.9	95.4	87.8	74.7	57.0	39.7	22.5	12.4	0.0
	Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 3b. For moulting barn swallows, distribution of moult stages for each primary feather for the sKZN and WC zones, by time period (period 1: 1990–2005, period 2: 2006–2011.). Values are the percentages for each primary feather of records with each moult score. Greyed-out values reflect data that were excluded from the data set so that only moulting birds were analysed. Rounding errors are present in the percentages.

	Moult stage	Percentage of records by primary feather in each moult stage								
		P1	P2	P3	P4	P5	P6	P7	P8	P9
sKZN, period 1 (n=2887)	0	0.0	1.0	8.4	16.3	22.5	28.5	42.6	58.0	79.4
	1	1.8	2.7	3.5	2.6	2.2	4.5	8.3	8.7	7.1
	2	1.9	2.2	2.4	1.9	1.9	3.5	4.5	6.8	3.8
	3	1.7	1.6	1.5	1.2	1.0	3.5	5.3	5.9	4.9
	4	2.9	3.0	3.5	2.4	3.9	8.0	9.6	8.0	4.7
	5	91.7	89.4	80.8	75.6	68.4	52.0	29.7	12.7	0.0
	Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
sKZN, period 2 (n=3803)	0	0.0	1.4	8.5	18.2	29.7	41.0	56.6	72.0	87.7
	1	3.0	3.9	5.4	5.7	5.8	7.3	10.3	9.3	5.8
	2	1.8	1.6	2.3	2.3	2.3	2.9	3.3	2.7	1.9
	3	1.5	1.4	1.5	2.3	2.1	3.7	4.4	3.6	2.2
	4	1.7	2.2	3.6	5.0	4.9	6.5	5.4	4.5	2.4
	5	92.0	89.5	78.7	66.6	55.2	38.6	19.9	8.0	0.0
	Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
WC, period 1 (n=374)	0	0.0	0.0	0.8	1.6	5.1	13.6	37.7	58.6	78.1
	1	0.0	0.8	0.3	1.3	1.6	5.9	6.1	4.5	4.0
	2	0.5	0.0	0.3	0.5	1.9	3.7	5.6	4.8	3.5
	3	0.0	0.0	0.3	1.1	3.5	7.5	5.3	7.2	5.3
	4	0.3	0.5	0.8	1.6	4.3	10.2	8.3	8.0	9.1
	5	99.2	98.7	97.6	93.9	83.7	59.1	36.9	16.8	0.0
	Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
WC, period 2 (n=2725)	0	0.0	0.0	1.1	3.2	9.7	22.9	45.8	66.7	86.1
	1	0.1	0.3	0.9	3.0	6.1	9.5	11.7	10.4	6.2
	2	0.1	0.2	0.6	1.6	2.5	5.0	6.7	5.4	2.3
	3	0.2	0.3	0.6	2.1	4.4	6.6	6.8	4.0	2.5
	4	0.4	0.7	2.8	5.4	9.3	13.0	10.1	7.0	2.9
	5	99.1	98.5	94.1	84.7	68.0	43.0	19.0	6.5	0.0
	Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 4. Durations of moult, percentage feather mass grown per day, and standard deviation in mean start date for South African barn swallows. Estimates in days unless otherwise specified. SE: standard error. PFMG.d^{-1}: percentage feather mass grown per day.

Portion of tract	Data Type	Duration (SE)	Duration 95% CL	Moult rate (% FMG.d^{-1})	Standard deviation on start date (SE)
Full tract	3	123 (0.73)	122–125	0.81%	17 (1.41)
P1	4	21 (1.83)	17–25	0.23%	21 (3.78)
P2	2	32 (0.99)	30–34	0.20%	23 (3.44)
P3	2	24 (0.55)	23–25	0.32%	20 (2.46)
P4	2	23 (0.42)	22–23	0.38%	18 (1.97)
P5	2	23 (0.35)	22–23	0.47%	17 (1.79)
P6	2	25 (0.31)	24–26	0.49%	18 (1.76)
P7	2	25 (0.30)	25–26	0.56%	18 (1.82)
P8	2	28 (0.34)	27–28	0.59%	18 (1.84)
P9	5	16 (0.64)	15–18	1.16%	14 (1.70)
Estimates for entire primary tract based on per-feather models	n/a	134	127–141	0.75	n/a

Table 5. Mean start and end dates of moult for South African barn swallows, and 95% confidence limits.

Portion of tract	Start day (SE)	Start date (95% CL)	End day (SE)	End date (95% CL)
Full tract	121 (0.43)	29 Nov (28 Nov–30 Nov)	244 (0.36)	01 Apr (01 Apr–02 Apr)
Primary 1	96 (2.69)	03 Nov (29 Oct–09 Nov)	117 (1.03)	25 Nov (22 Nov–27 Nov)
Primary 2	87 (1.21)	25 Oct (23 Oct–28 Oct)	119 (0.66)	26 Nov (25 Nov–28 Nov)
Primary 3	114 (0.59)	22 Nov (21 Nov–23 Nov)	138 (0.41)	16 Dec (15 Dec–17 Dec)
Primary 4	132 (0.41)	10 Dec (09 Dec–11 Dec)	155 (0.31)	02 Jan (01 Jan–02 Jan)
Primary 5	150 (0.34)	27 Dec (26 Dec–28 Dec)	172 (0.25)	19 Jan (18 Jan–19 Jan)
Primary 6	166 (0.28)	13 Jan (12 Jan–13 Jan)	191 (0.21)	07 Feb (06 Feb–07 Feb)
Primary 7	185 (0.23)	01 Feb (31 Jan–01 Feb)	211 (0.23)	26 Feb (26 Feb–27 Feb)
Primary 8	200 (0.21)	16 Feb (15 Feb–16 Feb)	228 (0.29)	15 Mar (15 Mar–16 Mar)
Primary 9	213 (0.26)	01 Mar (28 Feb–01 Mar)	230 (0.83)	17 Mar (16 Mar–19 Mar)

Table 6. Kurtosis and skewness of the distribution of projected individual start dates for barn swallows ringed in South Africa from 1990 to 2011, for several possible moult durations. Linear progress of moult was assumed. The kurtosis of a standard normal distribution is 3 and the skewness is 0.

Duration (days)	Kurtosis	Skewness
103	3.197	−0.273
113	3.151	−0.178
123	3.106	−0.126
133	3.049	−0.118
143	2.970	−0.140

Table 7. Moult phenology estimates for 34 barn swallows captured in South Africa twice within the same moulting season, and with an increase in percentage feather mass grown between first and second capture of at least 10%. Standard deviation in start date describes the spread of the start dates in the sample. Extrapolated duration was calculated as the difference between mean start and end date. Standard errors of means obtained using linear modelling with no explanatory variable.

Method	Mean start date (SE)	Mean end date (SE)	Duration (SE)	Standard deviation in start date	Standard deviation in end date
Extrapolation	129 (3.94) 7 Dec	247 (3.90) 04 Apr	118	22.97	22.73
Moult model	124 (9.50) 02 Dec	244 (6.93) 1 Apr	120 (15.38)	15.5 (6.25)	n/a

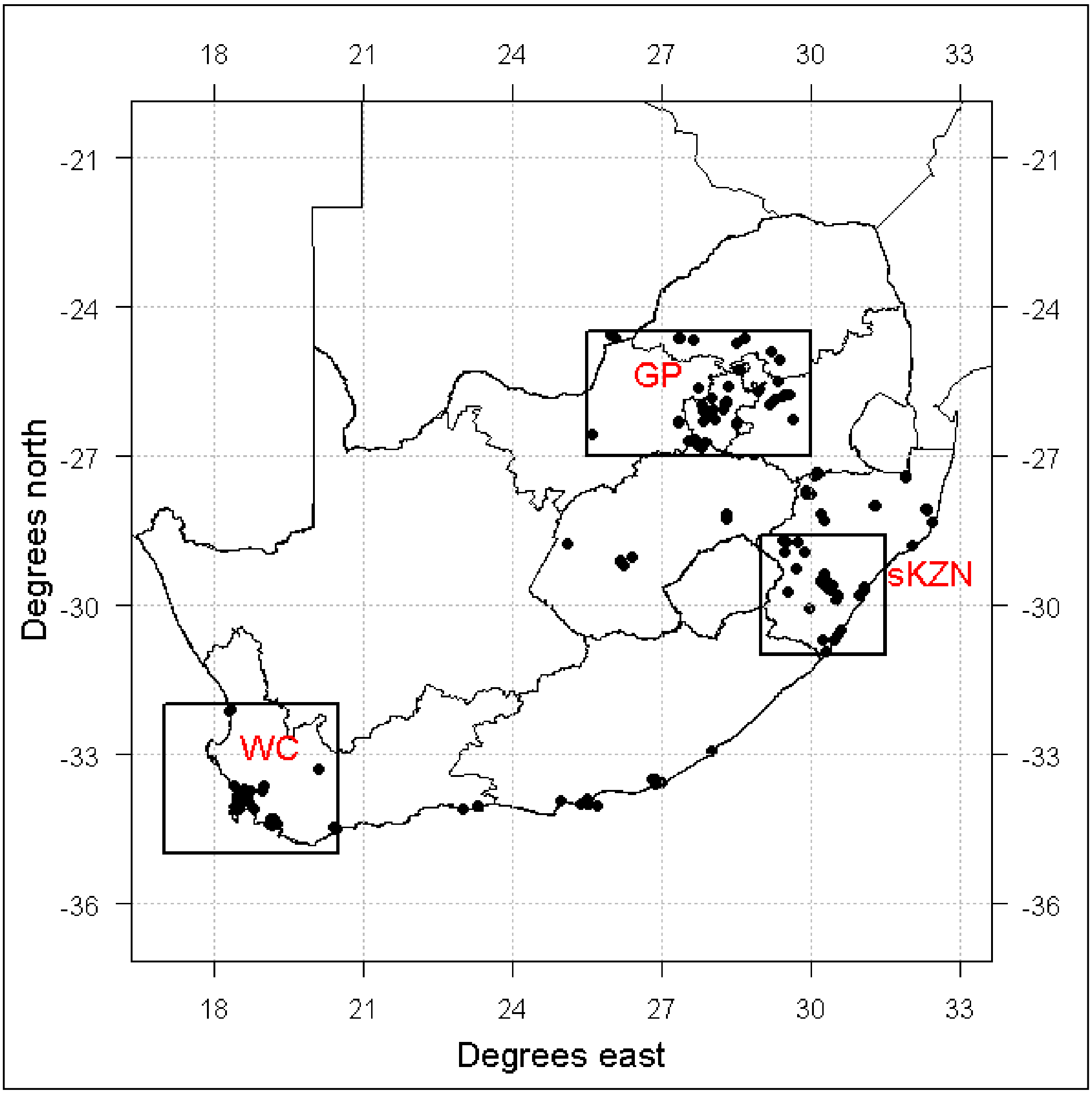

Figure 1. Map of South Africa showing the ringing locations of the barn swallow records used in this study. Points represent locations of records. Solid boxes enclose the zones used in this study, where most of the records were collected: GP: Gauteng; sKZN: Southern KwaZulu–Natal; WC: Western Cape.

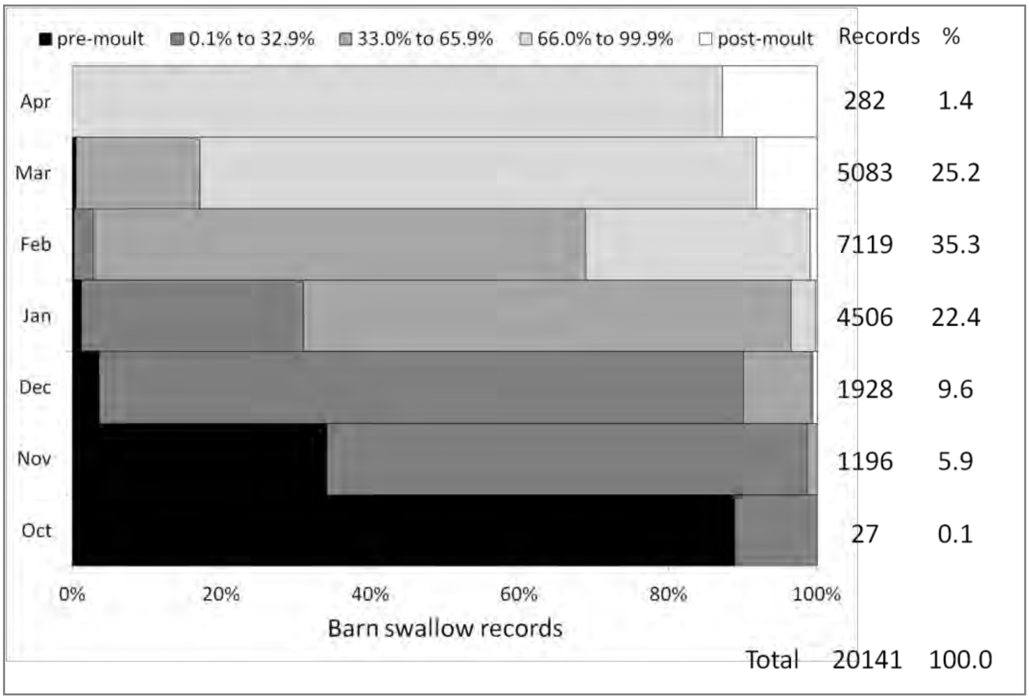

Figure 2a. South African barn swallow moult records collected between 1990 and 2012, for all birds for which moult and age data were available, by month and stage of moult.

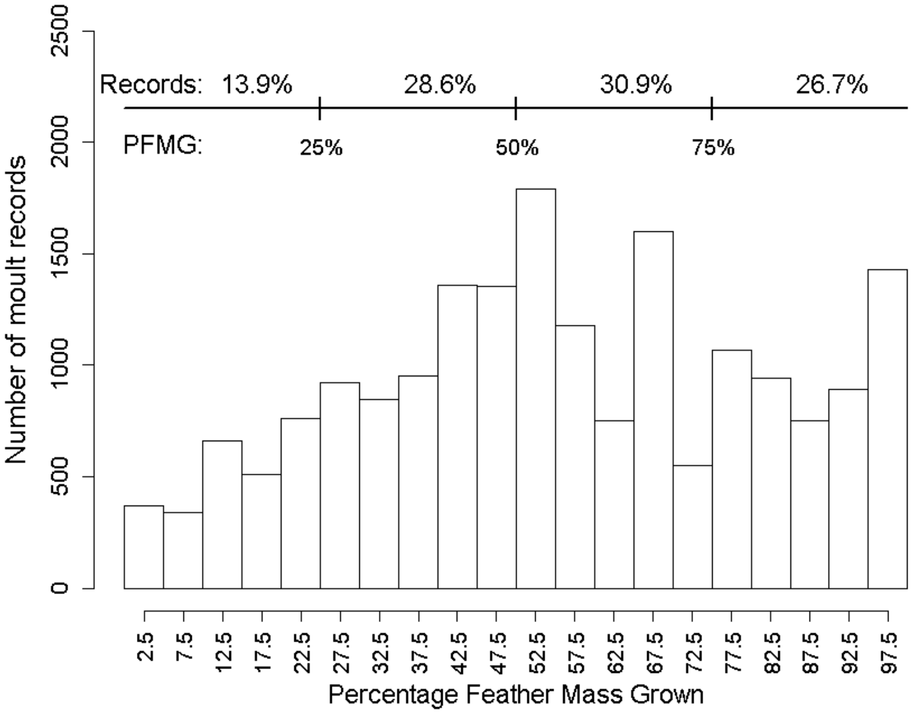

Figure 2b. Frequency of barn swallow moult records according to percentage feather mass grown (PFMG) for in–moult records (n = 19007).

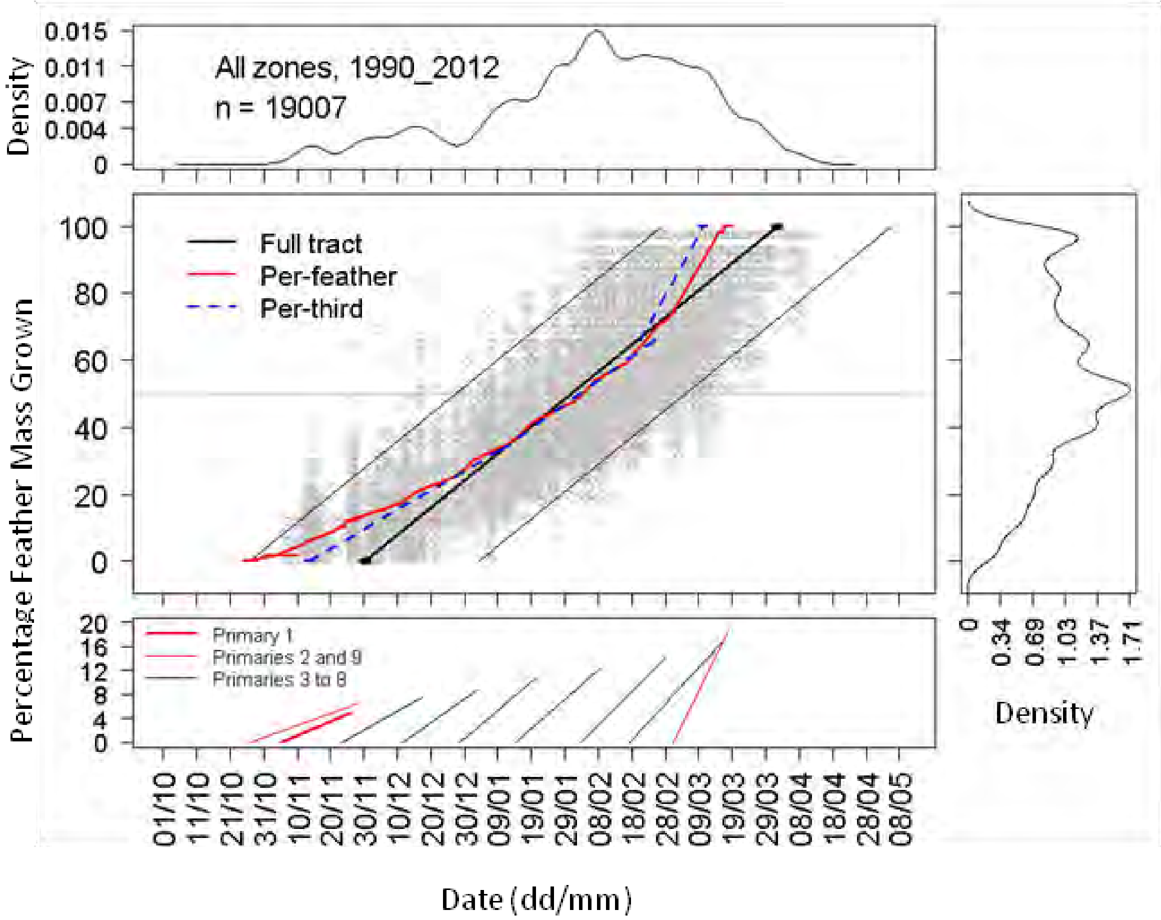

Figure 3. Barn swallow moult progress against date, shown separately for the full tract, per-feather, and per-thirds of feather mass growth models. Points represent the raw data. Thin black lines parallel to the full-tract plot show the 95% confidence intervals derived from the standard deviation in start date. Kernel density plots indicate distributions of ringing dates (x-axis) and PFMG scores (y-axis). The 95% confidence intervals based on estimated standard errors are shown as horizontal lines (in some cases these are too narrow to be distinguished from the modelled line or curves).

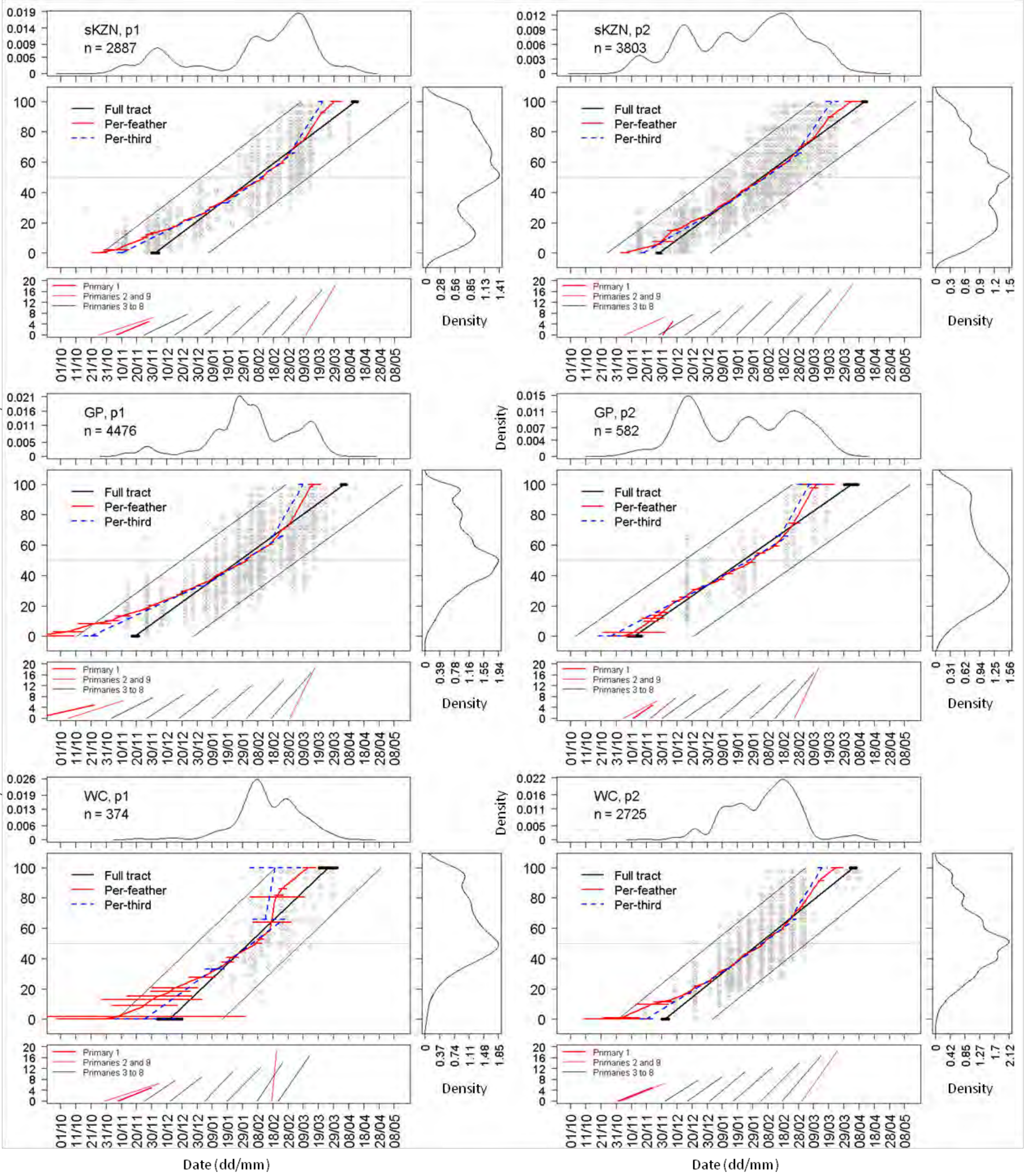

Figure 4. Barn swallow moult progress against date, shown separately for the full-tract, per-feather, and per-thirds of feather mass growth models. The data for each zone and time period were modelled separately. Time periods: p1: 1990–2005, p2: 2006–2011. Kernel density plots indicate distributions of ringing dates (x-axis) and PFMG scores (y-axis). GP: Gauteng; sKZN: southern KwaZulu-Natal; WC: Western Cape. For the description of points, lines and confidence limits see Figure 3.

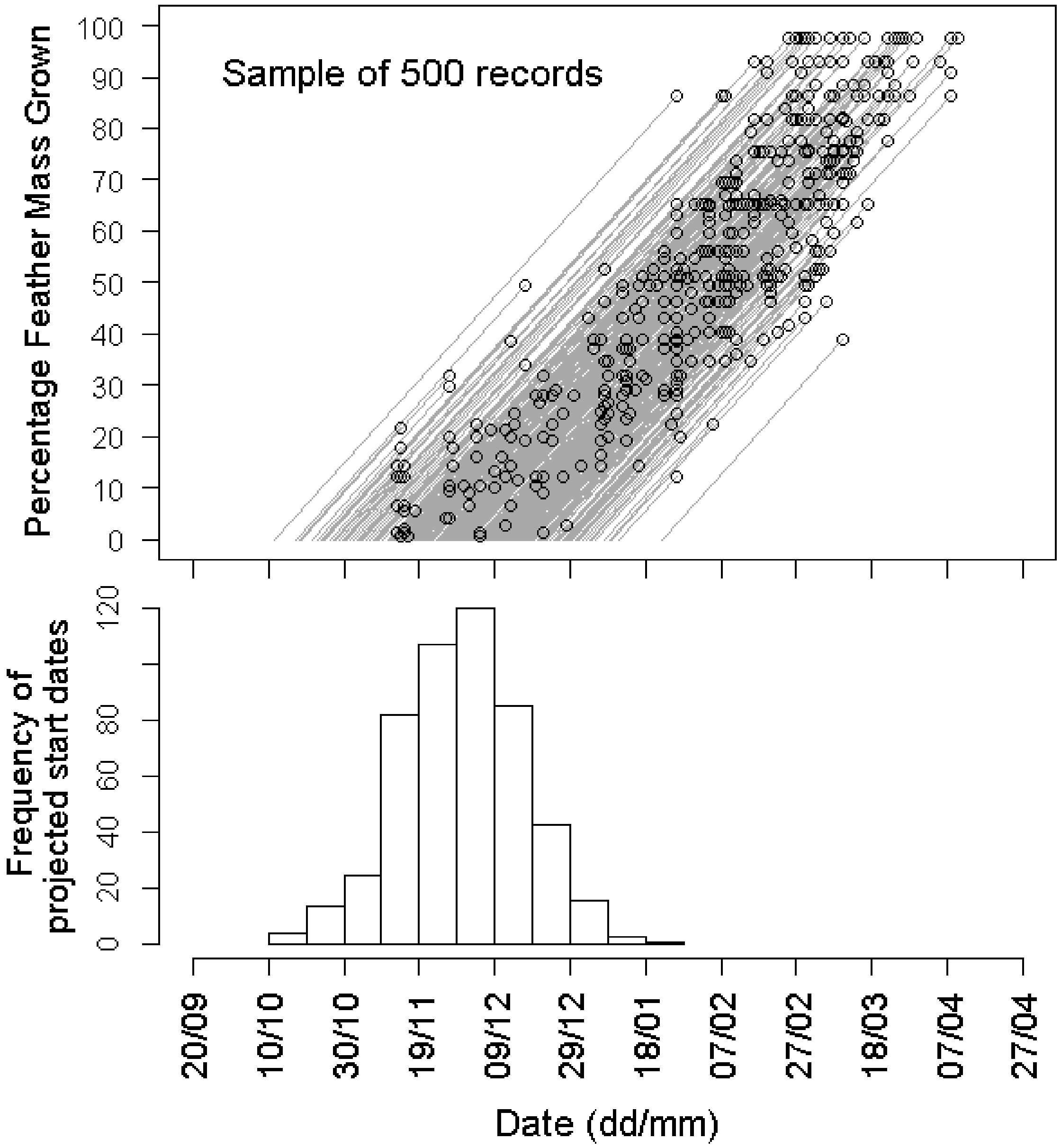

Figure 5a. The relationship between the observations (circles), the projections back to the start date for each record (gray lines), and the resulting distribution of the projected start dates, for a random sample of 500 barn swallows ringed in South Africa from 1990 to 2011. A duration of 123 days was used, and linear progress of moult assumed.

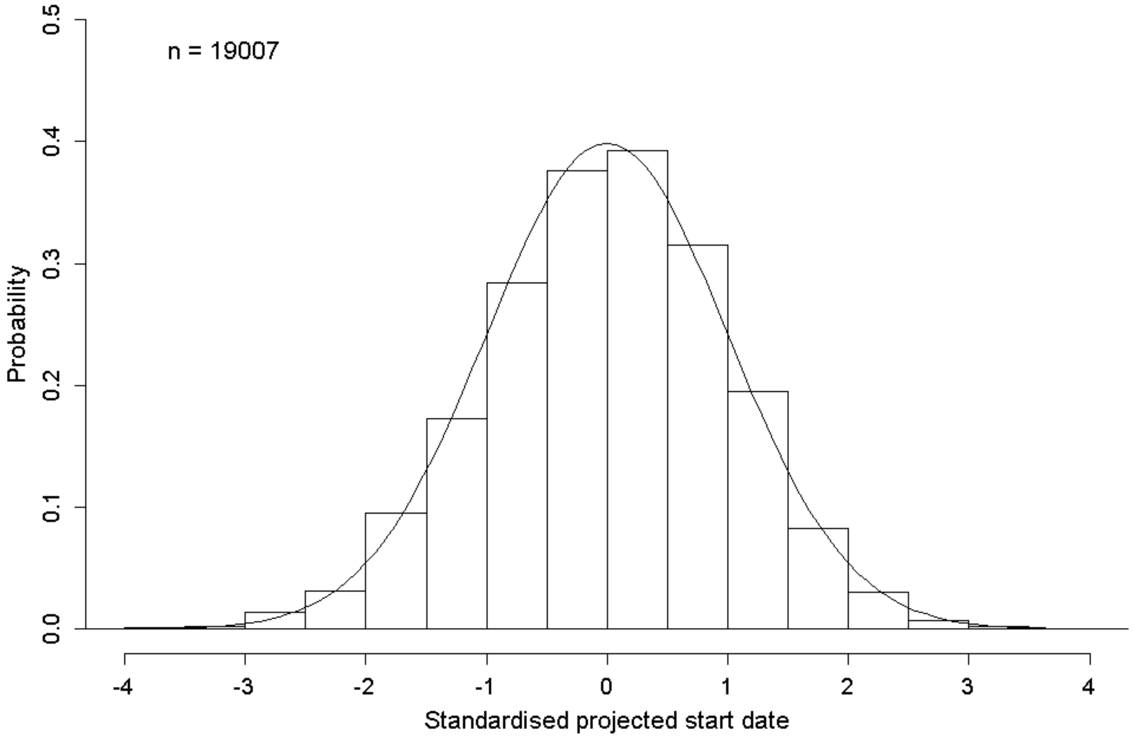

Figure 5b. Distribution of standardised projected start dates, with a normal curve overlaid, for barn swallows with moult data, ringed in South Africa from 1990 to 2011. A duration of 123 days was used, and linear progress of moult assumed. See Table 6.

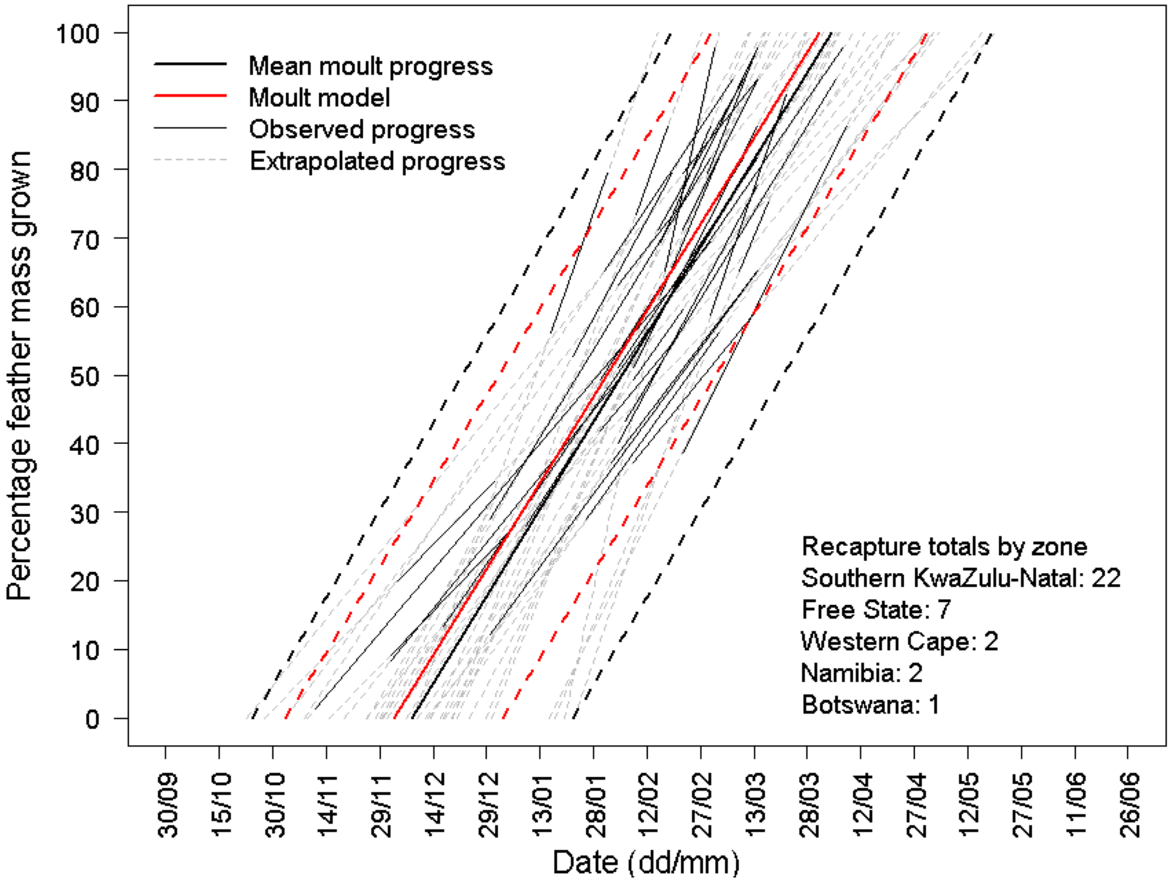

Figure 5. Progress of moult in the 34 barn swallows (same–season recaptures) which had a change in PFMG of more than 10%. Red dashed lines are confidence limits estimated by the moult model, between which 95% of the population was estimated to be moulting. Black dashed lines are 95% confidence intervals based on the mean extrapolated start and end dates.

Appendix

Table S1. Barn swallow feather masses (g) used in this thesis. Four samples were used: a skin in the collection of the National Museum in Bloemfontein (R. Nuttall, pers. comm.) and three skins from of Polish birds, an adult and two juveniles (M. Remisiewicz, pers. comm.). n/d: no data.

Primary	Bloemfontein	Adult left	Adult right	Juvenile 1 left	Juvenile 1 right	Juvenile 2 left	Mean
1	0.0101	0.0098	0.0098	0.0078	0.0075	n/d	0.0090
2	0.0131	0.0126	0.0126	0.0095	0.0094	0.0072	0.0107
3	0.0156	0.0157	0.0154	0.0119	0.0115	0.0085	0.0131
4	0.0181	0.0179	0.0183	0.0141	0.0140	0.0110	0.0156
5	0.0223	0.0199	0.0203	0.0170	0.0169	0.0127	0.0182
6	0.0253	0.0228	0.0233	0.0205	0.0204	0.0151	0.0212
7	0.0287	0.0264	0.0265	0.0248	0.0246	0.0181	0.0248
8	0.0341	0.0310	0.0310	0.0291	0.0284	0.0219	0.0292
9	0.0380	0.0342	0.0344	0.0321	0.0301	0.0261	0.0325
Total	0.2053	0.1902	0.1916	0.1666	0.1629		0.1743

Chapter Four

Misclassification of barn swallow age classes in South Africa and its impact on moult phenology estimates

Abstract

The original Underhill & Zucchini moult model assumed that all individuals moult at the same rate. Hence, one should separate groups that might have biologically important differences in moult duration. Failing to do so could cause the estimates to be inaccurate. Immature (first year) barn swallows are known to arrive at the non-breeding grounds, moult, and depart, several weeks later than the adults. There are contradictory reports about whether immature barn swallows moult at a different rate to adults; one study found that they moult slightly faster than adults, while another reported no difference. The first purpose of this study was therefore to estimate separately the moult phenology of immature and adult barn swallows ringed in South Africa from 1990 to 2012, using the South African Bird Ringing Unit (SAFRING) data set. Fully-moulted immatures look like adults, and are easily misclassified as adults by less experienced ringers, and such misclassification biases estimates of the moult parameters. I therefore explored the evidence for and implications of age misclassification, taking spatial variability into account. Data were analysed together as well as grouped into provinces: Western Cape, Eastern Cape, northern and southern KwaZulu-Natal, Gauteng, and the Free State. Overall, and in all zones separately, the percentage of immatures in the sample increased initially and decreased towards the end of the moult season, suggesting that there was misclassification. I then compared two moult models, assuming a different mean start date of moult (as indicated by the literature): the first model estimated a common duration for the age classes, whereas the second estimated different durations. The second (more complex) model was better supported, with immatures taking 22 days longer to moult than adults. However, I preferred the simpler model for two

reasons. First, the apparent difference in moult duration could itself be caused by the misclassification. Second, the difference in mean start date according to the simpler model (immatures started moult 22 days (SE 0.3) later than adults) was consistent with the literature, whereas the difference according to the more complex model (immatures started moult 9 days (SE 0.8) later than adults) was less than reported in the literature. Further, there was no difference in duration of moult between 21 immature and 13 adult barn swallows that were recaptured during the same non-breeding season. Hence, I regarded the simpler model as the more reliable.

Introduction

The Underhill & Zucchini moult model (Underhill 1985, Underhill & Zucchini 1988) is a maximum-likelihood approach that was developed specifically to estimate moult phenology within an appropriate statistical framework. The Underhill & Zucchini (1988) model made the important assumption that all individuals in a group moult at the same rate – here I address this key assumption as it relates to barn swallow moult phenology in South Africa. Support in the SAFRING barn swallow data set for the other three assumptions of the Underhill & Zucchini (1988) moult model – that stage of moult does not affect an individual's chances of being captured; that moult score (with or without correction for differences in feather mass), or a transformation thereof, increases at a constant rate (linearly); and that the start dates of individuals are normally distributed – was addressed in the Chapter Three. The linear "full-tract" model, as opposed to the non-linear cumulative growth curve (Remisiewicz *et al.* 2009) obtained by modelling the primary feathers separately (Underhill 2003), was found to be appropriate for use with the SAFRING barn swallow data; the assumption of normally distributed individual start dates was reasonable (Chapter Three).

The Underhill & Zucchini (1988) moult model estimates the expected start date, spread of start date and duration of moult for the population. Following from the assumption that individual start dates are normally distributed, the estimated start date and spread are taken to be the mean and standard deviation of the start of moult. The model assumes that all individuals moult at the same rate and estimates the average duration but, importantly, does not estimate the spread of duration. Hence, if there is large unexplained variability in moult duration in a sample, there is the risk that all the estimates will be biased or imprecise because the model uses all three parameters to explain the variability in duration. The negative correlation between duration and mean start date (Underhill & Zucchini 1988) means that both these parameters will be affected. Small differences in duration between individuals will not affect the moult model, but large differences such as those that could exist between, for example, widely separated populations or different age groups, could cause the assumption to be violated if the effect of group differences is not accounted for.

The assumption that all individuals have the same duration of moult is not completely satisfied because individuals do differ (e.g. the recaptured barn swallows; Chapter Three). Further, an important difference in duration between groups can exist for biological or ecological reasons; in this case, the groups should be separated to avoid violations of the assumption. The timing of moult is known to differ between immature (defined as being in their first year) and adult barn swallows, with arrival and moult occurring later in first year birds (de Bont 1962, Broekhuysen & Brown 1963, de Bont 1970, Møller *et al.* 2011). However, there are conflicting reports on differences in duration, with a difference being reported for barn swallows in the Congo (de Bont 1962, 1970), but no difference reported for barn swallows in Botswana (van den Brink *et al.* 2000). Age class should therefore be used as one of the explanatory variables for mean start date of moult, and potentially also for duration. In barn swallows age is difficult to determine in the hand, and there is a particular risk later in the moult season that immatures that have moulted into adult plumage are misclassified as adults (Broekhuysen & Brown 1963, Turner 2006). If age has been widely misclassified, it becomes impossible to assess reliably whether the age classes have different moult durations, because difference in duration between the ages could result from misclassification alone, as I will discuss later. In this chapter I describe the moult phenology of immature and adult barn swallows ringed in South Africa, taking into account the risk of misclassification. Geographic differences in moult phenology will be addressed in Chapter Five.

Methods

Barn swallow ringing records collected between 1990 and 2012, with primary moult and age-class data, were extracted from the SAFRING data base (Underhill & Oatley 1994) on 5 June 2012. The age classes used were ‘immature’ for birds considered to be in their first year of life, and ‘adult’ for all older birds. Barn swallows were mostly trapped on arrival at roosts in the evenings using mist nets, according to methods described in the SAFRING Bird Ringing Manual (de Beer *et al.* 2001). Moult was scored in the hand by qualified ringers using the British Trust for Ornithology technique (Ginn & Melville 1983). Instead of raw moult scores, the proportion feather mass grown was used as a moult index (Summers *et al.* 1983, Underhill & Joubert 1995, Underhill 2003), and for convenience was multiplied by 100 and reported as a percentage (‘PFMG’). Feather masses (Table 1) were obtained from an adult barn swallow skin in the collection of the National Museum in Bloemfontein (R. Nuttall pers. comm.). The calculation of PFMG uses relative feather masses. I assumed that the relative feather masses did not differ on average between immatures and adults. Immature barn swallows undertake the same migration as adults, so they should be expected to have the same wing-shape (and hence the same relative feather masses) as adults. Further, for species with similar wing-shapes, the Underhill-Zucchini (1988) model estimates are relatively insensitive even to inter-species differences in primary feather weights (Bonnevie 2010). However, given the small sample of feather weights available, it was not possible to test this assumption. To assess potential age misclassification I describe the proportion of immatures in the sample by geographic zone (Figure 1), and within each zone by month of the moult season.

The Underhill & Zucchini (1988) moult model was used to estimate the key moult parameters – the duration and mean start date of moult and standard deviation in start date. Only moulting birds were analysed, and hence data type three (which ignores birds that have not started moulting or have completed moult) was specified in the moult model. The simplest model, using the pooled data with no explanatory variables, is included for completeness, although the later arrival and moult of first year barn swallows at the non-breeding grounds has been well established (de Bont 1962; Broekhuysen & Brown 1963; de Bont 1970; Møller et al. 2011). Hence, the objectives being to estimate the difference between ages in mean start date and to determine whether a difference in duration was supported, I compared two models which included age class as an explanatory variable for mean start date, using the pooled data set. In the first model, a common duration was estimated for the age classes; in the second, separate durations were estimated. A common spread (standard deviation) of start date was assumed in both models. I used AIC model selection as a guide (Akaike 1974).

Barn swallows recaptured in South Africa within the same non-breeding season provided a further opportunity to estimate the different timing of moult in immatures and adult barn swallows. The start and end dates for individual recaptured birds were extrapolated, assuming a constant rate of moult within individuals (Chapter Three). Using these extrapolated start and end dates, the mean start and end days, and mean duration, were then estimated with their standard errors, for each age class. I then compared, for the age groups, the means of the extrapolated moult parameters and the estimates of the Underhill & Zucchini (1988) moult model.

Finally, I used a Students T-test to compare the extrapolated durations of individual adult and immature birds. All Underhill-Zucchini (1988) moult models (using single-capture data) were fitted using the R (v. 3.2.2) (R Core Team 2015) package ‘moult’ (v. 1.4) (Erni *et al.* 2013). Kernel density plots were used to illustrate the distribution of sampling days and PFMG. The density of PFMG is approximate because PFMG is a constrained variable, whereas kernel density plots are unconstrained.

Results

The data set consisted of 19007 records (Table 2). Summarised by month, for the entire sample, 60% of the records in November were aged as adults; by December, immatures comprised 73% of records (Table2). In January and February respectively, 71% and 68% were aged as immature; this decreased to 47% immatures in March and 41% immatures in April (Table 2). The proportion of immatures was consistently high throughout the non-breeding season in Southern KwaZulu-Natal, from 53% in November to 78% in December and 75% in January, and declining to 55% in March; in Gauteng the proportion of immatures increased from 11% in November to 64% in January, then declined to 39% in March (Table 2). Similar patterns occurred in the other zones. In the Free State, Western and Eastern Cape and Northern KwaZulu-Natal, the proportion of immatures was high (55%–88%) from December to February (Table 2). In March, the proportion of immatures declined in northern KwaZulu-Natal to 0%, in the Free State to 44%, whereas it remained high (65%–73%) in the Western and Eastern Cape (Table 2). In April, the proportion of immatures was greater than 50% only in southern KwaZulu-Natal, where it was 76% (Table 2).

The model which estimated different moult durations for immatures and adults had the lower AIC score (Table 3). According to the simpler model (model 1), duration was 134 days (SE 0.7) for both groups, and immatures started and ended moult 22 days (SE 0.3) later than adults (Table 4). Using the more complex model, immatures had a duration of 142 days (SE 0.8), adults a duration of 120 days (SE

1.1), and immatures started moult nine days (SE 0.8) later and ended moult 32 days later (Table 4; Figure 2). For both models the standard deviation in start date was 16 days (SE 1.3).

There were 34 same-season recaptures with an increase in percentage feather mass grown of at least 10% (Figure 3). Immatures took on average four days longer to moult than adults, started moult 16 days after adults, and ended moult 21 days after adults; the difference in duration was not significant, and the spread of duration, start date and end date were similar (Table 5, Figure 3).

Discussion

The proportion of immatures in the sample declined over the moult period, particularly in the last two months; this suggests widespread misclassification of immatures in adult plumage as adults. For the barn swallow population at the non-breeding grounds, immatures should comprise about two-thirds of the population, and towards the end of the season many adults will have completed moult and departed, leaving mostly immatures (de Bont 1962, 1970; Broekhuysen & Brown 1963); hence, the proportion of immatures should increase as the non-breeding season progresses. My results showed the opposite trend. Barn swallows are relatively easy to age early in the moulting season, before immatures have moulted into adult plumage; however, classifying age becomes difficult later in the season when many immatures are in adult plumage (Broekhuysen & Brown 1963, Turner 2006). Hence, there is an increasing risk of misclassification as the season progresses, and the results shown here are consistent with this.

According to the more complex model, immatures took 22 days longer than adults to moult the primary tract. This was probably caused by misclassification: if immatures in adult plumage are classified as adults, the early and faster moulting immatures would be removed from the pool of immatures, and the remainder would be the late or slower moulters – this would cause the appearance of the longer duration. Further, immatures (particularly those from second or third broods) might actually moult slightly faster, not slower, than adults (de Bont 1962, 1970), although other evidence suggests little or no difference in duration (van den Brink *et al.* 2000). The apparently longer duration in immatures is thus inconsistent with the literature, and is explained by misclassification.

The difference in start dates according to the simpler model, with immatures starting moult on average 22 days after adults, was generally consistent with reports that the life-cycle stages of barn swallows in their first year are later than adults: immatures begin fattening before the southward migration several weeks later, and at a slower rate (or over a longer period), than adults (in Italy and the UK; Pilastro & Magnani 1997, Coiffait *et al.* 2011). Immatures arrive at the breeding grounds several weeks after, and more gradually, than adults, and depart later than adults (De Bont 1962, 1970; Broekhuysen & Brown 1963). The more gradual arrival of immatures could reflect the finding that immatures take longer than adults to store sufficient fuel for migration (Pilastro & Magnani 1997). Immatures start primary moult several weeks later than adults (de Bont 1962, Broekhuysen & Brown 1963; de Bont 1970; Ginn & Melville 1983). Further, the results of my analysis of the recaptures are consistent with there being no difference between first year birds and adults in duration, but a difference in mean start date of two to three weeks.

For these reasons I regard the simpler model, estimating one duration for the age classes, as more appropriate. Further, the difference in duration between the age classes, if there is any, is probably much less than the 23 days difference found in model two, and closer to zero (based on the analysis of recaptures), and age-class can safely be excluded from the model. In Chapter Five I relate changes in the mean start and end of moult to changes in migratory timing which were modelled using bird atlas data (Altwegg *et al.* 2012). The bird atlas data does not distinguish between age-classes; hence, to compare moult phenology with those results, it was beneficial to disregard age class. I have therefore combined the age classes in all further analyses. Combining the age classes is done with the caveat that there might actually be a difference in moult duration, which these analyses did not detect, between the age classes. However, I believe that the analyses used were appropriate for the intended purpose. Further, based on these results and their interpretation, I believe that estimating separate moult durations for the age classes would result in unreliable duration and mean start date estimates when using this barn swallow data set.

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Tables and Figures

Table 1. Barn swallow primary feather masses, relative feather mass, and cumulative relative mass, obtained from a skin of an adult bird in the collection of the National Museum in Bloemfontein, South Africa (R. Nuttall, pers. comm.).

Primary	Mass (g)	Relative mass	Cumulative relative mass
1	0.0101	4.9%	4.9%
2	0.0131	6.4%	11.3%
3	0.0156	7.6%	18.9%
4	0.0181	8.8%	27.7%
5	0.0223	10.9%	38.6%
6	0.0253	12.3%	50.9%
7	0.0287	14.0%	64.9%
8	0.0341	16.6%	81.5%
9	0.0380	18.5%	100.0%
Full tract	0.2053	100.0%	100.0%

Table 2. Number of barn swallow records in each age class, by zone and month. Percentages of immatures and adults in each month are shown. Only moulting birds were included. Barn swallows were ringed in South Africa between 1990 and 2012.

Countrywide data set

Month	Immature		Adult		Total
Oct	0	0%	3	100%	3
Nov	314	40%	474	60%	788
Dec	1343	73%	504	27%	1847
Jan	3159	71%	1282	29%	4441
Feb	4757	68%	2276	32%	7033
Mar	2201	47%	2448	53%	4649
Apr	100	41%	146	59%	246
Total	11874	62%	7133	38%	19007
Southern KwaZulu-Natal					
Oct	0	0%	3	100%	3
Nov	266	53%	234	47%	500
Dec	934	78%	268	22%	1202
Jan	753	75%	246	25%	999
Feb	1681	71%	698	29%	2379
Mar	830	55%	667	45%	1497
Apr	84	76%	26	24%	110
Total	4548	68%	2142	32%	6690
Gauteng					
Nov	27	11%	230	89%	257
Dec	184	51%	176	49%	360
Jan	1111	64%	616	36%	1727
Feb	954	63%	556	37%	1510
Mar	468	39%	732	61%	1200
Apr	2	50%	2	50%	4
Total	2746	54%	2312	46%	5058
Northern KwaZulu-Natal					
Nov	17	77%	5	23%	22
Dec	28	67%	14	33%	42
Jan	22	81%	5	19%	27
Feb	57	55%	47	45%	104
Mar	0	0%	51	100%	51
Total	124	50%	122	50%	246

Table 2. continued.

Month	Immature		Adult		Total
			Free State		
Dec	1	100%		0%	1
Jan	330	65%	174	35%	504
Feb	814	58%	594	42%	1408
Mar	646	44%	807	56%	1453
Apr	13	16%	70	84%	83
Total	1804	52%	1645	48%	3449
			Western Cape		
Nov	3	38%	5	63%	8
Dec	130	88%	18	12%	148
Jan	763	81%	176	19%	939
Feb	1229	77%	373	23%	1602
Mar	229	65%	124	35%	353
Apr	1	2%	48	98%	49
Total	2355	76%	744	24%	3099
			Eastern Cape		
Nov	1	100%	0	0%	1
Dec	66	70%	28	30%	94
Jan	180	73%	65	27%	245
Feb	22	73%	8	27%	30
Mar	28	29%	67	71%	95
Total	297	64%	168	36%	465

Table 3. Model specification and AIC model selection coefficients for barn swallow moult models estimated using the Underhill & Zucchini (1988) moult model, for the pooled data set. dAIC: difference in AIC score between the model with the most statistical support (lowest AIC score) and every other model.

Model	Covariates for Duration	 Mean start date	Number of parameters	AIC	dAIC	Log likelihood
2	age class	age class	5	-33197	0	16604
1	none	age class	4	-32876	321	16442
0	none	none	3	-26877	6320	13441

Table 4. Moult parameter estimates for adult and immature barn swallows, modelled using the Underhill & Zucchini model, comparing two models: model 1 – single duration estimate; model 2: different duration estimates for the age classes. For duration estimates see Figure 2. For both models, the standard deviation in start date was 16 (SE 1.3) days. Estimates are in days from 1 August.

	Duration (SE)	Mean start day (SE)	Mean end day (SE)
Model 1			
Immature	134 (0.7)	123 (0.4)	257 (0.4)
Adult	134 (0.7)	101 (0.5)	235 (0.3)
Model 1: age difference	n/a	22 (0.3)	22
Model 2			
Immature	142 (0.8)	119 (0.4)	261 (0.4)
Adult	120 (1.1)	109 (0.7)	229 (0.7)
Model 2: age difference	22	9 (0.8)	32

Table 5. Moult phenology estimates for barn swallows recaptured in South Africa within the same season, with an increase in percentage feather mass grown between first and second capture of at least 10%. Estimates were based on the start and end dates extrapolated from the observed moult progress of recaptured individuals. Estimates are in days from 1 August. Sample size for immatures: 21; adults: 13. Difference in duration was not significant: $t = -0.31$, $p = 0.38$, degrees of freedom = 32; equal variance assumed). Alternative hypothesis: duration in adults < duration in immatures.

				Standard deviations		
	Duration (SE)	Mean start day (SE)	Mean end day (SE)	Duration	Start	End
Immature	119 (7.9)	135 (4.8)	255 (4.5)	29.7	19.4	17.3
Adult	115 (10.0)	119 (6.1)	234 (5.7)	44.8	25.3	25.3
Difference (ratio for SD)	4	16	21	0.7	0.8	0.7

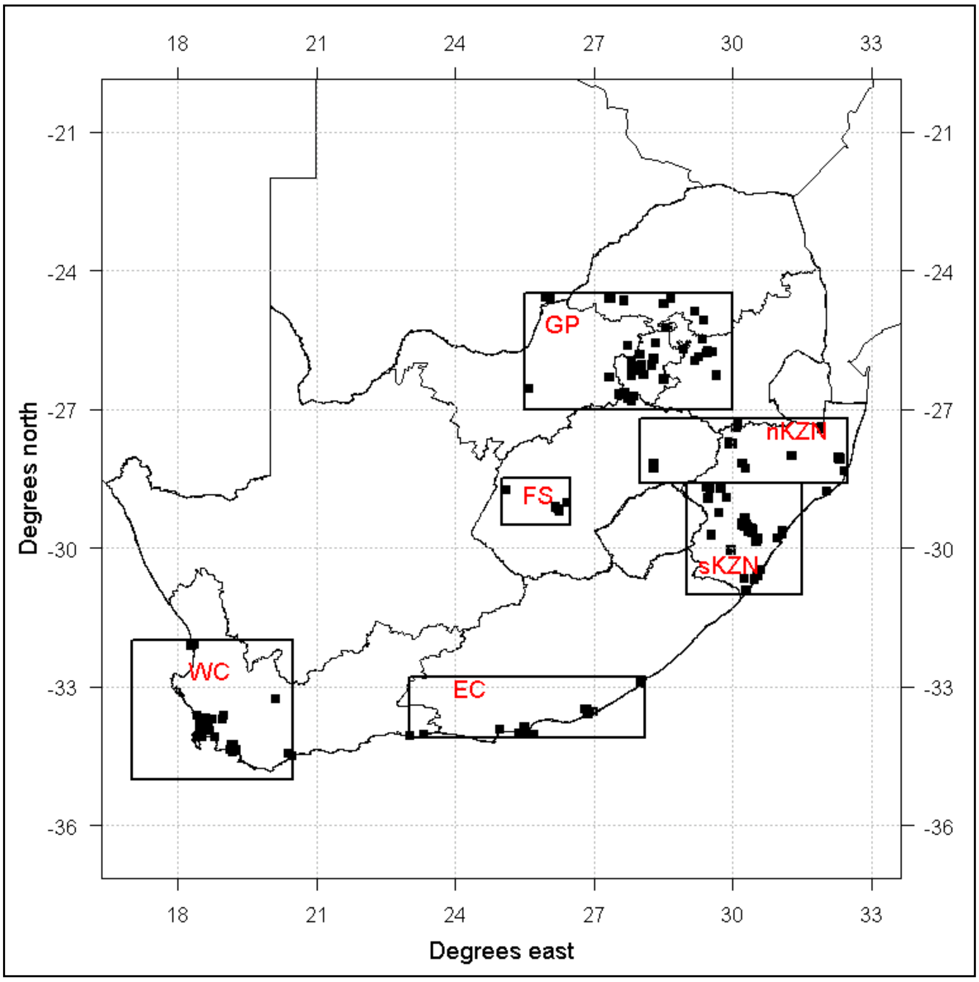

Figure 1. Map of South Africa showing the ringing locations of the barn swallow records used in this study. Points represent locations of records. Solid boxes enclose the zones where most of the records were collected: GP: Gauteng; sKZN: southern KwaZulu-Natal; nKZN: northern KwaZulu-Natal; FS: Free State; EC: Eastern Cape; WC: Western Cape.

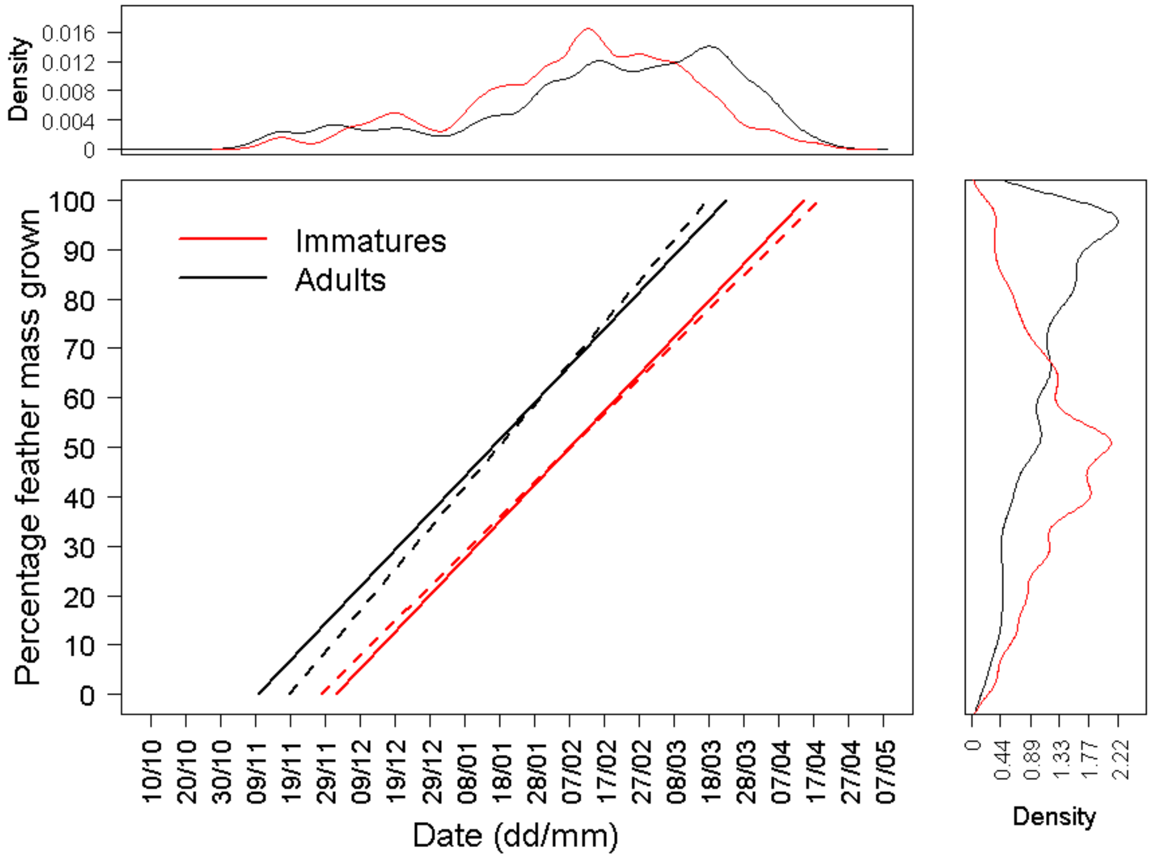

Figure 2. Moult parameter estimates for adult and immature barn swallows, modelled using the Underhill & Zucchini model, comparing two models: model 1 (solid lines) – common duration estimate; model 2 (broken lines) – different duration estimates for the age classes (see Table 4).

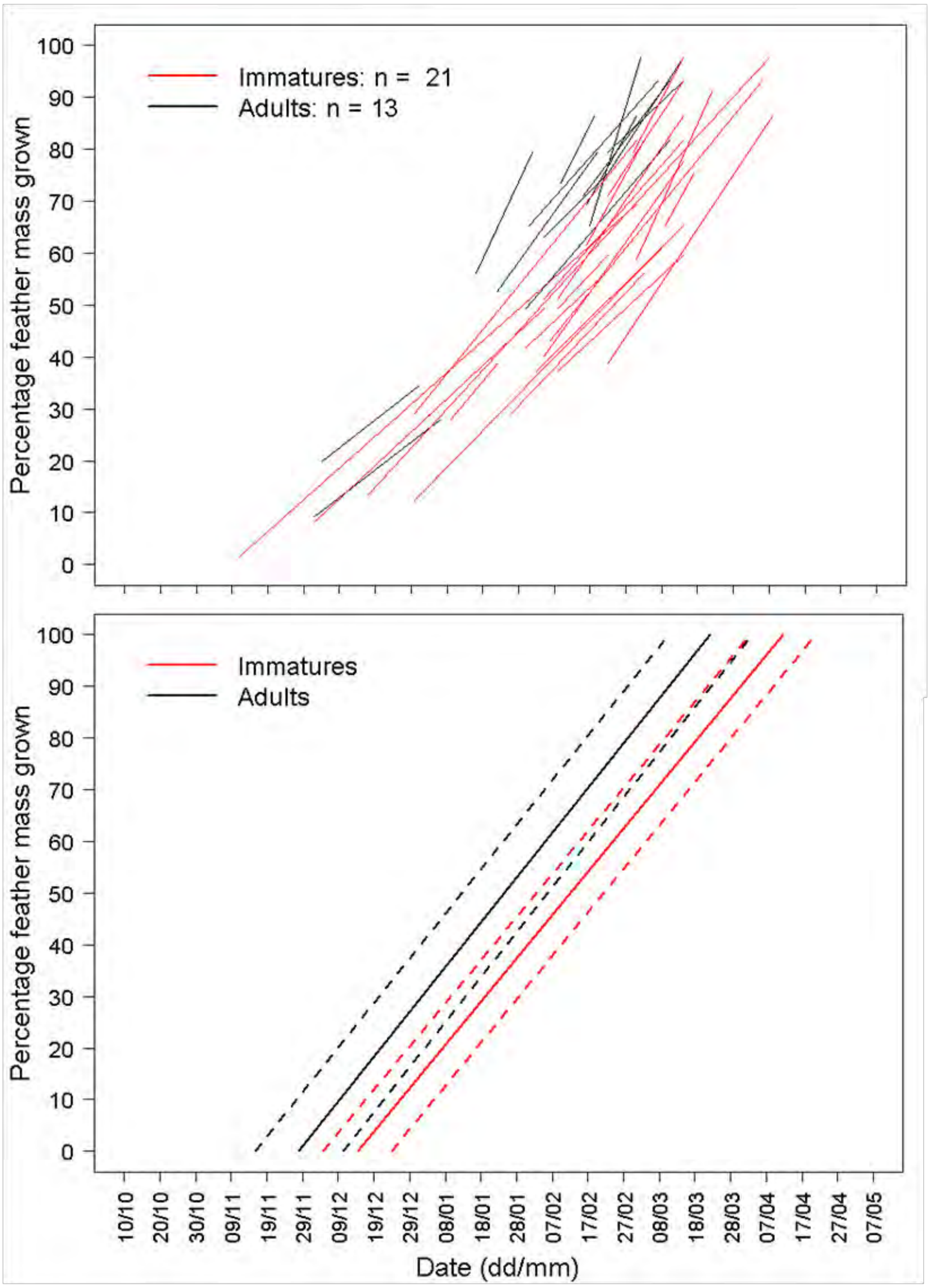

Figure 3. Individual progress of moult (above) and mean progress (below) in barn swallows recaptured during the same non-breeding season in South Africa, comparing immature (first year) and adult birds. Broken lines enclose the 95% confidence intervals that reflect the precision of the mean start and end date estimates.

Chapter Five

Spatial and temporal variation in flight feather moult phenology of barn swallows in South Africa

Abstract

Human-induced climate change has caused warmer and earlier springs in the northern hemisphere over the last 20 years, with many documented ecological effects. Palearctic climate changes have been linked to phenological changes in birds, including migratory birds, in which the life-cycle stages (breeding, migration and moult) are separated. For example, warmer and earlier Palearctic springs enable some bird species to begin breeding earlier. Climate change thus poses a particular risk for long-distance migrant birds - lengthening of one stage can cause it to continue into the time needed for another stage. Most barn swallows which breed in the Palearctic during the boreal summer spend the austral summer in Africa, many in South Africa, where they undergo complete moult. Barn swallow ringing moult records were obtained from the SAFRING data base. I explored changes in barn swallow primary (flight) feather moult phenology in six zones in South Africa, and in two time periods, between 1990 and 2012, using the Underhill-Zucchini moult model, which estimates the duration, mean start date, and variability in start date of moult. The first period consisted mostly of years during the 1990s, and in several zones up to 2005. The second period started in 2006 for Gauteng, KwaZulu-Natal and the Western Cape, and in 2002 for the Eastern Cape and the Free State. For four of these zones there were previously published phenological changes in barn swallows in South Africa. I used these reported changes as hypotheses about change in moult phenology in South Africa - in Gauteng, end of moult should shift eight days earlier; in the Western Cape, it should shift five days later; in Southern KwaZulu-Natal, it is unclear what to expect; and in the Free State, end of moult should shift later. In the Western Cape, Gauteng, Free State and Southern KwaZulu-Natal zones the changes in moult phenology between the periods were generally consistent with the expectations based on reported changes in migratory phenology and moult. In the Western Cape moult shifted on average later by two days, in northern KwaZulu-Natal earlier by one day, and in southern KwaZulu-Natal earlier by three days between the periods. In the Gauteng zone moult was on average six days earlier in the second period than in the first period. In the Eastern Cape and Free State zones, moult shifted five and seven days later respectively in the second period. These results were broadly consistent with hypothesised changes, and provide further evidence of geographically variable changes in barn swallow phenology at the non-breeding grounds.

Introduction

The Palearctic barn swallow *Hirundo rustica rustica* underwent geographically variable phenological changes at their breeding grounds in the late decades of the 20th century (Møller 1989, Sparks & Braslavská 2001, Robinson *et al.* 2003, Sparks & Tryjanowski 2007). Whereas many long-distance Palearctic migrant species declined over this period, some severely, the barn swallow population remained generally stable (Walther *et al.* 2011). This suggests that barn swallows might be more resilient to shifting seasons than other species. Changes in barn swallow moult and migratory phenology at the South African non-breeding grounds have also been reported (Møller *et al.* 2011, Altwegg *et al.* 2012), and these are thought to be caused by climate changes at the breeding grounds (Altwegg *et al.* 2012, Bussière *et al.* 2015). Adjustment of migratory phenology in response to Palearctic climate change is likely to be constrained by the need to complete (or almost complete) moult at the non-breeding grounds before departure (Møller *et al.* 2011). Hence, exploring changes in barn swallow moult phenology in South Africa should help to explain the contradictory changes in migratory phenology.

There are energetic, physical and time constraints between moult and migration which keep these life-cycle stages mostly separated (Ginn & Melville 1983, Earnst 1992, Jenni & Winkler 1994, Hedenström & Sunada 1999, Hall & Fransson 2000, Pérez-Tris *et al.* 2001, Echeverry-Galvis & Hau 2012). As such, most Palearctic barn swallows begin primary moult after arriving at the non-breeding grounds (Ginn & Melville 1983; Pérez-Tris *et al.* 2001; Jenni & Winkler 1994). In contrast, many barn swallows leave the non-breeding grounds while still moulting their ninth (outermost) primaries (de Bont 1970, Jenni & Winkler 1994, Turner 2006), even though there is a potentially high cost of migrating with incomplete moult (Rayner & Swaddle 2000). The fact that this costly overlap of moult and northward migration occurs reflects the importance to barn swallows of not delaying departure.

From the reported changes in migration and moult phenology in South Africa (Møller *et al.* 2011, Altwegg *et al.* 2012), some simple and testable hypotheses arise about shifts of the timing of moult in South Africa over the period: in Gauteng, the end of moult should shift 8 days earlier; in the Western Cape, end of moult should shift 5 days later; in Southern KwaZulu-Natal zone, where the period of residence was reported to extend in both directions, it is unclear what to expect; in the Free State, a shift towards later end of moult would be expected. The Northern Kwa-Zulu Natal zone lies between Gauteng and the Southern Kwa-Zulu Natal, so the shift in moult should be intermediate between the two, and likewise in the Eastern Cape which lies between the Western Cape and Southern Kwa-Zulu Natal. Further, if migration phenology is constrained by moult phenology, one would expect to see changes in moult phenology that are similar to the observed changes in migratory phenology, but the changes in the timing of end of the moult would potentially be less than the changes in timing of departure. The Synthesis chapter deals in depth with the relationships between moult, migration and pre-migratory weight gain. Hence, this chapter is limited to describing geographic patterns and temporal change in barn swallow moult phenology in South Africa. The discussion relates these patterns to previously published barn swallow phenological changes in South Africa. The evolutionary mechanisms behind these changes are briefly considered.

Methods

Barn swallow ringing records from 1990-2012 with primary moult data were extracted from the SAFRING data base (Underhill & Oatley 1994) on 5 June 2012. Barn swallows were mostly trapped on arrival at roosts in the evenings using mist nets, according to methods described in the SAFRING Bird Ringing Manual (de Beer *et al.* 2001). Moult was scored in the hand by qualified ringers using the British Trust for Ornithology technique (Ginn & Melville 1983) in which a worn feather is scored as 0, a growing feather from 1–4, and a replaced feather as 5. I classified an entirely worn primary feather tract (all the flight feathers of one wing) as 'pre-moult', an entirely replaced primary feather tract as 'post-moult', and a tract showing active moult as 'in-moult'.

Mean primary feather weights (per primary feather) were obtained from four specimens – one from the National Museum in Bloemfontein (Rick Nuttall pers. comm.) and three from Poland (Magda Remisiewicz, pers. comm.) (Table 1). Using these feather weights, the raw moult score was transformed into percentage feather mass grown (PFMG) (Summers *et al.* 1980, Summers *et al.* 1983, Underhill & Joubert 1995, Underhill 2003). The Underhill and Zucchini (1988) moult model, which uses maximum likelihood estimation (MLE), was used to estimate the key moult parameters for the population (duration of moult, mean start date, standard deviation in start date) and the correlation between these estimates, with mean end date of moult being a derived estimate (Underhill 1985, Underhill & Zucchini 1988, Underhill *et al.* 1990). I analysed only birds with actively moulting primaries, so the data set corresponds to data type three of the Underhill-Zucchini (1988) moult model. This data type is generally appropriate for migratory birds that begin moult on arrival and continue to moult throughout their stay until departure (Underhill & Zucchini 1988). Preliminary analysis of the data set (Chapter Three) informed this choice.

Models were fitted using the R (v. 3.2.2) (R Core Team 2015) package 'moult' (v. 1.4) (Erni *et al.* 2013), which implements an extension of the Underhill & Zucchini (1988) moult model that enables the three parameters to be modelled as a function of explanatory variables. The estimates of the mean start date and the duration have negative correlation (Underhill & Zucchini 1988). Maximum likelihood estimates obtained for large data sets have a bivariate normal joint distribution, hence I present these distributions as 95% confidence ellipses, using the R function ‘ellipse’ of the package ‘car’ (Fox & Weisberg 2011). These ellipses illustrate the uncertainty on the estimates more accurately than error bars based on the standard errors of the estimates, because they reveal the negative correlation between the parameters.

Of the six geographic zones used in this analysis (Figure 1), four – Gauteng (GP), Southern Kwa-Zulu Natal (sKZN), Western Cape (WC), and Free State (FS) – were chosen to coincide with the zones or location used in the two earlier studies on changes in barn swallow phenology in South Africa (Møller *et al.* 2011, Altwegg *et al.* 2012). I expanded the zones used in Altwegg *et al.* (2012) to include more ringing locations and records (Figure 1). I included two other intermediate zones, the Eastern Cape (EC) and Northern Kwa-Zulu Natal (nKZN).

Ringing dates were grouped into ringing years, between October and April (1990 thus refers to October 1990 to April 1991). For comparison with other published results, it would have been ideal to divide the data into the time periods of the first and second South African Bird Atlas Projects (SABAP; Harrison *et al.* 1997, Animal Demography Unit 2016): 1987 to 1991, and 2007 to 2011; however, the moult data were almost all collected after 1996, so this was not possible. Nonetheless, I was able to divide the data into two periods, with the second period starting in 2006 for four of the groups, and 2002 for the other groups (Table 2). These different time period definitions were chosen for two reason: first, so that the second period could start as near to 2007 as possible in those zones for which comparison with the migratory phenology results (Altwegg et al. 2012) was possible; second, to provide a better distribution of the number records in each time period within each zone, and to avoid any groups containing just one year of sampling. Groups with too few records, or with records from just one year, would risk reflecting short-term or local variability, rather than more general population patterns. The use of different time periods imposes some limitations that will be addressed in the Discussion. Specifically, the estimated mean start dates of moult for the Free State and Eastern Cape might not be directly comparable with that in other zones. This will be discussed further. To estimate the impact on the Free State and Eastern Cape results of using the same time period divisions for all zones, the model was run again after changing the start of the second period to 2006 in all zones.

The Underhill-Zucchini (1988) moult model allows one to estimate moult parameters for different groups by using grouping variables (Erni et al. 2013). For this study, geographic zone and time period were included as explanatory variables. I estimated one duration of moult for all groups (thereby assuming the same rate of moult for all groups), for reasons discussed in Chapters Two and Three. AIC scores (Akaike 1974) were used to guide model selection. I calculated the pooled variance of the estimates of mean start date in order to obtain the standard errors and 95% confidence intervals for the shifts between the time periods.

Because the countrywide barn swallow data set is particularly heterogeneous, it was not possible to compare changes in start and end date separately (which would have been optimal), by estimating different durations for each zone. In the Discussion I thus refer to shifts of the entire primary moult period, rather than in mean start or mean end of moult.

Results

The data consisted of 18060 moult records, collected in six zones within South Africa, for birds in active primary moult. For all zones except the Eastern Cape and Free State, period one ended with the 2005 moult season, while for the Eastern Cape and Free State zones, period one ended with the 2001 moult season (Table 2). The overlap of time periods was almost complete for the Free State and northern KwaZulu-Natal zones, and the Free State and Western Cape zones (Table 2). Period one records comprised 57% and period two 43% of the data (Table 2). The span of years in each time period with at least 20 records per year ranged from one year in northern KwaZulu-Natal, second period, to 11 years in southern KwaZulu-Natal in the first period.

In the model best supported by AIC, mean start date varied with zone, time period and the interaction between these (model 5, Table 3). Mean moult duration was 128 days (SE 0.8). Standard deviation in mean start date was 17.7 days (SE 1.5) (Table 4). For the Eastern Cape and Free State, the date of mean start of moult ranged from 16 November (SE 0.76) in the Free State during the first time period to 4 December (SE 1.55) in the Eastern Cape during the second time period (Table 4). Comparing the other zones, the earliest mean start of moult was 18 November (SE 0.89) in Gauteng in the second period, and the latest estimate was 4 December (SE 0.60), for southern KwaZulu-Natal in the first period. Because duration was assumed to be constant, the same patterns held for the mean estimated end of moult. From the first to the second period, the moult period shifted 6.8 (SE 0.03) days later in the FS zone, and 6.0 (SE 0.04) days earlier in the GP zone, and the shifts in the other zones were between these (Table 4; Figure 2). I expected the neighbouring Northern Kwa-Zulu Natal and Gauteng zones to exhibit similar shifts; the confidence limits for these zones did in fact overlap, with the Northern Kwa-Zulu Natal having a wider limits (and far fewer records) (Figure 2). The mean start dates for the moult period in the Eastern Cape fell between those for the neighbouring Western Cape and southern KwaZulu-Natal zones.

When the start of the second period was aligned to 2006 in the Free State and Eastern Cape to be consistent with the divisions used in the other zones, the estimated mean start of moult in the Free State in the first period was three days later than using the original model, whereas the estimate for the second period was unchanged (Figure 2). The change of period therefore reduced the delay in mean start date between the periods from 6.8 (SE 0.03) days to 3.5 (SE 0.17) days. The effect of using the aligned time periods for the Eastern Cape was to bring the estimates for the time periods closer together, reducing the delay from 4.9 (SE 0.14) to 3.3 (SE 0.19) days (Figure 2). The mean moult duration using the aligned time periods was 127 (SE 0.8) days. For the other zones, using the aligned time periods made less than one day's difference to the estimates, because for these zones the period divisions remained unchanged.

Discussion

Rapid climate change in recent decades, and its reported effects on ecological systems, has made it a priority to analyse and assess phenological shifts, especially those in the Southern Hemisphere (Chambers *et al.* 2013). The observed phenological patterns for barn swallows in South Africa seem to be counter-intuitive, with the average shifts in nearby zones – the Free State and Gauteng – being large and in opposite directions. Conversely, there were much smaller average shifts in the two coastal regions, the Western Cape and southern KwaZulu-Natal. However, these patterns make sense in the light of reported changes in moult and migratory phenology (Møller *et al.* 2011; Altwegg *et al.* 2012), and the expected shifts were largely supported. Specifically, the estimated shift towards an earlier (advanced) moult period in Gauteng was close to the shift of departure from that zone (Altwegg *et al.* 2012). In the nearby Free State, the estimated shift towards a later (delayed) moult period was consistent with the delayed end of moult predicted by Møller *et al.* (2011) for that zone. In southern KwaZulu-Natal the slight advance in estimated moult period was consistent with the estimated advance in the mid-point of departure (Altwegg *et al.* 2012), although Møller *et al.* (2011) reported later departure from that zone. In the Western Cape, the slight delay in the moult period was consistent with the slight delay in the mid-point of departure from that zone (Altwegg *et al.* 2012).

The *ad hoc* nature of the choice of sampling dates meant that there were gaps in the data, making it unfeasible to analyse the changes on a continuous scale. Because of the averaging that resulted from grouping the data into time periods, the scale of the phenological shifts quite probably underestimates the real shifts that occurred over the study period. However, Altwegg *et al.* (2012) reported changes in the mid-point of arrival and mid-point of departure, hence it was useful to compare averages. The implications and assumptions of this decision will be discussed below.

Moult and migration are generally separated, because of the competing physiological and physical requirements of each activity (Jenni & Winkler 1994). Barn swallows therefore probably experience time-pressure to finish moult (or at least to reach an advanced stage) before leaving the non-breeding grounds; if the timing of departure shifts earlier, there will be selective pressure to end moult earlier. If the timing of arrival does not change, or shifts later, the period available for moult will be reduced; this would have negative consequences in a region such as the Western Cape, where the mean period of residence is only about two weeks longer than the estimated duration of moult. These dynamics are addressed further in the synthesis chapter.

Immature barn swallows depart later than adults (Møller *et al.* 2011), and most immatures depart before completing the ninth primary (de Bont 1962, Jenni & Winkler 1994, Turner 2006), presumably out of necessity; hence, adults are probably better predisposed to cope with the selective pressure to depart earlier. In the Western Cape where the period of residence is already short (Altwegg *et al.* 2012), the selective pressure against both age classes, but especially immatures, might be worse than in the other zones. To assess whether this were true, one would need to model moult phenology separately for adult and immature barn swallows. However, the age classes were not analysed separately, for the key reason that there was systematic misclassification of age classes during sampling (Chapter Two), making it impossible to obtain accurate estimates when separating the ages.

Unexplained variability might reflect differences in factors such as age, sex, year, breeding population, ringer, date, or ringing location; however, I did not consider these factors here. The data used by Altwegg *et al.* (2012) did not permit separation by age class or sex, meaning that their estimates contain similar unexplained variability compared to these moult estimates. Further, Møller *et al.* (2011) found that the delay in the end of moult was more pronounced for immatures than adults, and for females than males. Such differences were hidden in my analysis.

The GP, WC and sKZN zones have different durations of residency (Altwegg *et al.* 2012). Hence, it is possible that there were similar differences in moult duration between the zones; further, duration might have changed between the time periods. Estimating different durations for either the zones or the time periods would allow for differences between the changes in mean start dates and mean end dates. Changes in duration are largely mediated by changes in the number of feathers growing simultaneously, rather than changes in the rate of feather production at the follicle (Rohwer & Rohwer 2013). The rate of feather production at the follicle is linked to metabolic rate (Lindström *et al.* 1993); hence, a reduced metabolic rate (for example, due to hypothermia or reduced prey availability) would slow moult, but it would also reduce survival. However, I assumed the same duration for all groups – this was necessary because of the heterogeneity of the data amongst the zone-period groups I compared.

In a study of passerine species (mostly residents) in the UK, it was found that, within species, individuals with the potential to raise an extra clutch generally start moult later and moult faster after breeding, by moulting more feathers simultaneously (Morrison et al. 2015). Similarly, barn swallows probably have the phenotypic plasticity (or genetic variability, or both) to moult faster under increased time constraints, such as in the Western Cape where the estimated residence period is already nearly as short as the estimated mean moult duration. If birds moult faster than is optimal, however, this can result in produce poor quality plumage (Hall & Fransson 2000, Vágási *et al.* 2012), which could reduce survival, leading to population declines. It would therefore be valuable to test this by monitoring plumage quality in addition to moult in South Africa. For birds in the Western Cape, an alternative to rushing moult would be to remain further north at the non-breeding grounds (Altwegg et al. 2012), where a longer period of residence is possible.

The changes reported here are consistent with a process of microevolution in response to change in the timing of Palearctic spring. Barn swallow arrival date at the breeding grounds is genetically controlled (Møller 2001), and variability (polymorphism) in the genes controlling barn swallow phenology has been further described (Saino *et al.* 2013). Selection favours Individuals that have the phenological plasticity to survive changes that occur within their life-spans. The generally high consistency between my findings on change in the timing of moult and other published changes (Møller *et al.* 2011; Altwegg *et al.* 2012), therefore probably reflects successful adaptation to changes that have occurred over the 21 years from 1990 and 2011. However, there is probably very little phenological plasticity in the minimum time required for successful moult (Lindström *et al.* 1993); hence, in the Western Cape in particular, barn swallows might already have reached their threshold for change, and we might expect populations to decline in this area between 2010 and 2020. In Southern Kwa-Zulu Natal, however, the population increased by 10% over the period, whereas in Gauteng there was a 5% decrease (Altwegg *et al.* 2012). Spatially variable demographic changes such as these, which might well be early responses to global climate change, urgently need to be monitored.

The results presented here are generally consistent with the published changes in barn swallow phenology in South Africa (Møller *et al.* 2011, Altwegg *et al.* 2012). This consistency provides some support for the analytical approach used here, which was to compare the mean start of moult in two time periods. This method had two assumptions – first, that the estimated phenological changes were linear (constant in rate and direction of change), and second, that these patterns continued linearly beyond the ends of the data in some cases, at least for the duration of the period covered by Altwegg et al. (2012). The second assumption was necessary because for most of the zones, the number of years with data was limited to a portion of the 1990s and 2000s, and the sampling years did not always overlap between zones. The consistency of the shifts in mean start of moult with the migratory phenology results suggests that the shifts were real and were representative of shifts over the longer period (the 1990s and 2000s), rather than being artefacts of the uneven distributions of data within each time period and between zones, or of using imperfectly matched time periods. Throughout this thesis, I have considered the results to be valid hypotheses of change, based on the high level of consistency found between the different sets of results. However, it is possible that a different analytical approach would produce different results and conclusions. These findings should therefore be studied further and tested using other models and methods.

There were opposite shifts in mean start of moult for Gauteng and the Free State, with moult shifting earlier in Gauteng, and later in the Free State. However, these zones had different time period divisions, with years in the first period for Gauteng falling into the second period for the Free State (for reasons described earlier). The second time period started at 2006 in four of the six zones, and 2002 in the Free State and Eastern Cape. Therefore, it is possible that this difference was an artefact of the choice of time period. When the time periods were aligned so that the second period started at 2006 in all the zones, the magnitude of the delay in both Free State and Eastern Cape was reduced. This difference in magnitude has a straightforward explanation – it suggests that the change over the period was linear, as it was assumed to be. If there is a linear trend towards later mean start of moult, and one extends the first period, the estimated mean start of moult in the first period will shift later – which was observed to happen in this case. If the second period is reduced, the precision of the estimates will be reduced, as was reflected by the wider ellipses for both zones when using the later start of the second period. This suggests that, although the magnitude of the shifts was affected, the direction of shifts in the Free State and Eastern Cape was estimated correctly. This therefore suggests that the comparison of shifts is valid, in spite of the use of different time period divisions. Further, the shifts for these two zones derived from the unmatched time periods are better supported than the smaller shifts obtained using the matched periods, because in the former case, the period divisions were chosen to balance the number of records in each time period.

Weather patterns can influence the timing of birds' life-cycles – for example, barn swallows in Botswana moulted slowest in years of drought, and faster when there was sufficient rainfall (van den Brink *et al.* 2000). Good conditions earlier in the season might enable the entire moult period to shift earlier (or enable a slower, less time-constrained moult), whereas a dry and hot summer in South Africa might delay the mean start of moult. The discussion up to now has mainly considered the support for the hypothesis that these results reflect real phenological changes over the 1990s and 2000s, and the mechanisms by which these changes could occur. Nonetheless, given the relatively short time periods used in some zones, an alternative hypothesis – that some of these results reflect short term variability – cannot be ruled out at this stage. This aspect was not investigated, and should be considered in future research.

This study describes, for the southern hemisphere, large-scale spatial and temporal variability in the moult phenology of a Palearctic migrant passerine. It is challenging to explain geographically variable population-level responses to climate change in long-distance migrants. However, the complex life-histories of such species, whilst making them difficult to analyse, also makes them particularly sensitive indicators of climate change, and thus all the more worth studying. In the final chapter I relate the moult phenology findings of this chapter to changes in the timing of pre-migratory weight gain (Chapter Six), and to other changes in the barn swallow life-cycle reported elsewhere. The migratory connectivity patterns reported in the second chapter provide a further level of explanation for the changes. I will return to this in the synthesis.

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Tables and Figures

Table 1. Average barn swallow primary feather weights used in this study. Four birds were used: a skin in the collection of the National Museum in Bloemfontein (Rick Nuttall, pers. comm.) and three skins from Polish birds (M. Remisiewicz, pers. comm.).

Primary	Average weight (g)	Sample standard deviation (g)
1	0.0090	0.00126
2	0.0107	0.00237
3	0.0131	0.00294
4	0.0156	0.00298
5	0.0182	0.00339
6	0.0212	0.00352
7	0.0248	0.00363
8	0.0292	0.00411
9	0.0325	0.00409
Full tract (sum of average weights)	0.1743	

Table 2. Barn swallow data used in this study. Data consisted of South African barn swallow records with moult scores (extracted from the SAFRING data base, on 5 June 2012) ringed in the six zones of South Africa (see Figure 1 for zone descriptions). Only moulting birds were included. In the Eastern Cape and Free State zones (*), the time periods were divided so that the second period starts in 2002, whereas in all zones without an asterisk, the second period starts in 2006. Amount of data per year is indicated by text shade. Gray text: 1 to 19 records per year; black text: 20 or more records per year. In years that are grouped, the shading indicates amount of data in each year separately.

	Period One			Period Two			
Zone	Ringing year	Records	Span of years with at least 20 records	Ringing year	Records	Span of years with at least 20 records	Grand Total
EC*	1995–1997, 1998, 1999	311	5	2002, 2003, 2005, 2007, 2009, 2011	155	8	466
FS*	1998–2001	2165	4	2002–2003, 2005, 2007	1232	6	3397
GP	1998, 1999, 2000–2005	4509	8	2006, 2007, 2008, 2009, 2010, 2011	616	5	5125
nKZN	2000–2001, 2002–2004, 2005	151	3	2006, 2008, 2009, 2010, 2011	96	1	247
sKZN	1990–1994, 1995, 1998, 1999–2000, 2001–2005	2886	11	2006–2011	2842	6	5728
WC	1994, 1996, 1998–2000, 2001–2005	375	5	2006–2010, 2011	2722	5	3097
Grand Total		10397			7663		18060

Table 3. AIC model selection coefficients for barn swallow Underhill-Zucchini (1988) moult models. The '+' indicates that the covariate was included additively. A '*' indicates an interaction between the covariates surrounding it. dAIC: difference in AIC score between the model with the most statistical support (lowest AIC score) and every other model.

Model	Covariates for mean start date	Number of parameters	AIC	dAIC	Log Likelihood
5	zone * period	14	-26653	0	13340
4	zone + period	9	-26487	166	13253
3	zone	8	-26489	164	13252
2	period	4	-25481	1172	12745
1	None	3	-25424	1228	12715

Table 4. Estimated mean start and end dates of moult, and shift in mean start over time, for barn swallows ringed in South Africa between 1990 and 2012. Different time periods were used: the second time periods starts in 2002 for the Free State and Eastern Cape zones, and in 2006 for all other zones. Moult duration was 128 (SE: 0.8). Standard deviation in mean start date was 17.7 days (SE 1.5). Values less than 0.05 were rounded to 0.0.

Zone	Period	Mean start day (SE)	Mean end date (SE)	Shift in mean start date (p2–p1) (SE)
Free State	p1	16 Nov (0.76)	24 Mar (0.53)	6.8 (0.03)
	p2	23 Nov (0.74)	31 Mar (0.63)	
Eastern Cape	p1	29 Nov (1.17)	06 Apr (1.22)	4.9 (0.14)
	p2	04 Dec (1.55)	10 Apr (1.59)	
Western Cape	p1	28 Nov (1.08)	05 Apr (1.02)	1.6 (0.06)
	p2	30 Nov (0.55)	06 Apr (0.53)	
Southern KwaZulu-Natal	p1	04 Dec (0.6)	10 Apr (0.51)	–2.9 (0.02)
	p2	01 Dec (0.54)	08 Apr (0.58)	
Northern KwaZulu-Natal	p1	26 Nov (1.70)	03 Apr (1.68)	–1.3 (0.25)
	p2	25 Nov (2.06)	01 Apr (2.06)	
Gauteng	p1	24 Nov (0.53)	01 Apr (0.46)	–6.0 (0.04)
	p2	18 Nov (0.89)	26 Mar (0.9)	

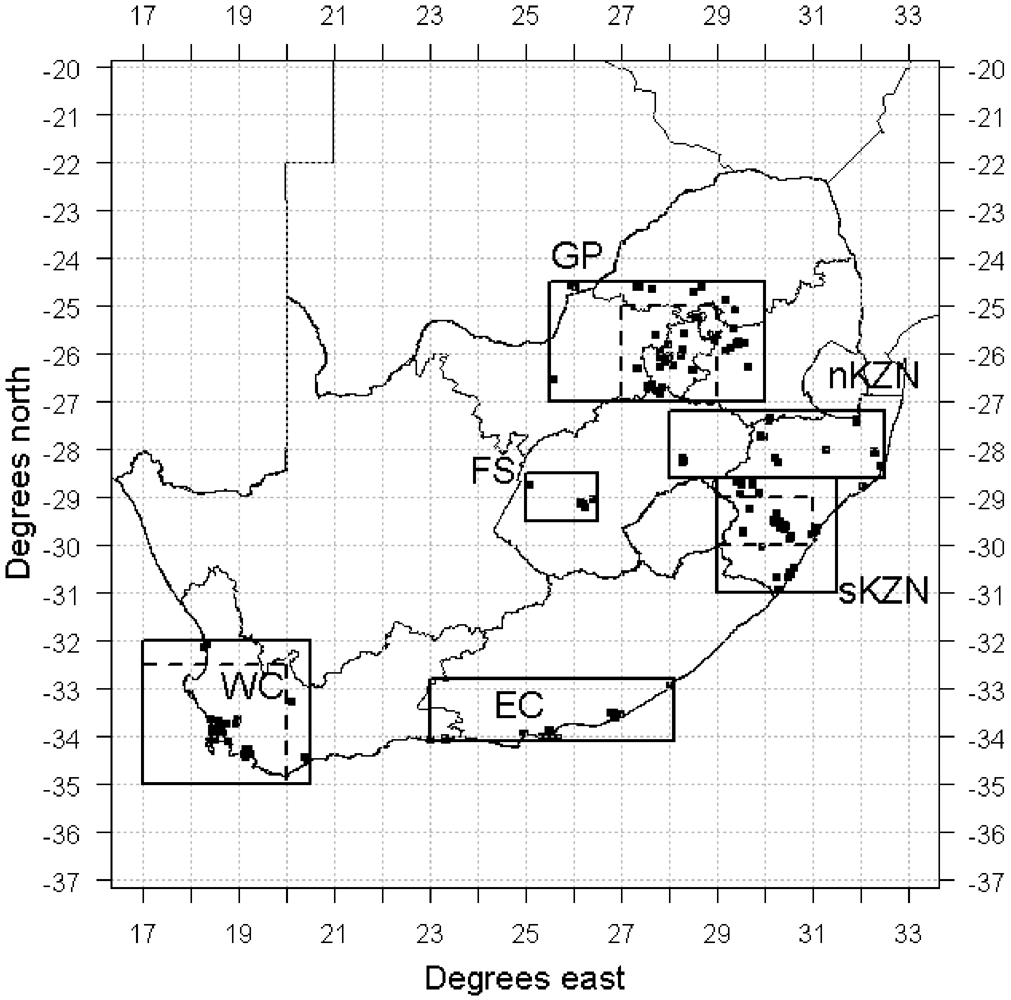

Figure 1. Map of zones and locations of barn swallow records within the zones used in this study. Dashed boxes are zones used by Altwegg *et al.* (2012). Solid boxes indicate zones used in this moult analysis. Zones: Western Cape ‘WC’, Southern KwaZulu-Natal ‘sKZN’, Northern KwaZulu-Natal ‘nKZN’, Gauteng ‘GP’, Free State ‘FS’ and Eastern Cape ‘EC‘. Points indicate locations where barn swallows were ringed. Data consisted of South African barn swallow ringing records, ringed between 1990 and 2012, with moult scores (see Table 2). Records lying outside the boxes were excluded.

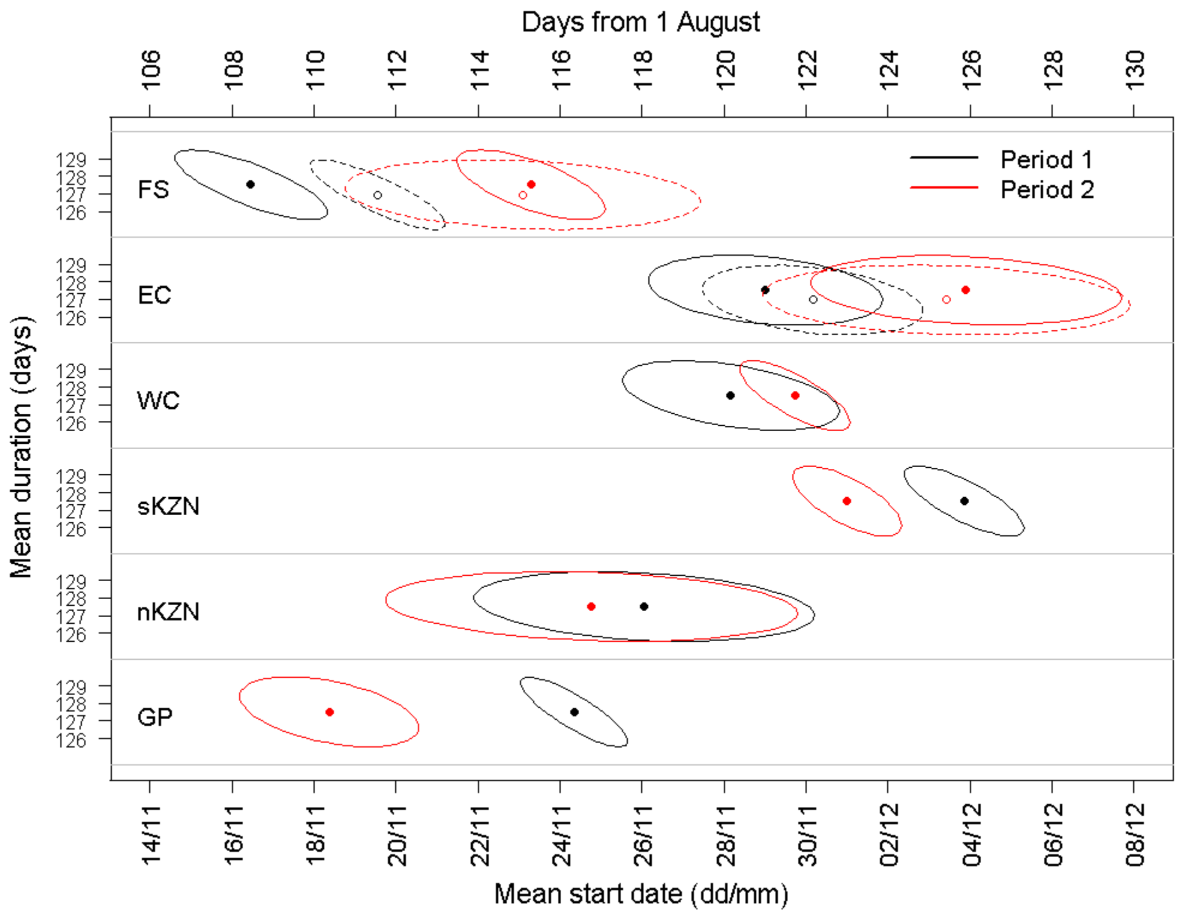

Figure 2. Barn swallow mean duration and start date estimates by zone, for birds ringed in South Africa between 1990 and 2012. Solid line and filled point ellipses reflect the results of model using different time period divisions: for the Free State and Eastern Cape period two started at 2002, and for the other zones period two started at 2006. Dashed line ellipses and open points reflect results of model in which period two started at 2006 in all the zones. Duration was estimated at 128 (SE 0.8) days for the first model and 127 (SE 0.8) days for the second model. The 95% confidence ellipses illustrate the covariance between the duration and mean start date parameters. These Underhill-Zucchini (1988) moult estimates are derived from model five (Table 3). For zone descriptions see Figure 1.

Chapter Six

Pre-migratory weight gain patterns in Palearctic barn swallows in South Africa

Abstract

Changes in the physiological processes that occur during and between life-cycle activities such as breeding, migrating and moulting can reveal the different needs and constraints imposed by each activity or stage within the activity. Knowledge of these changes and constraints is required to understand a species' capacity to adapt to rapid climate change. For the Palearctic barn swallow *Hirundo rustica* I describe geographic and temporal differences in seasonal weight patterns before northward migration from South Africa. Within each geographic zone, weight patterns for two time periods between 1986 and 2012 were compared, using data from the South African Bird Ringing Unit. Patterns were described using locally weighted linear regression. The minimum weight attained was used as an estimate of the start of pre-migratory weight gain and of lean body weight in each zone. Further, to detect a change in the weight pattern between the first and second period within each zone, the start of pre-migratory weight gain in each time period was estimated directly using break-point analysis. In two of the four zones (Gauteng and Western Cape) there was an initial decrease in weight during the non-breeding season, followed by an increase before departure. In the southern Kwa-Zulu Natal zone, weight did not change much before January, but increased before departure in February–April. From the first to the second time period, the start of weight gain in Gauteng shifted 13 days earlier, and two days earlier in the Western Cape. Start of weight gain shifted nine days later in southern Kwa-Zulu Natal, and 15 days later in the Free State, in the second period compared to the first. The geographic variation in the seasonal patterns in weight is probably caused by the different

durations of residence and resulting rates of moult in each zone, with moult being less rushed in some zones than others. The Kalahari region forms a wide east-west band across much of southern Africa where standing water is scarce, and insect abundance is unpredictable even at stopover sites. Many of the barn swallows in the Western Cape, Free State and Gauteng would cross the Kalahari region during migration. Birds in these zones were carrying larger fuel reserves, probably as insurance against unpredictable conditions in the Kalahari. Those in southern KwaZulu-Natal arrived and departed with small fuel reserves, probably reflecting the fairly predictable availability of prey along the eastern sub-tropical regions of southern Africa through which they migrate. Estimated departure fuel loads in South Africa ranged from 15.9% in southern KwaZulu-Natal to 17.5% in the Gauteng, and were 0–5% greater than fuel loads before the start of pre-migratory weight gain. These fuel loads, which are 8–22% of lean body weight below those of barn swallows about to cross the Mediterranean and Sahara desert, suggest that pre-migratory weight gain in South Africa provides a buffer against unpredictable conditions during northwards migration, rather than preparation for crossing a migratory barrier where food is unavailable.

Introduction

From the early 1990s to the late 2000s barn swallow *Hirundo rustica* populations experienced phenological changes in South Africa: timing of migration changed in southern KwaZulu-Natal, and timing of moult changed in the Free State (Møller *et al.* 2011). Further, there were changes in migration phenology between the first and second South African Bird Atlas Projects (SABAP1 and SABAP2 up to 2011) that displayed unexpected geographic variability (Altwegg *et al.* 2012). The changes in moult phenology (Chapter Five) were similar to, but not entirely consistent with, the changes reported by Altwegg *et al.* (2012). These inconsistencies suggested that it would be useful to investigate the phenological changes in another aspect of the life-cycle, the period of pre-migratory weight gain. Pre-migratory weight gain is possibly the only other predictable seasonal event in the long-distance migratory life-cycle, after breeding, migration and moult. Pre-migratory weight gain is a periodic short-term trend within the annual weight pattern, which reflects changes in body composition (mostly fat storage) before migration (Biebach 1996, Jenni & Jenni-Eiermann 1998). To investigate the timing of pre-migratory weight gain, one must first examine the seasonal weight pattern to determine whether pre-migratory weight gain actually occurs. Further, by exploring the seasonal weight pattern, one can detect geographic differences not only in phenology but in fat storage levels.

Seasonal weight patterns, including winter fattening and pre-migratory weight gain, have been well described for waders (Charadrii) (e.g. Summers & Waltner 1979, Rogers *et al.* 1996) and for passerines (e.g. King 1961, Smith 1965, Ormerod 1991, Coiffait *et al.* 2011, Pettersson & Hasselquist 2011), mostly for the Northern Hemisphere (but see Yohannes *et al.* 2008). There has been much interest since the 1960s in the weight differences associated with the long desert and ocean-crossing of the Sahara and Mediterranean (e.g. Moreau 1969, Moreau & Dolp 1970, Moreau 1972, Pilastro & Spina 1997, Pilastro *et al.* 1998, Grattarola *et al.* 1999, Rubolini *et al.* 2002). However, there are few regional studies on the seasonal weight dynamics of Palearctic migrant passerines at their non-breeding grounds (Yohannes *et al.* 2008). Barn swallows are the most widely distributed, widely ringed and well studied long-distance Palearctic passerine in South Africa. The available studies of seasonal weight patterns in barn swallows (Broekhuysen & Brown 1963, Mendelsohn 1973, Loske & Lederer 1988, van den Brink *et al.* 1995, van den Brink *et al.* 1997) have relatively restricted geographic ranges and report either monthly or daily averages and standard deviations, which makes it difficult to detect a pattern. Timing of pre-migratory weight gain in barn swallows has so far not been estimated at a regional level in southern Africa. Aside from an analysis of weight patterns throughout the non-breeding season in Acrocephalus warblers in Nigeria (Aidley & Wilkinson 1987), there seem to be few studies which consider weight pattern during the entire non-breeding season or have a broad geographic scope.

There is thus a large knowledge gap regarding seasonal weight dynamics of populations of Palearctic passerines at their non-breeding grounds, and of the pre-migratory weight accumulation during the northward migration (Yohannes *et al.* 2008). The objective of this study was to address this gap by describing phenological changes between two time periods in the weight dynamics of barn swallows in South Africa from 1986 to 2012. In doing so, the evidence for pre-migratory weight gain in South Africa and geographic variability in the weight patterns are explored.

Methods

Barn swallow ringing records, collected between 1986 and 2012, were obtained from the South African Bird Ringing Unit (SAFRING) data base (Underhill & Oatley 1994). This data set included SAFRING records from six other African countries: Botswana, Zambia, Malawi, Mozambique, Zimbabwe and Namibia. Barn swallow weights from one other location (Ngulia Lodge, Tsavo West National Park, Kenya) were provided by David Pearson (pers. comm.). The Kenyan records were collected only during November and December, as part of the ongoing research project at Ngulia. In all other zones the ringing occurred on an ad-hoc basis.

Barn swallows were mostly trapped on arrival at roosts in the evenings using mist nets, according to methods described in the SAFRING Bird Ringing Manual (de Beer *et al.* 2001). The weight measurements were made with a precision of 0.1g. As such, the estimates and their standard errors were rounded to 0.1g and values less than 0.05 were rounded off to 0.0. To eliminate likely data capture errors, I excluded weight scores below 10g or over 30g. Weights were analysed by the process of ‘synchronised averaging’ (Gardner 1986): data for many non-breeding seasons were superimposed and analysed as though they belong to one period. All ringing was done on an ad-hoc basis, making it necessary to pool records from many locations into zones to have enough records in an area to analyse changes in seasonal weight patterns. Barn swallow body weight estimates reported in the literature are presented for comparison (Table S1).

Records were restricted to birds ringed during the non-breeding season, from October to April (season 1990 thus refers to October 1990 to April 1991). For the analysis of phenological change, I aggregated records into two time periods guided by the number of records per ringing season in each zone, and report weight patterns for four zones within South Africa: Gauteng (GP), southern KwaZulu-Natal (sKZN), Western Cape (WC) and Free State (FS) (Figure 1). For convenience, zones are referred to by the names of the South African provinces where most of the records in each zone were collected.

In this chapter, unlike in the previous chapters, the zones were extended to include the entire province (except in southern KwaZulu-Natal where only the southern part of the province was used). This was done so that the estimates would be more representative of the entire region, and to increase the number of available records in each time period. For the same reasons, for this analysis a relatively small number of records from the surrounding provinces were incorporated into the Gauteng data set. The northern KwaZulu-Natal zone was excluded from this analysis because it was decided to focus exclusively on the four zones (Free State, Gauteng, the Western Cape and southern KwaZulu-Natal) for which the moult and weight trend results can be compared with other published findings of phenological change in barn swallows in South Africa (Møller *et al.* 2011, Altwegg *et al.* 2012).

I tried to keep the size of the two time periods within a zone roughly equal, by using the median ringing year as the start of the second period for most zones. For the countries other than South Africa, and for the remaining South African provinces, there were either too few records or the sampling periods were too short to study changes in average weight over time. Hence, for those countries and provinces, only the average weights are described. Because of the apparent misclassification of first year birds as adults (Chapter Four) the ages were pooled.

Analysis of the seasonal weight pattern in each zone

Locally weighted linear regression (Summers *et al.* 1985, Summers *et al.* 1992, Mullers *et al.* 2009) was used to describe the seasonal weight patterns during the non-breeding season in each zone. This method estimates a flexible curve by applying a weighted ordinary least squares regression (body weight as a function of day) successively to each day (the 'target day') in the time series. The flexible curve is the line connecting the predicted body weights for each day. To determine the degree of smoothing, one must specify the smoothing factor. Scarce data (sections with few or no records) cause the method to over-fit the model, and to smooth over large gaps one can use a higher value smoothing factor. By trial and error I chose a smoothing factor of 17 days on either side of the target day.

From the locally-weighted linear regression curves, I used the minimum estimated weight during the second half of the non-breeding season as an indicator of the mean start of pre-migratory weight gain. To obtain confidence intervals on the start of weight gain estimate, I used non-parametric bootstrap sampling with replacement (with 1000 bootstrap samples) (Efron 2000) and repeated the locally weighted linear regression procedure for each bootstrap sample. For each bootstrap sample a new estimate of the start of pre-migratory weight gain for each sample was generated. Bootstrap samples were taken after grouping the data by zone. From the distribution of the bootstrapped estimates, the interval from the 2.5th to the 97.5th percentile was used as a 95% non-parametric confidence interval.

Estimating departure fuel load

To estimate the departure fuel load, one needs an estimate of lean body weight, because weight in excess of lean body weight is considered to be the fuel load (Alerstam & Lindström 1990, Pilastro & Spina 1997). A standard method to estimate lean body mass is to take the mean mass of birds with a fat score of zero (no visible subcutaneous fat) (Alerstam & Lindström 1990, Pilastro & Spina 1997). However, fat scores were not recorded for barn swallows, so in the absence of other suitable methods or data, I used an untested method – I assumed that the minimum weight attained during the season, which is also the weight at the start of pre-migratory weight gain, approximated the lean body weight of birds in each zone. To determine whether the estimated minimum weights were reasonable estimates of the lean body weight, I compared them with the reported lean body weights for barn swallows from the United Kingdom (Coiffait *et al.* 2011) and Italy and Spain (Rubolini *et al.* 2002).

The mean body weight of the heaviest 25% of birds was taken to be the mean body weight at departure (Alerstam & Lindström 1990). Departure fuel load is estimated as the difference in means between estimated lean body weight and the body weights of the birds in the upper quantile, that is, the heaviest 25% of birds (Alerstam & Lindström 1990). To gain more insight into the seasonal weight pattern, I compared estimated departure fuel load with the estimated fuel load before the start of pre-migratory weight gain. To estimate the fuel load before pre-migratory weight gain, I used only the heaviest 25% of birds ringed before pre-migratory weight gain, and used the minimum weight estimate at the start of pre-migratory weight gain as a proxy for lean body weight. This latter method is not in the original method (Alerstam & Lindström 1990) and has not been tested before as far as I know, but I include it because it is a potentially useful approach.

Estimating the shift in the start of pre-migratory weight gain

To estimate directly the starting date (and weight) of pre-migratory weight gain in each zone, I used a linear break-point detection method (hereafter ‘break-point method’), using R (R Core Team 2015) package ‘segmented’(Muggeo 2008). The break-point method simultaneously estimates the parameters for the segments and the break-points at which they connect, and generates a covariance matrix for the weight and date at the start of weight gain.

The break-point method assumes that the turning point estimate of the independent variable (in this case, the start of weight gain) is asymptotically normally distributed, and the method generates symmetrical confidence intervals based on this assumption. There was no way to test this assumption.

Bootstrapped confidence intervals, which do not assume asymptotic normality of the estimates, were thus provided as an alternative description of the uncertainty in the estimates.

Difference in body size

It is sometimes useful to adjust body weight for differences in body size. Wing-length, which also differs with body size, is often used to do this (Mayr 1956, Hamilton 1961). However, there is only value in such a correction if the variable used to do the adjustment actually varies more than the variable being adjusted. To test whether there would be any value in using wing-length to adjust body mass for differences in body size, I compared the amount of variation in each of these biometrics. The coefficients of variation ('CV') were calculated as CV = standard deviation/mean. For the comparison, I assumed that if the CV of wing length was several times less than the CV of body mass, there was no value in using wing length to adjust for body size.

I used ordinary least squares linear regression to estimate mean body weights before and during pre-migratory weight gain, and used a post-hoc Tukey test to find the zones in which that difference was significant. All analyses were done using R statistical software (v. 3.2.2) (R Core Team 2015).

Results

The data set consisted of 32025 weights of barn swallows ringed between October and April in southern Africa between 1986 and 2012 (Table 1). The smallest mean weight of barn swallows in South Africa was 18.1g in southern KwaZulu-Natal, and the largest was 12% greater at 20.3g in the Eastern Cape. In other southern African countries, the smallest mean weight was 16.8g in Kenya, and the largest was 20% greater, at 20.2g, in Mozambique (Table 1).

To assess differences between the time periods, a subset of 23425 birds ringed in the Free State, Western Cape, southern KwaZulu-Natal and Gauteng was used. Depending on the zone, the first period started in 1986 or 1988 and lasted until 2000 or 2004, and the second period started in 2001 or 2005 and ended in 2007 or 2011 (Table 2, Figure 1).

In each zone barn swallows were estimated to increase in weight before departure (Figure 2). Particularly in the Western Cape, the increase occurred after an initial decrease in weight between October and February (Figure 2). In all zones except the Free State, a maximum mean weight was reached in late March or early April, and in the Western Cape and southern KwaZulu-Natal there was a subsequent decrease (Figure 2). The Free State birds were estimated to be heaviest at the start of pre-migratory weight gain at 19.4g, and those in southern KwaZulu-Natal were 8% lighter at 17.9g (Table 3, Figure 2).

The minimum mean weight during the non-breeding season was estimated to occur earliest in Gauteng on 9 February, then in the Free State five days later on 14 February, southern KwaZulu-Natal three days later on 17 February, and in the Western Cape two weeks later on 4 March (Table 3; Figure 2). The bootstrapped 95% confidence intervals of the estimates were narrow, ranging from three to five days (Table 3; Figure 2).

Analysis of pre-migratory weight gain

The analysis of pre-migratory weight gain is based on average weights within each zone (both time periods pooled). In the Free State and Western Cape, birds were estimated to be on average 0.5g heavier during pre-migratory weight gain than before it, whereas there was no estimated difference in mean weight in the other two zones (Table 4). Estimated departure fuel load ranged from 15.9% of mean minimum weight in southern KwaZulu-Natal to 17.5% of mean minimum weight in the Western Cape (Table 5).

The minimum weights at start of weight gain (Table 3; Figure 2) in the Western Cape, Gauteng and southern KwaZulu-Natal differed by at most 0.8g from the lean body weight for this species in Italy and Spain, estimated at 17.9g (Rubolini *et al.* 2002). Many of the birds in Western Cape and most in

Gauteng were estimated to come from western Europe, so it made sense to compare the minimum weights in these zones with the lean body weight for Italy and Spain. Further, the minimum weight in the Free State was closer to the lean body weights for barn swallows from the UK (juveniles: 19.61g and adults: 20.23g; Coiffait *et al.* 2011) than to values for Spain and Italy, and a large proportion of the birds in this zone were estimated to come from the UK and western Europe (Chapter Two). This suggests that the minimum weight estimates were reasonable estimates of lean body weight for the purpose of estimating the departure fuel loads.

Comparison of time periods

To obtain reasonable estimates of the start of the weight gain period in each zone using the break-point model, it was necessary to remove outliers from the data set. This was done by finding the 0.5th and 99.5th percentiles of the distribution of weights, and excluding records outside this 99% interval. For the Western Cape, Gauteng and southern KwaZulu-Natal zones, I then excluded records collected before 29 November, during the period when many of the birds were still arriving. For the Free State I excluded records before 29 December because few records were collected before this date.

The start of weight gain in the first period ranged from 24 February to 21 March in the first period, and from 1 March to 24 March in the second period (Table 6; Figures 3 & 4). The Start of weight gain shifted earlier in Gauteng and the Western Cape, and later in the Free State and southern KwaZulu-Natal (Table 7; Figure 3). Although the confidence intervals produced by the break-point method were narrow, the intervals produced by bootstrapping reflected an apparently large level of uncertainty in most groups (Figure 5).

The coefficients of variation were 0.1 for body weight and 0.03 for wing-length. The three times greater variability in body weight suggests that an adjustment using wing-length would have little value, so this was not done.

Discussion

The main findings of this analysis are, first, that barn swallows experienced pre-migratory weight gain in South Africa during February and March; second, that the mean date of start of pre-migratory weight gain changed between the two time periods (roughly between the 1990s and late 2000s) with regional variability; and third, that there were regional differences in the seasonal weight patterns. The first section of the discussion deals with the patterns in the estimated barn swallow weight trends, and how they relate to published estimates from other parts of Africa. In the second section, the evidence presented here for pre-migratory weight gain in South African barn swallows is discussed. The departure fuel load estimates are compared to those for other groups and species, and to those reported for birds before and after crossing major migratory barriers, such as the Sahara desert and the Mediterranean. The implications of the levels of departure fuel loads observed in South Africa are discussed, and possible impacts of South African climatic conditions during migration on fuel loads are considered. The estimates of change in timing of pre-migratory weight gain are discussed briefly – these will be considered in more depth in the Synthesis Chapter. The discussion then focuses on several factors related to the methods, the analytical approach and choice of time periods, and the choice of models. Finally some conclusions are presented.

Barn swallow weight variability within Africa

In general, the estimated mean weights observed in this study were similar to those observed for the rest of Africa (comparative mean weights are provided in Table S1). Mean weights in Botswana after drought were near the lower weight limits for barn swallows (van den Brink *et al.* 1997), similar to those expected and observed in Senegal (Loske 1990) and the central Sahara (Bairlein 1985). The mean weight of birds in Morocco, after northward crossing of the Sahara, was similarly several grammes less than the lean body weights estimated in this study and in Europe (Pilastro & Magnani 1997, Coiffait *et al.* 2011), as would be expected following a difficult desert crossing. Barn swallows at the start of the non-breeding season in southern KwaZulu-Natal were apparently not carrying much in the way of fuel reserves. It is unlikely that birds arriving in southern KwaZulu-Natal were lean as a result of being exhausted, because many of these birds would have flown south through the sub-tropical parts of the east coast of southern Africa, where one might expect conditions to be good for insect abundance throughout the non-breeding season. Good foraging conditions can reduce the need to carry fuel reserves, because when food is abundant fat reserves become less important (McLeod *et al.* 2008). Alternatively, the low mean weight of barn swallows arriving in KwaZulu-Natal could reflect a response to predation pressure – for example, starlings *Sturnus vulgaris* were on average leaner when food was more abundant, but were also leaner when predation pressure, measured by relative abundance of raptors, was higher (McLeod *et al.* 2008). Barn swallows are preyed on, particularly when congregating at their roosts, for example by the African hobby *Falco cuvieri* (Bijlsma & van den Brink 2005), and predation probably occurs at both stop-over sites and at the destinations in South Africa. However, before attributing geographic weight differences to predation pressure, it would be necessary to determine how barn swallow predation pressure varies geographically in South Africa. This has not yet been studied.

The fact that mean weights of barn swallows captured in eastern and north-eastern Egypt during northward and southward migration were near to those observed in southern KwaZulu-Natal is also consistent with an alternative explanation, however. KwaZulu-Natal generally became cooler and drier over the study period (Cunningham *et al.* 2015), and barn swallow populations could have been negatively affected if the cooling and drying led to reduced insect abundance. This climate change pattern possibly extended along the east African coast through Mozambique, potentially causing poorer conditions for barn swallows crossing that region. It would require a closer analysis of insect abundance and rainfall and temperature patterns in the region to determine which response was more likely.

The higher mean weights after good rains recorded in Botswana in 1992 and 1993, of 18–22g (van den Brink *et al.* 1997), reveal that the Kalahari region can sometimes provide excellent feeding conditions for barn swallows, and sometimes harsh drought (Table S1). Barn swallows found in the Free State and Gauteng presumably cross the Kalahari, and the departure fuel loads observed for these zones are consistent with crossing an unpredictable, but not always harsh, barrier. Parts of the Free State experienced hotter and drier conditions over the study period (Cunningham *et al.* 2015), but the mean weight for this zone was nonetheless the highest of all the zones; this suggests that weather conditions did not limit foraging on average.

An alternative and intriguing possibility for future testing is that barn swallows from the Free State, which originate mostly in western Europe (Chapter Two), actually have a larger body size than those from further east at the breeding grounds. The zone with the lowest mean body weight, southern KwaZulu-Natal, also had the largest proportion of birds originating from Siberia. Hence, there could be a negative correlation between body weight and longitude in the Palearctic.

Barn swallows captured at their non-breeding grounds in Zambia (Loske & Lederer 1988) and Nigeria (Bijlsma & van den Brink 2005) weighed on average 17–18g (Table S1), mostly less than those ringed in South Africa, but more than those ringed on southward migration through Kenya. The low average weight of the birds in Kenya might reflect the fact that they were captured mostly during November and December, which is during their southward migration – most barn swallows captured at Ngulia are still on migration (Colin Jackson, pers. comm.). The low mean weight of barn swallows at Ngulia could mean that they arrive there with depleted fat reserves, or that they do not need to carry large fat reserves at this stage of the journey. November and December coincide with a rainy season in Kenya, which provides good conditions for migrants, and many species spend some time refuelling in Kenya (Pearson *et al.* 1992). Similarly, conditions in Nigeria and Zambia were probably generally mild, enabling these birds to avoid carrying much in the way of fuel reserves. However, this was not the case in Malawi, Zimbabwe, Namibia and Mozambique, where the mean weights were between the lightest in South Africa (southern KwaZulu-Natal) and the heaviest (Eastern Cape). The consistently higher mean weights in southern Africa probably reflect the relatively dry and unpredictable conditions across the region, because birds are predicted to carry extra reserve as a buffer against unpredictable foraging conditions (Biebach 1996).

Most of the mean weights in Africa (except for Mozambique) were less than the mean weights during pre-migratory weight gain before the southward crossing of the Mediterranean and Sahara from Italy and Spain (Pilastro & Magnani 1997, Rubolini *et al.* 2002). This is to be expected because conditions in most of southern Africa during the austral autumn are relatively mild and do not require the size of reserves necessary for an obligate ocean and desert crossing of 3000km. The amount of weight loss during the desert crossing is illustrated by the drop from 17.2g in the north Sahara to 15.0g roughly 500km south in the central Sahara (Bairlein 1985). Further, the effect of crossing the Sahara in Morocco is illustrated by mean weights of 19.1g before the crossing (Moreau & Dolp 1970), and 15.9g after the crossing (Moreau 1969) (Table S1).

Pre-migratory weight gain

In each zone there was an increase in mean weight towards the end of the non-breeding season, suggesting that pre-migratory weight gain occurred in each zone. In two of the four zones the trends reached a maximum mean weight late in the season, followed by a rapid decline in weight. This decline suggests that the birds leave as soon as they have gained enough weight, causing the mean weight to be reduced. This would be consistent with the expected benefits of returning to the breeding grounds to begin breeding as soon as possible (Alerstam 1990). Comparing mean fuel load before pre-migratory weight gain with the fuel load over the entire season revealed that there were lower mean fuel loads before the start of pre-migratory weight gain in three of the four zones – southern KwaZulu-Natal, Western Cape and the Free State. For the Free State, however, the start of the trend suggests that the estimate for the first part of the season might be unreliable. However, for the other zones, the presence of lower mean fuel loads before the point of minimum weight provides support for the hypothesis that there was some degree of pre-migratory weight gain. This analysis of fuel loads depended on estimated lean body masses which might have been over-estimated, because they were based on the mean lowest point of the trends for each zone (excluding the end points). For example, the lowest quartile of weights during the period surrounding the minimum point (rather than the mean) might give a better reflection of the real lean body mass.

It was originally thought, based on relatively small data sets available in the 1950s and 1960s, that no appreciable fuel loads were deposited before northward migration in South Africa (Broekhuysen & Brown 1963, Mendelsohn 1973). The present analysis, based on a large data set collected over a much longer period, 1986 to 2012, has revealed a clear pattern of pre-migratory weight gain in South Africa.

For passerine migrants that are not preparing to cross a migratory barrier, the estimated departure fuel load is on average 24% of lean body weight, up to 70% (n=55 species), whereas in waders it is 55%, up to 100% (n=32 species) (Alerstam & Lindström 1990). When preparing to cross migratory barriers, however, the estimated departure fuel load is 50% (40–70%) of lean body weight in passerines (n=63 species) and 66% (50–90%) in waders (n=17 species) (Alerstam & Lindström 1990). The South African results presented here therefore seem to reflect the former situation, in which there is no immediate migratory barrier to cross. The barn swallow reserves presented here are thus lower than the average fuel reserves for passerines by 7–8% of lean body weight, relative to the passerine average of 24% fuel reserve (Alerstam & Lindström 1990). The barn swallow is similar in this respect to the red-backed shrike *Lanius collurio*, which weighs about 10g more on average than the barn swallow and has a fat content of 16.8% of mean weight (n=40). Mean fat content is effectively a measure of fuel load, because lean body weight is assumed to be the weight of a bird with no visible fat. A range-wide comparison for other passerine species of seasonal weight patterns and pre-migratory weight gain, especially at the non-breeding grounds, would be valuable.

Body weight depends on the amount of time spent foraging, which in turn depends on the energetic demands of the current life-stage, weather conditions, food availability, and predation risk (Houston &

McNamara 1993). Fat reserves enable birds to survive anticipated food shortages or cold weather both at a daily and seasonal level, and both ‘winter fattening’ and pre-migratory weight gain are examples of this (King & Farner 1966, Biebach 1996). The amount of fat gained before migration is related to several factors including the size of the migratory barriers that must be crossed (Lindström 1991, Rubolini *et al.* 2002), the scheduling of migration in the life-cycle (Ormerod 1991, Coiffait *et al.* 2011) and the existing level of fat reserves (Biebach 1996). The estimated departure fuel loads for barn swallows leaving South Africa were about half as much as those carried by birds from Italy and Spain, less by about 8–22% of estimated lean body weight (Rubolini *et al.* 2002). Conversely, estimated departure fuel loads for barn swallows leaving South Africa were greater than those in the United Kingdom (Coiffait *et al.* 2011) by about 5% of lean body weight (Table S1). The Sahara desert and the Mediterranean present a mostly inhospitable region of 1500–4000km wide from north to south, with limited opportunities for passerine migrants to refuel at infrequent oases (Moreau 1972, Rubolini *et al.* 2002, Turner 2006). The fuel reserves of South African barn swallows thus represent an intermediate state between the low reserve condition of birds in the United Kingdom and the high reserve condition of birds about to cross the Mediterranean and Sahara.

A fat load of 2g (about 10% of the lean body weight of a barn swallow) can theoretically allow an 800km non-stop flight (Pilastro & Spina 1997), and barn swallows about to cross the Mediterranean and Sahara in September deposit 5–8g of fat (Rubolini *et al.* 2002), which thus permits a crossing of 2000–3200km without refueling (Pilastro & Magnani 1997). Barn swallows were estimated to leave South Africa with reserves of 2.8–3.2g (on average 17% of estimated lean body mass) – on such reserves they are probably capable of crossing the Kalahari region or Namib desert, approximately 1500–2000km from north to south, with only a little foraging along route. Alternatively they can retain or supplement their reserves by migrating along the seashore, where insects are more abundant. There are also ephemeral rivers and lakes in the Kalahari region which support large numbers of barn swallows (up to three million at some roosts) when conditions are good, and which may be almost abandoned in dry years (van den Brink *et al.* 1995). During those good years, the northward migration could potentially be faster than average, enabling birds to reach the Sahara in optimal time, with good reserves already in place for the northward crossing.

Southern African conditions during migration

Barn swallows make their northward journey in as little as five weeks (Mead 1970), as opposed to several months for the southward journey (Cramp 1988) – carrying a larger fuel reserve would help to achieve this by facilitating longer flights and reducing time spent refuelling at stopover sites. The fact that the observed fuel reserves were relatively small, suggests that conditions during the northward migration are not on average particularly harsh. The eastern half of southern Africa, divided at 26E, is a summer rainfall region and is home to more Palearctic passerines than the western half (Underhill *et al.* 1998). The western half of South Africa is drier, in some parts receiving less than 200mm of rain in a year (Underhill *et al.* 1998), and insect populations are therefore less reliable. One might thus expect barn swallows leaving the eastern half to require lower departure fuel reserves than those leaving the western half – this was observed for birds from southern KwaZulu-Natal, which had the smallest mean departure fuel load, but not for birds from Gauteng, which had the largest mean departure fuel load. Birds leaving southern KwaZulu-Natal might therefore continue to gain weight, or remain lean and be able to feed regularly, during the early stages of their northward migration. Birds from Gauteng, however, might be prepared for harsher conditions during early migration, or might make the journey to stopover sites in the tropics relatively fast, compared to birds leaving from southern KwaZulu-Natal. Barn swallows could migrate along the coastline, or fly directly across the dry regions, or stop at oases. Some of those departing the Free State and Western Cape are probably able cross the Kalahari region directly because they carry sufficient reserves to cope with the unpredictable presence of water and prey. Those birds that have not been able to gain enough weight might alter their course to fly through more mesic regions or along the coast line where insects are more abundant. Birds crossing the Kalahari should be prepared for conditions that are relatively inhospitable, but nonetheless not as harsh than the deserts of the Middle East, the Sahara, or the Mediterranean Sea crossing. The pre-migratory weight gains described here therefore suggest that the Kalahari belt presents a moderate but not harsh migratory barrier to barn swallows migrating directly north from South Africa (as opposed to migrating north-east along the coast). The same logic could explain the relatively large average weights on arrival for barn swallows in Gauteng and the Western Cape (the arrival weight could not be estimated for the Free State zone) – in most years they can refuel regularly during southward migration and maintain the fuel reserve as a buffer against unpredictable conditions, but in years of drought the buffer is probably exhausted.

Barn swallows originating from eastern Europe and Siberia, of which southern KwaZulu-Natal and the Western Cape had the highest proportions (Chapter Two), presumably migrate along the east coast of southern Africa, where they would experience relatively high prey abundance compared to in the arid conditions further west. There are therefore probably barn swallows in the Western Cape that have much smaller fuel loads than the mean for that zone (18.7%) and migrate along the east coast of Africa to Siberia, and those with much greater fuel loads, which migrate northwards through the semi-arid Northern Cape and arid Namib desert.

The decrease in average weight after arrival in each zone except southern KwaZulu-Natal could have several causes. Two of the reasons why weight might decrease after arrival operate at the individual level. First, to retain large fuel reserves birds would need to spend more time foraging, and carrying the extra weight makes it harder to escape from predators (McLeod *et al.* 2008). Hence, there is no apparent advantage to retaining the large arrival weights in Gauteng and the Western Cape, where prey-availability is probably sufficient throughout most of the summer except in unusually hot and dry or cold and wet years, when barn swallow mortality can be high (Broekhuysen 1953, Skead & Skead 1968). Second, some of the decrease in weight could reflect the high energetic costs of moulting (Jenni & Winkler 1994).

Other sources of variability

Body weight partially reflects body size (Hamilton 1961), so it can differ within a species between groups such as juveniles and adults, or males and females, which differ in body size (Møller 1994, Rubolini *et al.* 2002, Turner 2006). Because sex and age were not included as explanatory variables, these changes in the age and sex composition of the samples could bias the weight patterns. First year birds are on average lighter than adults (Rubolini *et al.* 2002), and first year birds are about twice as numerous as adults by the middle of the non-breeding (Chapter Four). However, even if the initial decrease was caused by the progressive arrival of immatures, adults become more scarce later in the season (de Bont 1962) so the subsequent weight increase is not related to the change in age-ratio. Males (which are heavier than females) arrive earlier at the breeding grounds (Møller 2004) and hence probably leave the non-breeding grounds earlier. Hence, any change in the sex-ratio during the end of the non-breeding season would result in an apparent decrease in average weight during the end of the non-breeding season – the fact that an increase was observed indicates that any effect of change in sex ratio was swamped by the signal of pre-migratory weight gain. Further, no adjustment for body size was made, firstly because there was little variability in wing-length, and secondly, migratory distance is correlated with both wing-length (Marchetti *et al.* 1995, Nowakowski *et al.* 2014) and wing-pointedness (Baldwin *et al.* 2010). Hence, any adjustment made using wing-length could reflect differences in migratory distance rather than body size.

Another factor that could bias weight trends is that the weight of an individual can vary widely during the day, for example, because of breeding, weather and prey availability (Jones 1987, Ormerod 1989), and the presence of predators (Rogers & Smith 1993, McLeod *et al.* 2008). However, the barn swallow body weight records were collected in different locations, at different times of day, over many years, and throughout the non-breeding season, hence they presumably form a representative sample of the variability in weight. As a result, the estimates should not be biased by, for example, individual differences in the amount of weight lost between capture and weighing, or differences between zones in barn swallow responses to weather. However, the impacts of weather were not investigated in this study, so it cannot be ruled out that unusual weather conditions in particular years might have influenced the estimates. For example, barn swallows in Italy, in the weeks leading up to southward migration, gained weight more slowly when conditions were unusually cold and dry than during years with better conditions (Pilastro & Magnani 1997). However, there was a reasonably high number of years in each period in each zone, thereby reducing this risk. The possibility that South African weather variability influenced the results is discussed further in the Synthesis.

Phenological changes over time

The estimated patterns of geographically variable phenological changes in the mean start of pre-migratory weight gain were partially consistent with the estimated changes in primary moult phenology (Chapter Five) – for the two zones in which there were large shifts in the mean start of moult, there were large shifts, in the same direction, in mean start of pre-migratory weight gain. In the zones which had smaller shifts in moult phenology – the Western Cape and southern KwaZulu-Natal, the shifts in pre-migratory weight gain were less consistent. Specifically, there were opposite shifts of about two weeks in mean start of pre-migratory weight gain, earlier in Gauteng and later in the Free State, and there were there were similar opposite shifts in mean start of primary moult in these zones (Chapter Five), although the magnitude was nearer to one week than two. The shift in mean start of moult was earlier in southern KwaZulu-Natal by about three days, whereas the shift in mean start of pre-migratory weight gain was later by nine days. In the Western Cape, mean start of moult shifted about two days later, whereas mean start of pre-migratory weight gain shifted two days earlier. In summary, there were generally large and clear phenological trends in Gauteng and the Free State, whereas there were smaller and less clear patterns for the other two zones.

The greater magnitude of the shift in Gauteng in mean start of pre-migratory weight gain, compared to the shift in primary moult, could reflect the fact that the weight analysis in Gauteng spanned a period nearly twice as long as the moult analysis for this zone. If the underlying patterns were actually linear (as this thesis assumes; Chapter Five), the longer period would give rise to a larger estimate of change. Also assuming linearity, the large shift to later start of pre-migratory weight gain in southern KwaZulu-Natal could reflect real differences in the changes due to different time-scales used – the weight analysis spanned nine years more than the moult analysis for this zone. However, time period differences cannot explain the difference in magnitude of change for the Free State, because the periods used for the two studies were roughly similar, of eleven and twelve years respectively. It is possible that the magnitude of shifts in pre-migratory weight gain was over-estimated by the break-point method (discussed below). The estimated changes in pre-migratory weight gain were also generally consistent with the published changes in barn swallow migratory phenology (Altwegg *et al.* 2012) in Gauteng, the Western Cape and southern KwaZulu-Natal, and in moult phenology in Bloemfontein in the Free State (Møller *et al.* 2011). The generally consistent directions, and to a lesser extent magnitudes, of the changes between these different sets of results suggests that these changes occurred in response to the same set of driving factors, which are likely to be related to Palearctic climate change (Bussière *et al.* 2015).

The approach used when describing phenological changes over time was to assume a constant rate and direction of change in each zone. Further, I assumed that the changes were generally representative of the changes in each zone over the longer period of 1990s and 2000s, even though different numbers of years and different quantities of data were available for each zone. In some cases, different time period definitions were used. The comparative approach and assumptions discussed in Chapter Five also apply here, and in the Synthesis Chapter. The consistency between the different sets of results adds weight to the argument that the methods and assumptions were valid.

Analytical approach

The analysis of seasonal weight patterns is complicated because it requires describing both the central tendencies and the variability over time. A well-fitted curve provides a realistic model of variability over time. The curves presented here reveal interesting regional differences, but the description is largely visual – curves do not lend themselves to simple quantitative comparison. Quantitative comparisons are relatively easy, however, when using averages, into which portions of the trends are pooled. These averages, however, have the disadvantage that they mask much of the real variability over time. Further, the two methods are affected differently by unevenness in the distributions of the data. For example, the dates at which pre-migratory weight gain was estimated to start in each zone (derived from the trends) are well supported because they occur during the period when most of the ringing occurred (February and early March). However, relatively little data were available for the early and late non-breeding season in each zone, so the sections of the trends for those periods (including the maximum mean weights) might reflect the influence of unrepresentative records or outliers. Using the averages, however, the influence of unrepresentative records is reduced, because many records are pooled within each average. Therefore, whereas the trends provide a better understanding of the real patterns of change, they might over-estimate the mean maximum weights, or provide faulty estimates for very early in the season. Conversely, whereas the means for each part of the non-breeding season provide reasonable estimates of average weights over each portion of the trend, it appears that they do not adequately describe the difference between the portions of the trends. These two methods used together provide a more complete description of the weight change patterns than either one does alone.

Choice of models

The smoothing method generated weight trends that appear to fit the data well, and I have assumed that these patterns are reasonably accurate. However, an alternative method – break-point analysis – was used to estimate the turning points, and from these the shifts in start date over time were derived. The shifts obtained by break-point analysis were largely consistent with shifts derived from other sources of data and methods, which suggests that they are valid estimates. However, for two of the zones – Gauteng and the Free State – the break-point method estimated dates of the start of weight gain in each period that were about a month later than the smoothing method estimates. For

Gauteng and the Free State, therefore, the method might have been less appropriate for estimating start of weight gain, or less well supported by the data. However, given the corroboration of the shifts for these two zones from two other sources of data, it seems likely that the shifts at least are reasonably accurate, even if the actual mean start dates of weight gain are somewhat later than they should be. The barn swallow weight patterns were mostly not clearly V-shaped, which would produce the best break-point estimates (Muggeo 2003). The flexible model revealed that the zones which had large discrepancies between the break-point and locally weighted linear regression estimates also had a gradual start of weight gain. The Western Cape, in which the V-shaped pattern was most pronounced, had the least discrepancy and probably the most accurate estimates. The real start dates are therefore probably nearer to the smoothing method estimates which were derived from well-fitted curves. The shifts derived from the break-point methods, however, reflect the relative differences in the estimates; it can reasonably be argued that the relative differences can still be correct, even if the absolute values are estimated to be later than they really are.

The narrow (non-bootstrapped) confidence intervals suggest that the real mean start of pre-migratory weight gain in each time period and zone falls within a reasonably narrow date range. Conversely, the wide (bootstrapped) confidence intervals suggest that the real mean start of pre-migratory weight gain could occur any time over a period of several weeks in some zones and periods. Either of these patterns could be true, and for the purposes of this thesis, I have assumed that the date ranges are better reflected by the narrow confidence intervals, and this assumption is supported by partial consistency with other results, as described. However, there are also some technical reasons for placing more trust in the narrower intervals. The narrow confidence intervals are based on the assumption that the mean start of pre-migratory weight gain is asymptotically normally distributed. It is unknown whether this assumption is supported. Bootstrapping was used as an alternative because it does not make this assumption. However, bootstrapping might be inappropriate for this data set, given the method used, and the uneven distribution of the data. This is because the break-point method is probably quite sensitive to the distribution of the data. When an unevenly distributed data set (such as that used here) is randomly and repeatedly sampled, the unevenness can by chance be highly amplified in some of the samples. In these instances, the break-point method could generate unrealistic results, leading to unreasonably wide bootstrapped confidence intervals. I therefore regard the narrower confidence intervals as more realistic for this data set. Nonetheless, future research might reveal that, in some years or periods, the mean start of pre-migratory weight gain in South African barn swallows occurs much earlier in the year (or more gradually) than is suggested by these estimates and narrow confidence intervals.

Choice of zone boundaries

The zones used in this chapter are defined differently to those used in the previous chapters, and to those used for the migratory phenology analysis (Altwegg *et al.* 2012). This was done in order to make use of all the available data, even though this meant that the zones were not perfectly comparable between chapters. Using all the available data helped to improve the representativeness of the estimates in each zone and period. In spite of the different boundaries, however, the zones are essentially comparable between chapters, because the regions within each zone where the bulk of the data were collected were always within the boundaries of the smallest of the zones being compared, those defined by Altwegg *et al.* (2012). The same principle applies to the other provinces used - most records come from the same parts of each zone, when comparing the zones used in different chapters.

Conclusions

These complex geographic differences and phenological changes in weight patterns provide a good basis for examining the phenological changes in moult and migration. These results suggest that there are constraints to phenological change at the level of physiological preparation for migration. For example, barn swallows arrive latest in the Western Cape (Altwegg *et al*. 2012) where the average period of residence is only two weeks longer than the average duration of moult (Chapter Three).

Moult in the Western Cape is thus probably constrained at both ends, and these birds probably have to invest more energy in order to moult at their fastest optimal rate, whereas those in Gauteng have a longer period during which to moult. The sharp and continuous decrease through the non-breeding season in weight in the Western Cape probably thus reflects the time constraints and the larger costs of moulting in the Western Cape where time is most limited. For the Western Cape, these constraints could also explain the late start, and rapid rate, of weight gain. In Gauteng and southern KwaZulu-Natal the decrease in average weight did not continue throughout the period leading up to pre-migratory weight gain; this could reflect a more relaxed moult in those zones, which have much longer residence periods.

Phenological changes in the start of pre-migratory weight gain could be readily studied in other species, and it is surprising that this has apparently not done, as far as I can tell. The break-point method works best when there is a clear difference in slopes (Muggeo 2003), so for species with rapid and large pre-migratory weight gain it would be effective. For barn swallows in South Africa, neither the rate nor extent of pre-migratory weight gain were particularly large, and this probably affected the estimates somewhat. The key advantage of exploring the timing of pre-migratory weight gain in South Africa is that most birds are not actually migrating during this period – departure from throughout South Africa is centred during the first three weeks of April, which is after the estimated start of pre-migratory weight gain. In southern Europe, however, changes in pre-migratory weight gain in could be masked by changes in the timing migration through the region.

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Tables and Figures

Table 1. Descriptive statistics of body weight (g) for barn swallows ringed between October and April in southern Africa from 1986 to 2012. SE: standard error; LCL and UCL: lower and upper limits of the 95% confidence intervals. SD: sample standard deviation. N: sample size. Values less than 0.05 were rounded off to 0.0. For the four zones which are analysed further in this chapter – the Free State, Western Cape, Gauteng and southern KwaZulu-Natal – the ringing locations and zone groups are reflected in Figure 1.

Zone	Abbreviation	Mean	LCL	UCL	SE	SD	Sample size
Free State	FS	19.9	19.8	20.0	0.0	1.8	3099
Western Cape	WC	19.4	19.3	19.5	0.1	2.0	1357
Eastern Cape	EC	20.3	20.2	20.5	0.1	2.3	578
Southern KwaZulu-Natal	sKZN	18.1	18.1	18.1	0.0	1.8	9830
Northern KwaZulu-Natal	nKZN	18.8	18.7	18.9	0.0	2.2	2114
Gauteng	GP	18.6	18.6	18.7	0.0	2.0	9139
Limpopo	LM	18.8	18.5	19.0	0.1	1.6	305
Mpumalanga	MP	18.9	18.4	19.4	0.3	1.7	57
Botswana	BW	17.3	17.2	17.4	0.1	1.6	731
Zambia	ZM	16.9	16.6	17.3	0.2	2.0	124
Kenya	KE	16.8	16.8	16.9	0.0	1.5	2674
Namibia	NA	19.3	19.1	19.5	0.1	1.8	503
Zimbabwe	ZW	19.3	19.2	19.4	0.1	1.8	1283
Mozambique	MZ	20.2	19.7	20.8	0.3	1.2	43
Malawi	MW	18.3	18.0	18.5	0.1	1.5	188
	Total						32025

Table 2. Ringing seasons included in each time period used in this analysis, for barn swallows ringed in South Africa. Amount of data per year is indicated by text shade. Gray text: 1 to 19 records per year; black text: 20 or more records per year. In years that are grouped, the shading indicates amount of data in each year separately.

Zone	Period One	Period Two
Free State	1988, 1992, 1996, 1997–1999, 2000	2001–2005, 2007
Western Cape	1986, 1988, 1989, 1990–1992, 1993–1998, 1999, 2000, 2001, 2002, 2003–2004	2005 –2010, 2011
Southern KwaZulu-Natal	1986–1989, 1990, 1991, 1992–1997, 1998–1999, 2000, 2001–2004	2005–2011
Gauteng	1986–1988, 1989, 1990, 1991–2000	2001–2006, 2007, 2008–2010, 2011

Table 3. Estimated date and weight at start of the weight gain period, for barn swallows in South Africa between 1986 and 2012. Estimates obtained using locally weighted linear regression, hence no standard errors are available for the start of weight gain date estimate. Non-parametric 95% intervals (95% CL) for date estimate obtained using bootstrapping. SE: standard error. Days are counted from 1 August. For zones see Table 1.

Zone	Day at start of weight gain period (95% CI)	Date at start of weight gain period (95% CI)	Weight at start of weight gain period (g) (SE)
FS	198 (196–200)	14 Feb (12 Feb–16 Feb)	19.4 (0.03)
WC	216 (214–219)	04 Mar (02 Mar–07 Mar)	18.7 (0.05)
sKZN	201 (198–203)	17 Feb (14 Feb–19 Feb)	17.9 (0.02)
GP	193 (192–195)	09 Feb (08 Feb–11 Feb)	18.3 (0.02)

Table 4. Mean weight (g) before and during pre-migratory weight gain, for barn swallows ringed in South Africa between 1986 and 2012. See Table 3 for the estimated start date of weight gain. 95% CI: 95% confidence intervals. The difference between the mean weight before and during pre-migratory weight gain was significant for the Free State and Western Cape zones (p < 0.005, ANOVA with Post-hoc Tukey test).

Zone	Before or during pre-migratory weight gain period	Mean	SE	LCL	UCL	Sample standard deviation	Difference in mean weight	Sample size
FS	Before	19.5	0.06	19.4	19.7	1.6	0.5	956
	During	20.1	0.04	20.0	20.1	1.9		2143
WC	Before	19.3	0.06	19.2	19.4	2.0	0.5	1054
	During	19.8	0.11	19.5	20.0	2.1		303
sKZN	Before	18.1	0.02	18.0	18.1	1.8	0.0	5965
	During	18.1	0.03	18.1	18.2	1.9		3865
GP	Before	18.6	0.03	18.6	18.7	1.9	0.0	5475
	During	18.6	0.03	18.6	18.7	2.0		3664

Table 5. Estimated fuel loads ('EFL') for the heaviest 25% (those above the 3rd quantile) of birds by zone before the start of pre-migratory weight gain period, and for the entire non-breeding season. Data consisted of barn swallows ringed in South Africa from 1986 to 2012. Estimated fuel load is given in grammes and as percentage of estimated lean body mass (mean weight at the start of pre-migratory weight gain). The second row of values for each zone represents the estimated departure fuel load ('EDFL'), because it includes birds ringed during the period of pre-migratory weight gain.

Zone	Excludes or includes period of weight gain	Third quantile of body weight	Mean EFL (SE) (g)	Mean EFL as % of mean weight at start of weight gain	Sample size
FS	Excludes	20.5	2.3 (0.08)	11.9	226
	Includes	21.0	3.2 (0.05)	16.5	606
WC	Excludes	20.5	3 .0 (0.07)	16.2	263
	Includes	20.6	3.2 (0.06)	17.4	336
sKZN	Excludes	19.0	2.8 (0.03)	15.6	1276
	Includes	19.0	2.8 (0.03)	15.9	2100
GP	Excludes	20.0	3.2 (0.04)	17.6	903
	Includes	20.0	3.2 (0.03)	17.5	1537

Table 6. Estimated day at start of weight gain in the first and second time periods, within each zone, for barn swallows ringed in South Africa between 1986 and 2011. Estimates derived using break-point method. See Methods section for details about data exclusions and time periods. LCL and UCL: lower and upper limits of the symmetrical 95% confidence intervals. SE: standard error. Days are counted from 1 August. For zones see Figure 1.

Zone	Period	Day				Weight (g)			Sample size
		Estimate (SE)	(date)	LCL	UCL	Estimate (SE)	LCL	UCL	
FS	p1	221 (1.8)	09 Mar	217	224	19.3 (0.1)	19.2	19.5	1481
	p2	236 (1.3)	24 Mar	233	238	19.6 (0.1)	19.4	19.8	1553
WC	p1	232 (5.6)	21 Mar	221	243	18.6 (0.1)	18.4	18.9	547
	p2	230 (1.5)	18 Mar	227	233	17.4 (0.1)	17.1	17.7	731
sKZN	p1	207 (2.6)	24 Feb	201	215	18.2 (0.1)	18.1	18.3	4367
	p2	216 (2.0)	05 Mar	212	220	17.1 (0.1)	17.1	17.2	4132
GP	p1	226 (0.8)	14 Mar	224	227	18.2 (0.1)	18.0	18.3	3845
	p2	213 (2.0)	01 Mar	209	217	18.5 (0.1)	18.4	18.6	4603

Table 7. Shift in the start of pre-migratory weight gain between the first and second period, within each zone, for barn swallows ringed in South Africa, between 1986 and 2011, estimated using a break-point method. Values less than 0.05 were rounded off to 0.0.

Zone	Shift in days (p2−p1)		Shift in weight (p2−p1)	
	Estimate	SE	Estimate	SE
Free State	15.1	0.1	0.3	0.0
Western Cape	−2.3	0.2	−1.2	0.0
Southern KwaZulu-Natal	9.0	0.1	−1.0	0.0
Gauteng	−13.0	0.0	0.3	0.0

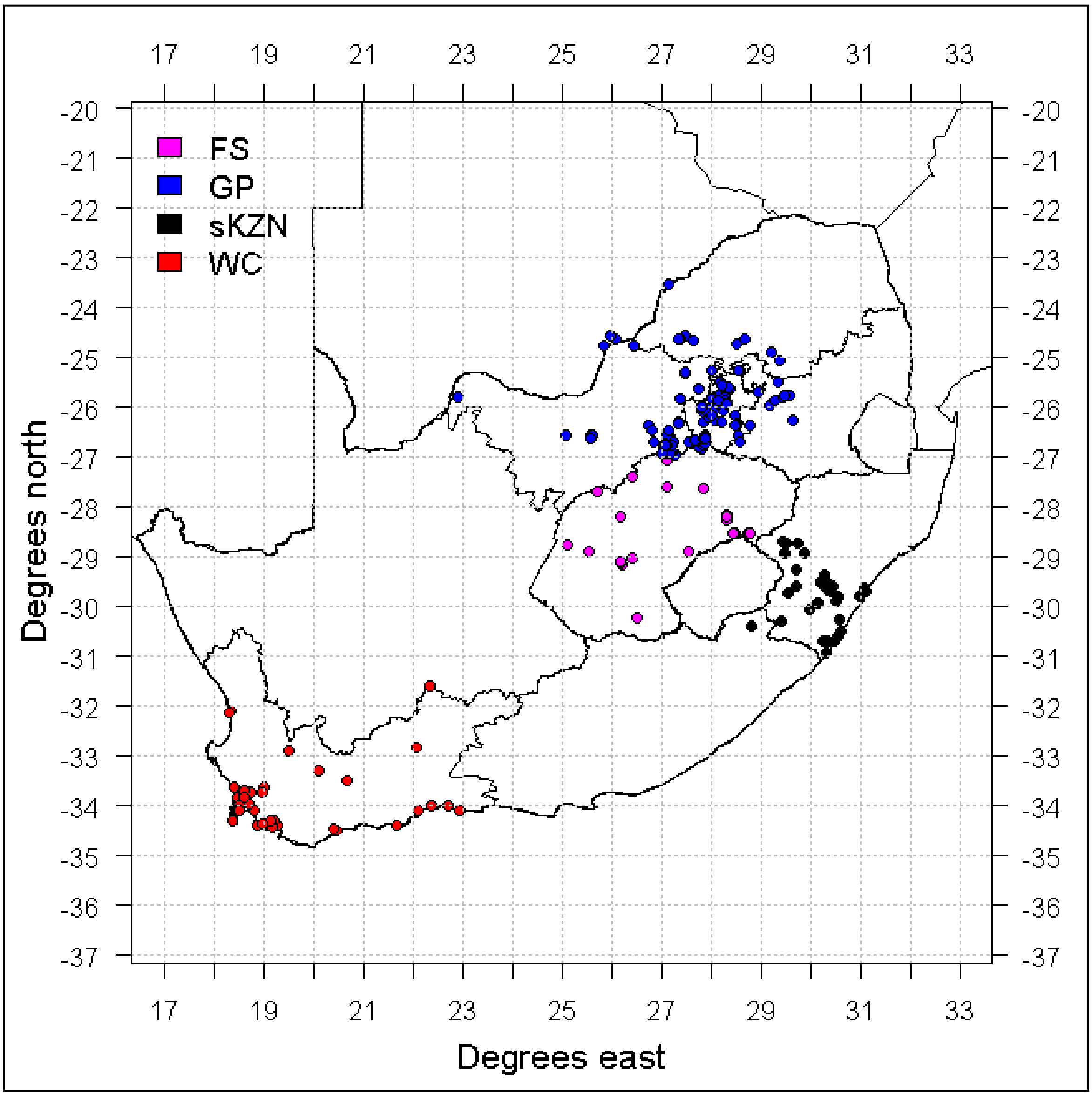

Figure 1. Map of South Africa showing the ringing locations of the barn swallow weight records used in this study, collected between 1986 and 2012, and the zones into which the locations have been grouped. Points reflect approximate ringing locations. Zones: FS: Free State; GP: Gauteng; sKZN: southern KwaZulu-Natal; WC: Western Cape.

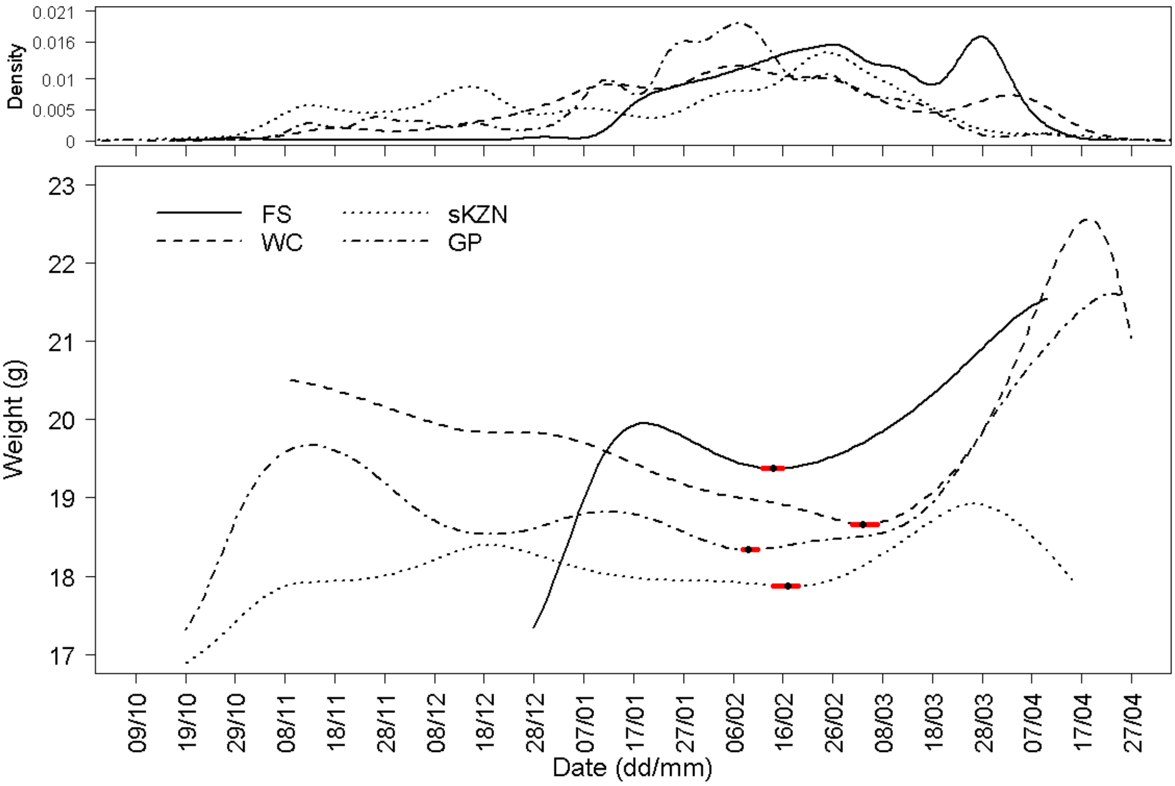

Figure 2. Patterns in weight against date derived by locally weighted linear regression for barn swallows ringed in South Africa, from October to April between 1986 and 2012 (n=23425). Solid points: estimated lean body weight. Red lines: bootstrapped 95% confidence limits for start of weight gain. See Figure 1 for description of zones. Data points are not shown to improve clarity.

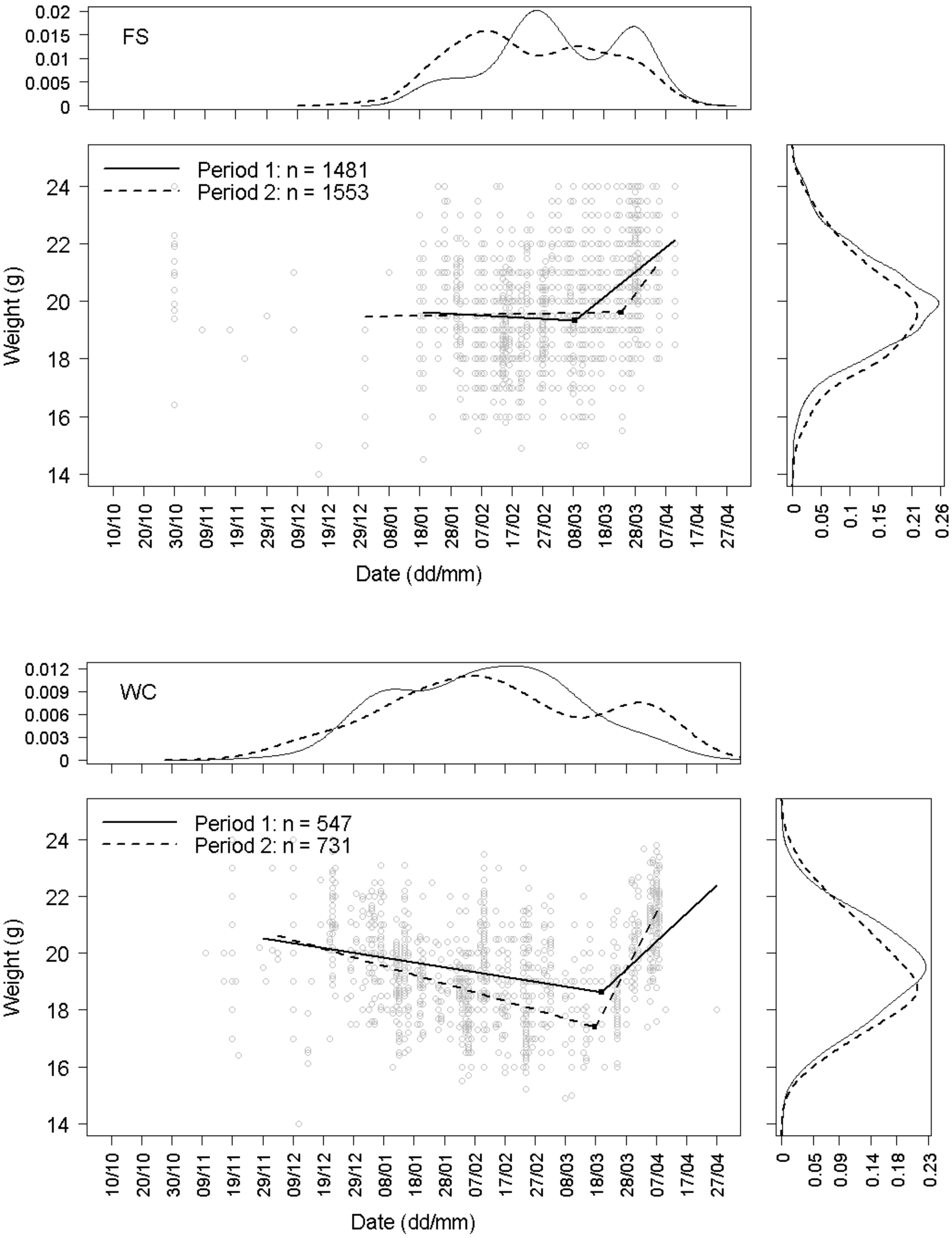

Figure 3. Break-point model of the pattern in weight for barn swallows ringed in South Africa, from October to April, between 1986 and 2012, modelled by time period and zone. For time periods see Table 2. For description of zones see Figure 1.

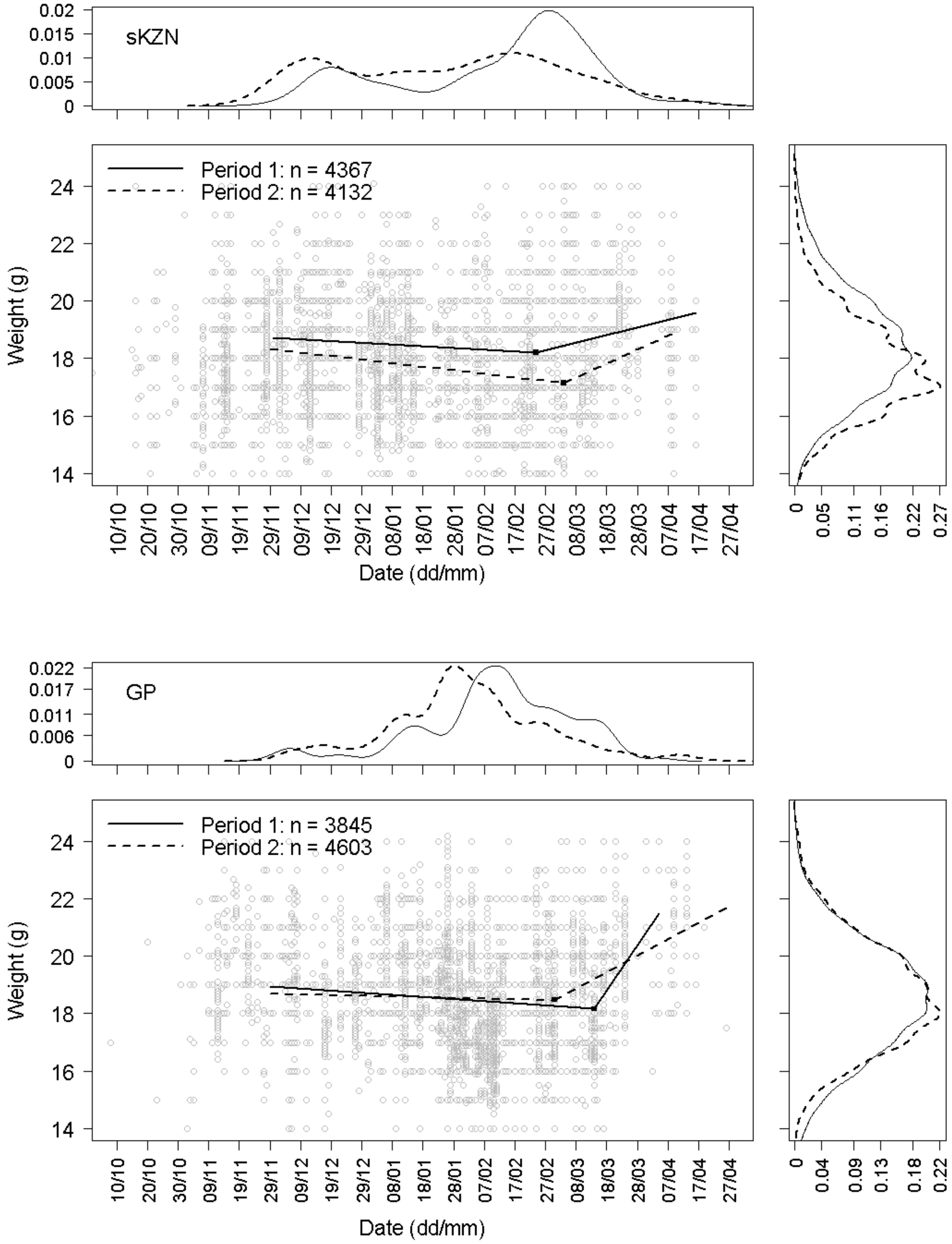

Figure 3 continued.

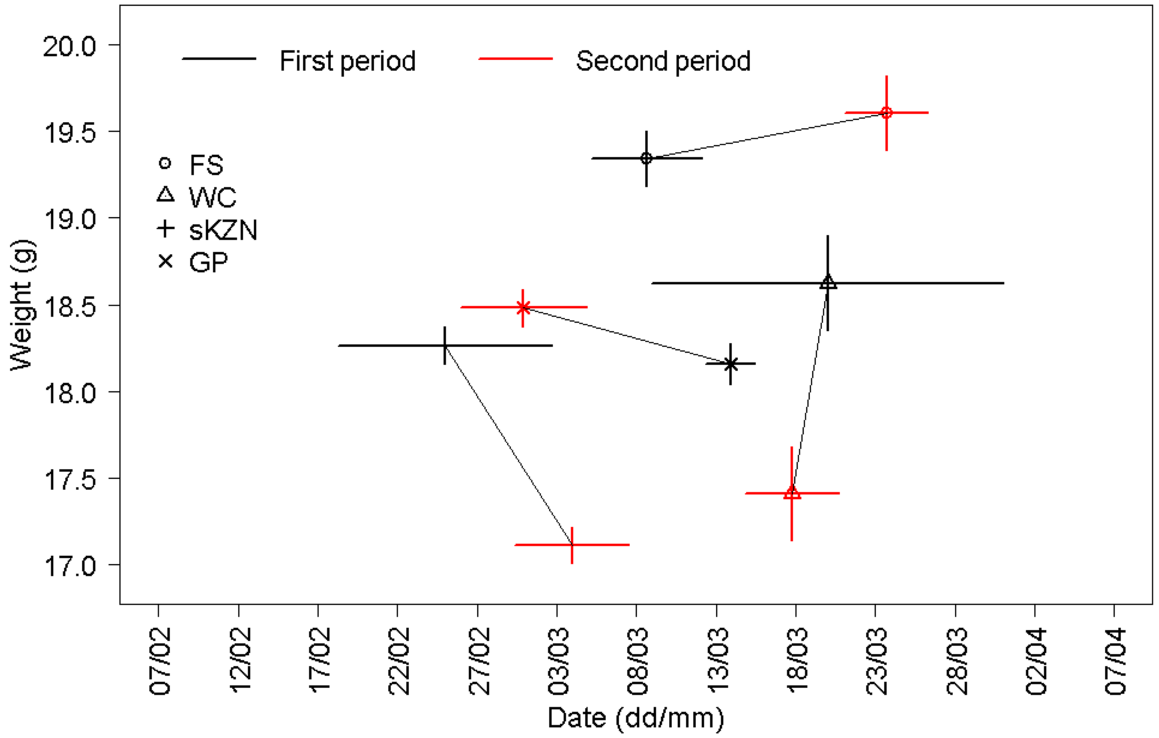

Figure 4. Weight and date estimates at the start of weight gain, for barn swallows ringed in South Africa from October to April between 1986 and 2012. For zones and time periods see Tables 1 & 2. Thin black lines connect the two estimates for each zone. The thick red and black lines are 95% confidence intervals for the weight and date estimates.

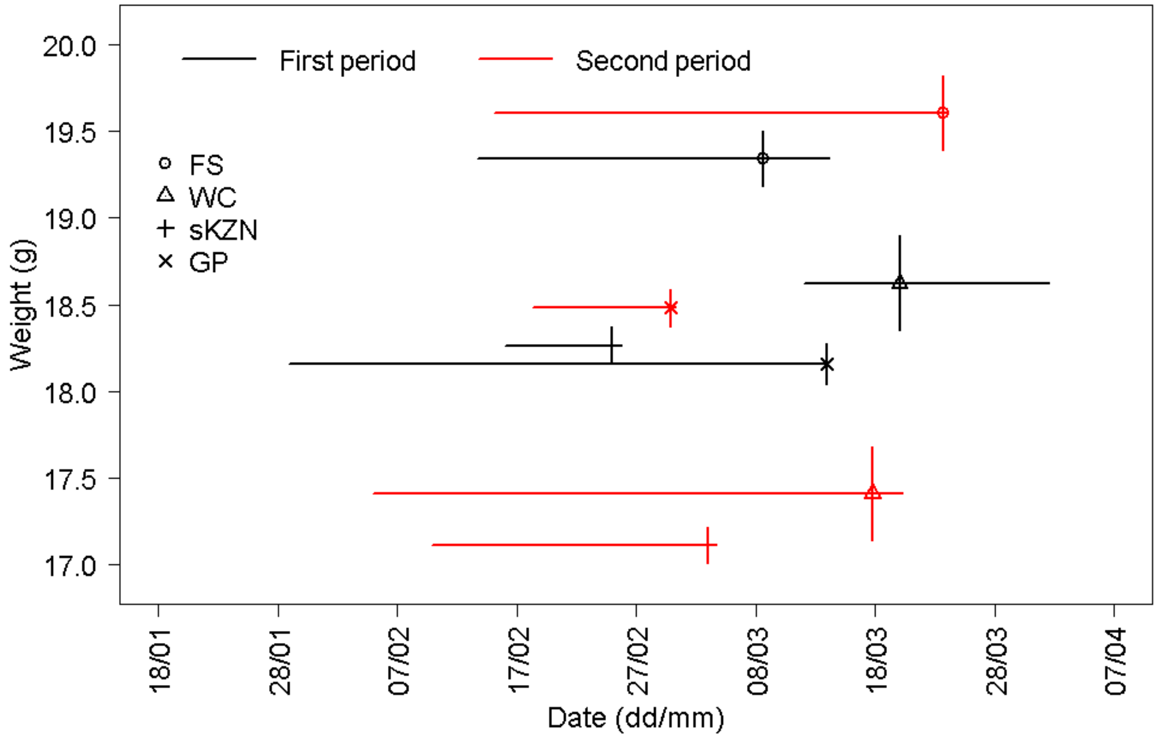

Figure 5. Weight and date estimates at the start of weight gain obtained using a break-point model, for barn swallows ringed in South Africa from October to April between 1986 and 2012. For description of zones and time periods see Tables 1 and 2. The horizontal lines are 95% non-parametric confidence intervals obtained using bootstrapping. The vertical lines are the symmetrical confidence limits. The location of the point estimates is the same as in Figure 4.

Supplementary Information

Table S1. Some barn swallow body weight data reported in the literature. Values are mean ± sample standard deviation (SD) or standard error (SE) or 95% confidence interval (CI), (range). Units: weight (g). LBM: lean body mass. EDFL: estimated departure fuel load. ‘Pre-migratory’: mean weight between start of pre-migratory weight gain and departure.

Location	Date	Mean weight (g)	Source
South Africa, Western Cape	1953 Apr Unseasonal cold / wet conditions	Wt, range: 13.6 (11.7 – 15.8) (n=28)	(Broekhuysen 1953)
South Africa, Limpopo Province	1968 Oct Unseasonal cold / wet conditions	Juvenile: 12.5 (10.9 – 14.9) (n=14) Adult: 13.0 (11.3 – 15.4) (n=51)	(Skead & Skead 1968)
Botswana (several sites) (n < 1000 per season)	1992 1993 1994 December 1995 January	20 – 22 (after rain) 18 – 21 (good rains) 19 (dry) 14 – 15 (drought)	(van den Brink *et al.* 1995) (van den Brink *et al.* 1997)
Zambia	1985 Feb–Mar	Wt ± SD, range: 17.4 ± 1.4 (15.2 – 21.0) (n=88)	(Loske & Lederer 1988)
Nigeria	2001 Jan–Feb	Juvenile wt ± SD: 16.6 ± 1.69 (n=254) Adult wt ± SD: 18.1 ± 2.31 (n=44)	(Bijlsma & van den Brink 2005)
Senegal	1986 Mar–Apr	Wt (range): 15.5 (12.4 – 18.2) (n=5)	(Loske 1990)
Sahara, north / central	1983 Aug–Oct	North: Wt ± SD (range): 17.2 ± 2.3 (12.1 – 23.1) (n=57) Central: Wt ± SD (range): 15.0 ± 1.6 (12.0 – 17.6) (n=21)	(Bairlein 1985)

Table S1. continued

Location	Date	Mean weight (g)	Source
Egypt, north-east	1965 Sep–Oct	Wt ± SE, range: 16.1 ± 0.57 (12.7 – 19.4) (n=8)	(Moreau & Dolp 1970)
Egypt, east	2006 Mar	Wt ± SD: 17.03 ± 1.27 (n=10)	(Hilgerloh & Raddatz 2009)
Morocco, south-east	Before southward crossing of Sahara	Wt: 19.1 (n=18)	(Moreau & Dolp 1970)
Morocco	After northward crossing of Sahara	Wt: 15.9	(Moreau 1969)
Cyprus / Malta	Before southward crossing of Med. Sea	Cyprus: 19.4 Malta: 20.3	(Moreau & Dolp 1970)
Italian Islands	1988 & 1989 Mar–May	16 – 18 (10.3 – 22.4) No seasonal trend in daily means	(Spina *et al.* 1993)
Italy	1996 Sep	Juvenile: 19.26g ± 1.76 (n=7028) Adult: 20.57g ± 1.93 (n=1562) 3rd quartile: Juvenile: 20.3g (EDFL: 24.1%) 3rd quartile: Adult: 21.8g (EDFL: 30.5%)	(Pilastro *et al.* 1998)
Italy, north	1992–1996 Jul–Sep	Juvenile: LBM ± SD: 17.36 ± 0.99 (n=469) Pre-migratory ± SD: 20.52 ± 2.30 (n=12784) Adult: LBM ± SD: 18.59 ± 1.08 (n=113) Pre-migratory ± SD: 22.03 g ± 2.70 (n = 1405)	(Pilastro & Magnani 1997)

Table S1. continued

Location	Date	Mean weight (g)	Source
Italy, central / southern	1997 & 1998 Jul–Oct	Juvenile: 21.1 ± 2.3 (n=4925) EDFL: 35.7% ± 5.8% (n=1233) Adult:22.5 ± 2.5 (n=858) EDFL: 43.8% ± 6.2% (n=220)	(Rubolini *et al.* 2002)
Spain	1997 & 1998 Jul–Oct	Juvenile: 19.6 ± 2.1 (n=3101) EDFL: 24.6% ± 6.5% (n=841) Adult: 21.1 ± 2.3 (n=320) EDFL: 33.9% ± 5.8% (n=80)	(Rubolini *et al.* 2002)
Britain	1988 Jul–Sep	Wt ± 95% CI: 19.5 ± 0.1	(Ormerod 1989)
Britain	2002–2006 Jul–Oct	Juvenile wt ± SD: 19.79 ± 1.4 (32670) LBM: 19.6 ± 1.4; EDFL: 10.37% ± 4.2% Adult wt ± SD: 20.86 ± 1.7 (5413) LBM: 20.2 ± 1.7; EDFL: 13.86% ± 4.4%	(Coiffait *et al.* 2011)

Chapter Seven

Barn swallow phenological changes in South Africa – a synthesis

Introduction

Breeding, migration and moult in long-distance migratory birds must be accomplished within a limited amount of time each year, most often in different places, and with little or no overlap (Jenni & Winkler 1994, Pérez-Tris *et al.* 2001). Climate change caused global temperatures to increase in the late 20th century (Vose *et al.* 2005), and temperature is a key climatic factor to which animal life-cycles respond (Berthold 1996). Climate change causes directional changes in seasonal timing (phenology) by shifting the date at which temperature thresholds (such as the thawing point) are reached in different places (Beniston 2014).

Phenological changes and their consequences are often complicated to explain because they can vary in direction and magnitude at many interacting ecological levels – for instance, between seasons (e.g. Adamík & Pietruszková 2008), between time periods and plant growth forms (Shen *et al.* 2015), between populations in different regions and between related species (Visser *et al.* 2003), and among different trophic levels (Both *et al.* 2009, Thackeray *et al.* 2010). Phenological changes in life-cycles can cause stages with competing energetic demands or physical requirements to shift towards each other in time, and the shift in one of the stages can then be blocked by the inability of another stage to shift – this is thought to be more likely for migrants than residents, because migrants have more constrained schedules than residents (Lehikoinen *et al.* 2004). Worsening phenological constraints are thought to be a cause of population declines, and this has been shown for North American migrant species (Jones & Cresswell 2010). However, population size can also change size for a variety of reasons that are unrelated to the timing of life-cycles. For example, habitat loss at the non-breeding grounds can cause population sizes to change through 'carry-over effects' on individual breeding success (Norris 2005). Prolonged drought, which is not uncommon in parts of Africa, is another non-seasonal event that can reduce population size of migrant birds (Walther *et al.* 2011), potentially outweighing or masking the effects on population size of phenological changes.

Temperature and rainfall during migration, or at the non-breeding grounds, have been linked to changes in breeding phenology and in breeding success – for example, warmer spring temperatures during migration through the Mediterranean region were associated with earlier breeding in Europe for the redstart *Phoenicurus phoenicurus*, spotted flycatcher *Muscicarpa striata*, and wood warbler *Phylloscopus sibilatrix*; and redstarts started breeding earlier in Europe after increased rain in the Sahel (Finch *et al.* 2014). In theory, better weather could enable individuals to maintain better physical condition, enabling them to prepare for migration faster, leave earlier, migrate faster, arrive earlier at the breeding grounds, start breeding earlier (and in better condition), and thus possibly have both the time and energy for an extra brood (Saino *et al.* 2004, Finch *et al.* 2014). Barn swallows were found to reach Europe earlier, and therefore start breeding earlier, in years when they had experienced better conditions at their non-breeding grounds (Saino *et al.* 2004). Further, earlier breeding can improve breeding output, in terms of increased fledgling survival – for example, in a breeding experiment using barn swallows, the survival of second brood fledglings was higher if the birds fledged earlier in the season (Grüebler & Naef-Daenzer 2010).

Structure of this synthesis

This synthesis does not conform to the typical structure of a scientific paper. Rather, it is presented as an essay or discussion that illustrates how the results of the previous chapters can be integrated with other information, to provide a global-scale context for interpreting the findings. In this synthesis I will attempt to draw together the strands of evidence for changes in Palearctic barn swallow *Hirundo rustica* phenology, and consider the potential causes and effects. First, I present a novel method (L. G. Underhill, pers. comm.) which transforms the average phenological changes in the mean start of moult in South Africa (Chapter Five) using the migratory connectivity estimates (Chapter Two). These transformed estimates reflect how birds migrating to different parts of the breeding grounds experienced the phenological changes in South Africa (Table 1). Second, to provide a simplified model of Palearctic phenological changes over the second half of the 20th century, I estimate average trends in spring phenology in the Palearctic, using plant phenological changes as an indicator of average spring trends (Figure 1). Then, assuming that barn swallows respond to phenological changes in the Palearctic and that these changes have carry-over effects in South Africa, I calculate predicted changes in barn swallow phenology in South Africa based on the average trends in the Palearctic (Table 2). Fourth, I present a visual summary (Figure 2) and discussion of the estimated changes in the timing of moult (Chapter Five) and start of weight gain (Chapter Six), in relation to earlier reports of the migration (Altwegg *et al.* 2012), and to the predicted changes in spring phenology. Finally, I discuss some implications of these findings.

Choice of geographic zones

The main objective of the Synthesis was to compare the estimated phenological changes reported in this thesis, and to relate these changes to reported changes in migratory phenology (Altwegg *et al.* 2012), and the change in moult phenology in Bloemfontein in the Free State (Møller *et al.* 2011). Hence, it made sense to focus on the four zones relevant to these comparisons – Gauteng, Western Cape, southern KwaZulu-Natal, and the Free State. Further, the bulk of South African barn swallow ringing has taken place in these zones. The other three zones – Northern Cape, Eastern Cape and northern KwaZulu-Natal – have been analysed in this thesis because they provided information about areas linking or adjoining the four zones on which these studies were focused. Further, phenological estimates for the Eastern Cape and northern KwaZulu-Natal zones have been included in the phenological calendar presented below, in order to provide a more complete estimate of the geographical patterns of phenological changes in South Africa.

Choice of time periods

The approach taken throughout this thesis is to assume that the phenological changes were on average linear, or constant in direction and rate of change, within each zone. The differences in mean start of moult between the periods (the shifts reported in Chapter Five) are therefore assumed to reflect changes from the late 1990s to mid 2000s (for the Free State and Eastern Cape) or to the late 2000s (for the other zones). The differences in mean start of weight gain (Chapter Six) reflect changes from the late 1980s to late 2000s (for Gauteng, southern KwaZulu-Natal and Western Cape), and late 1990s to mid 2000s for the Free State. The assumptions of linearity were applied in both the moult and weight-gain studies, for which data were available for only a portion of the period in each zone. The reasons for this approach, and validity of the assumptions, are discussed in Chapter Five. In essence, I consider these results to be valid hypotheses of change based on the high level of consistency found between the different sets of results. However, as already stated, a different analytical approach might generate different results and conclusions, and further analysis is warranted.

To estimate the changes that barn swallows would have experienced at their breeding grounds over the study period, estimates of shifts in early spring plant phenology in the Palearctic (derived from Ahas *et al.* 2002) were used; from these shifts, assuming linear change, the shift in phenology from 1989 to 2009 was predicted. The period from 1989 to 2009 was chosen because these years are the midpoints of two SABAP periods (1987–1991 and 2007–2011) that were compared by Altwegg *et al.* (2012). The shift from 1989 to 2009 therefore provides an estimate of change in Palearctic spring phenology over the entire period considered in this thesis. The estimated changes in Palearctic spring plant phenology are therefore based on a somewhat longer time period than that used to estimate changes in barn swallow moult phenology (Chapter Five), but similar to that used in the analysis of body weight (Chapter Six). In the phenological calendar presented below (Figure 2), the average timing of the start of the Palearctic spring over the period 1952 to 1998 (derived from Ahas *et al.* 2002), as it is experienced by birds from each of the South African zones, is presented for extra information – this period, which begins well before the start of the main study period of this thesis, is used because it provides a reliable long-term average. Further, including the estimated start of Palearctic spring in the phenological calendar, together with the estimated timing of migration, moult and pre-migratory weight gain in South Africa, helps to illustrate the time pressure which barn swallows are under to return to the Palearctic.

Using the phenological changes in South Africa to obtain patterns of change in the Palearctic

A central hypothesis of this project is that the estimated changes in barn swallow phenology in South Africa occurred in response to (or were driven by) Palearctic climate changes. To test this hypothesis, one could relate the estimated phenological changes at the non-breeding grounds to Palearctic climate changes or their effects on boreal spring phenology. This would be straightforward if we knew the breeding location of every bird - in that case, the supposed Palearctic drivers could be tested as explanatory variables in the models. Failing that, if we knew the breeding destinations for birds from different zones in South Africa, and knew that different breeding populations used different zones in South Africa, the relationships could be estimated by direct correlation. However, the breeding grounds are known only for a small fraction of birds, and barn swallow breeding populations are mixed within each part of South Africa (Rowan 1968, Oatley 2000; Chapter Two), making direct correlation impossible. The migratory connections estimated in Chapter Two provide a logical way of relating these changes, by making it possible effectively to regroup the birds by their estimated breeding zones. In this way, the estimated changes in South Africa are transformed so that they can be presented in terms of the estimated breeding zones, rather than as they were presented in Chapter Five, for each zone in South Africa. These new transformed estimates reflect how birds from each part of the Palearctic experienced the phenological changes when they were in South Africa. The transformed estimates of phenological change in South Africa can now be related directly to climate changes or phenological changes in the respective breeding zones.

This novel method applies a mathematical approach which uses the migratory connections (Chapter Two) to remove the effects of migratory mixing from the estimates of phenological change in South Africa (Chapter Five). The method applies least squares optimization, by setting up four linear inequalities (one for each South African zone), with the changes in mean start of moult as the left hand side (the responses), and the proportions potentially migrating to each Palearctic zone as the right hand side (the predictors). In this case there were four South African zones $(\mathrm{A} \ldots \mathrm{D})$ (Table 1), with changes in moult phenology (in days) represented by $\mathrm{d_A} \ldots \mathrm{d_D}$. There were three destination Palearctic zones $(1, 2, 3)$ (Figure 1) with the proportions potentially migrating from each South African zone to each Palearctic zone represented by $v_{1\mathrm{A}}, v_{1\mathrm{B}}, \ldots, v_{3\mathrm{D}}$. The set of three coefficients which will optimize these inequalities is the set of average phenological changes in South Africa, but presented from the perspective of the Palearctic zones ($\mathrm{x_1}$, $\mathrm{x_2}$, $\mathrm{x_3}$) to which the barn swallows from South Africa were estimated to migrate:

$$\mathrm{d_A} \approx \mathrm{x_1} v_{1\mathrm{A}} + \mathrm{x_2} v_{2\mathrm{A}} + \mathrm{x_3} v_{3\mathrm{A}} \qquad \mathrm{d_C} \approx \mathrm{x_1} v_{1\mathrm{C}} + \mathrm{x_2} v_{2\mathrm{C}} + \mathrm{x_3} v_{3\mathrm{C}}$$

$$\mathrm{d_B} \approx \mathrm{x_1} v_{1\mathrm{B}} + \mathrm{x_2} v_{2\mathrm{B}} + \mathrm{x_3} v_{3\mathrm{B}} \qquad \mathrm{d_D} \approx \mathrm{x_1} v_{1\mathrm{D}} + \mathrm{x_2} v_{2\mathrm{D}} + \mathrm{x_3} v_{3\mathrm{D}}$$

Least squares optimisation minimizes the sum of the squared deviations, and to apply this in R (using the lm() function; R Core Team 2015), I used a matrix formulation of the responses and predictors (see Table 1). The values used to generate the results, and the results of the optimisation, are provided in Table 2. Using the changes in mean start date of pre-migratory weight gain in South Africa to estimate the corresponding changes from the perspective of the Palearctic zones did not generate a useful model, so I have not included those results.

Table 1. Matrix formulation of the four inequalities comprising the changes in mean start date of moult in each South African zone (Chapter Five), and the proportions potentially migrating from South Africa to each Palearctic zone (Chapter Two). The coefficients that achieve the optimised least squares solution to the set of inequalities are the estimated average changes in mean start of moult in each Palearctic zone (last row). Solving these equations using the estimated coefficients provides new estimates of the changes in mean start of moult in the South African zones (last column). See Chapters Two and Five for details about zones. The time periods are approximately matched between the zones – first period: 1990s to early 2000s; second period: early to late 2000s (Chapter 5). Residual standard error of least squares optimisation: 0.83 days. Positive values indicate shift to later mean start of moult, negative to earlier mean start of moult.

South African zone	Change (days) in mean start date of moult between time periods	Proportion potentially migrating from South Africa to each Palearctic zone			Estimated change in mean start of moult between time periods (days, SE)
		western	central	eastern	
Free State	+6.8	0.760	0.240	0.000	+7.0 (0.80)
Western Cape	+1.6	0.284	0.312	0.404	+1.0 (0.52)
Southern KwaZulu−Natal	−2.9	0.053	0.386	0.561	−2.4 (0.68)
Gauteng	−6.0	0.146	0.794	0.060	−6.0 (0.83)
Coefficients that provide the optimal solution. Estimated change in mean start of moult in South Africa, but presented for the destination Palearctic breeding zones (days, SE)		+12.4 (1.17)	−9.9 (1.18)	+1 .4 (1.47)	

The estimates (Table 1, last column) of the response variable, change in mean start date between the time periods in the South African zones, were almost identical to the original response values (first column) – the estimated coefficients can thus be considered to be reliable. The Free State, where mean start of moult shifted on average seven days later, had the largest proportion of birds potentially migrating to (or originating in) the western Palearctic zone (74%); the Western Cape, where there was an estimated two day later start of moult, had the next largest proportion of birds originating in the western Palearctic zone (26%) (Table 1) (these proportions are taken from Table 3 of Chapter Two). Consequently, for barn swallows migrating to the western Palearctic from South Africa, the predicted average shift in the start of moult in South Africa was a large delay, of 12 days over the study period. Gauteng had the largest proportion of birds originating in the central Palearctic zone (81%), and hence had a large influence over the predicted mean start of moult (10 days earlier) experienced by birds migrating to the central Palearctic zone from South Africa (Table 1). Relative to the other South African zones, Southern KwaZulu-Natal and the Western Cape had large proportions originating in the eastern Palearctic zone (54% and 40% respectively; Table 1). As a result, the predicted change in the mean start of moult that barn swallows migrating to the eastern Palearctic zone would have experienced was just one day later (no change).

Summary of changes in the timing of spring in the Palearctic

Before considering the changes in phenology in South Africa, it is worth considering the phenological shifts in the Palearctic in some detail. Menzel *et al.* (2006), in a meta-analysis of more than one hundred thousand phenological time series, reported an average European phenological response of earlier start to spring, by 2.5 days per decade, and almost no change real to autumn phenology (a delay of 1.3 days per decade); start of spring shifted the most in the warmer European countries where spring starts earlier in the year, and earlier spring phases shifted earlier by more days per decade than later spring phases (Menzel *et al.* 2006). For comparison with the estimated changes in mean start of moult in the Palearctic (Table 1), I estimated the average shifts in each Palearctic zone using plant-phase phenological data (the mean start of flowering and leaf-unfolding) from a published study – Ahas *et al.* (2002). The longitudinal range assessed in that study coincided largely with the barn swallow breeding grounds. For each longitudinal Palearctic zone (Figure 1), I calculated averages of the reported shifts in the spring phases of six plant species, for the period 1951–1998 (Ahas *et al.* 2002).

There were several reasons why plant phenology, rather than bird phenology, was used as an indicator of the pressures faced by barn swallows at their breeding grounds. From a methodological perspective, I preferred to use the results of one study, in which one method and time period were used and with a broad geographic scope, rather than combining results from several studies. There were also biological reasons for using plant phenology. Changes in barn swallow phenology at the breeding grounds (Sokolov *et al.* 1998, Sparks & Braslavská 2001, Møller 2004, Sparks & Tryjanowski 2007) were not used as indicators because they already reflect the outcome of how those pressures have interacted with the constraints imposed by the long-distance migratory life-cycle. For the same reason, I avoided using changes reported for other bird species - all such changes reflect responses to climate change, rather than external pressures faced by birds. Plant phenology, on the other hand, reflects changes in the environment inhabited by birds, and therefore provides one way of estimating how spring conditions have advanced in those ecosystems. Further, plants and animals on average responded similarly to increases in temperature over the second half of the twentieth century (Root et al. 2003, Menzel et al. 2006). However, plant phenological responses are not unconstrained responses to temperature change - for example, in many tree species the start of new growth in spring, and start of preparation for winter, are related to changes in day length as well as changes in temperature, and the interactions between these cues can be complex (Way 2011). Further, given that trees do not always respond as strongly as other plants or as animals to increasing temperatures (Root et al. 2003), the changes in tree spring phenology that I derive from Ahas *et al*. (2002) might underestimate the expected changes in barn swallow phenology at the breeding grounds over the period. However, in spite of these constraints, using plant phenological responses might nonetheless provide a more realistic model of change in spring timing, as birds experience it, than using changes in temperature directly.

The six plant species for which spring phenology was estimated emerge from Palearctic winter dormancy progressively later the farther east one goes, in the following sequence: hazel *Corylus avellana*, colts-foot *Tussilago farfara*, Birch *Betula pendula*, lilac *Syringa vulgaris*, apple *Malus* *domestica*, and linden *Tilia cordata* (Ahas *et al.* 2002). For all the species except birch, the date of start of flowering was measured; for birch, the start of leaf unfolding was measured (Ahas *et al.* 2002). So that the averages reflected the timing of the start of spring in each zone, rather than average timing of spring and summer phases, I averaged different subsets of the data from Table 3 in Ahas *et al*. (2002). The species subsets from which I derived the mean start of spring date in each zone were chosen as follows: for the western zone, the start of spring flowering of the two species that flower earliest: hazel and colts-foot. The remaining four species were excluded from the estimate for the western zone because they produce new growth later in the season (mid-April to late June), and therefore their estimates would not reflect the early start of spring for the western zone. For the central zone, hazel was excluded because its estimated flowering date was not available for every station in this zone, and the next two species in the sequence – colts-foot and birch – were used, whereas the last three species were excluded for the same reason that the last four species were excluded from the estimate for the western zone. For the eastern zone, all the species for which data were available were included (that is, all except hazel); this was based on the logic that, of the nine sites for which data were averaged in this study, the start of spring occurs latest at the Ural Mountains. Therefore, even the latest new growth (that of linden) might still reflect spring (or possibly early summer) conditions in this region. The same subsets were used to derive the average rates of change for each Palearctic zone from the changes reported in Table 3 of Ahas et al. (2002), except that for the eastern zone, no rate of change for linden was available, so that species was excluded.

The plant phenology data were collected over 48 years, from 1951–1998 (Ahas *et al.* 2002). This time period is much longer than the time period I used to assess changes in barn swallow phenology; however, much of the warming in the second half of the 20th century occurred after 1970 (Walther *et al.* 2002, Menzel *et al.* 2006); similarly, early springs occurred more frequently after 1970 than before 1970 (Ahas *et al.* 2002). The shifts reported in Ahas *et al*. (2002), and the averages I have calculated from these shifts, therefore probably underestimate the actual shifts that occurred during the later decades of the 20th century and the 2000s, which are the focus of this thesis.

A core hypothesis of this thesis is that barn swallow phenology at the non-breeding grounds responded to seasonal changes at the breeding grounds. The average changes in plant phenology at the breeding grounds (Figure 1, derived from Ahas et al. 2002) provide a proxy for the seasonal climate changes that barn swallows would be exposed to at their breeding grounds. Barn swallows in South Africa come from different parts of the breeding grounds (Chapter Two), where they experience different climate changes. By reweighting the average plant phenological changes in each Palearctic zone, it is possible to estimate how much change at the breeding grounds the birds in each South African zone experienced, and therefore how much change should be expected in their non-breeding phenology in South Africa. The proportions of birds potentially migrating to each Palearctic zone (Chapter Two; Table 1) provide the weights to calculate the weighted averages of Palearctic phenological change as experienced by barn swallows from each South African zone (Table 2).

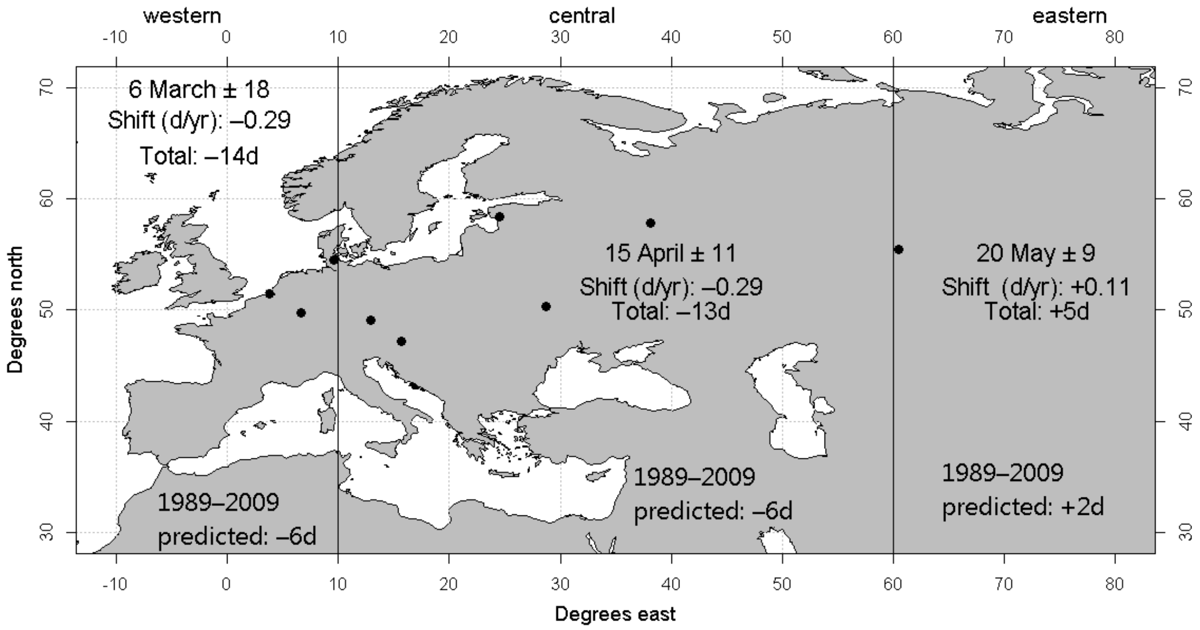

Figure 1. Average start dates, rates of phenological change, and total days of shift in the start of spring from 1951–1998, for longitudinal zones of the Palearctic: western: west of 10°E; central: from 10°E to 60°E; eastern: east of 60°E. The 1989–2009 predicted shifts assume that the same trends applied up to 2009. The location of monitoring stations (points) are derived from Tables 2 and 3 in Ahas (2002). Values relate to flowering or leaf unfolding, and reflect averages for each Palearctic zone, for starting date, rate and direction of phenological shift in days per year, and total number of days shifted over the 48 year period. See text for more details.

Table 2. Predicted starting date of spring (SD), regression slope (the change in start of spring in days per year, multiplied by 10 to provide days per decade), total days shifted from 1951–1998, and extrapolated total days shifted from 1989–2009, in the zones of South Africa. Predictions are the weighted averages of the estimates of early spring plant phenology in the Palearctic (Table 3 in Ahas *et al.* 2002), using the proportions potentially migrating from South Africa to the Palearctic (Table 1) as the weights.

Zone	Date	Days per decade	Total days (1951–1998)	Extrapolated total days (1989–2009)
Free State	17 Mar ± 16	−2.9	−14	-6
Western Cape	19 Apr ± 12	−1.3	−6	-3
Southern KwaZulu−Natal	01 May ± 10	−0.8	−4	-2
Gauteng	12 Apr ± 11	−2.7	−13	-6

Estimated phenological changes

Two earlier studies on barn swallow phenology in South Africa (Møller *et al.* 2011, Altwegg *et al.* 2012) revealed geographic patterns of phenological change which could not be easily explained, for example, by differences in latitude and longitude between the zones at the non-breeding grounds (and hence by distance from the breeding grounds). A key objective of this thesis was to find satisfactory explanations for these differences, by relating the patterns of moult and weight gain phenology observed in South Africa to climate changes at the breeding grounds. The first finding of this thesis was that the proportions of barn swallows going to different longitudinal sections (‘zones’) of the Palearctic breeding range differed between regions of South Africa. Second, the timing of moult and start of pre-migratory weight gain revealed phenological changes between the earlier and later study periods. Further, these changes varied between geographic zones in South Africa. The changes in moult and weight gain phenology were to some extent consistent with reported changes in moult phenology (Møller *et al.* 2011) and migratory phenology (Altwegg *et al.* 2012) – the inconsistencies, however, lead to interesting hypotheses which are discussed in this synthesis.

Free State

Mean start of moult (Chapter Five) and of pre-migratory weight gain (Chapter Six) shifted later by one to two weeks (mean start and end of moult: 7 days later; mean start of weight gain: 15 days later; Figure 2). This initially appears to be counter-intuitive, because barn swallows in the Free State originated mostly in the western Palearctic zone (74% originated west of 10°E) (Table 1; Chapter Two), where the start of spring shifted earlier between 1951 and 1998 by 14 days (Ahas *et al.* 2002, Turner 2009). Assuming that the weighted average trend in the start of Palearctic spring also applied to the period 1989–2009, spring started on average 6 days earlier over 1989–2009 in the western Palearctic zone, as well as 6 days earlier for birds using the Free State (Figure 1, Table 2). Earlier springs lead to a longer breeding season, which could enable migrants, including barn swallows, to produce an extra brood and leave the breeding grounds later (Jenni & Kéry 2003, Møller *et al.* 2008). Given that the mean start of moult and of pre-migratory weight gain shifted later in the Free State, it could be that barn swallows in this zone have already begun to experience increased selective pressures – the pressure to begin breeding earlier could continue to cause birds to depart earlier from the Free State; this would lead to a conflict developing between departure and moult and pre-migratory weight gain. Such a conflict might already have occurred.

However, conditions in the Free State also became warmer and drier during the 1990s and 2000s (Cunningham *et al.* 2015). This presents an alternative hypothesis for the estimated delayed mean start of moult and pre-migratory weight gain in the Free State (Figure 2). Barn swallows and their insect prey both require access to open water, and both function best at moderate temperatures (Cramp 1988). Therefore, warmer and drier conditions that reduce insect activity and restrict water availability probably cause moult to slow down, by reducing the amount of energy available for it. Barn swallows in Europe that are preparing for migration increase their foraging intensity during pre-migratory weight gain (Pilastro & Magnani 1997), and it seems likely that a similar increase in foraging intensity would occur at the non-breeding grounds. Further, barn swallow pre-migratory weight gain in South Africa coincided with the final stages of primary moult (Figure 2), suggesting that these processes would compete for energy when prey is limited. Stressful weather conditions might therefore delay the start of moult, delay the start of pre-migratory weight gain, and slow down both processes. Under such conditions, birds might be forced to delay departure, or to depart in less than optimal condition.

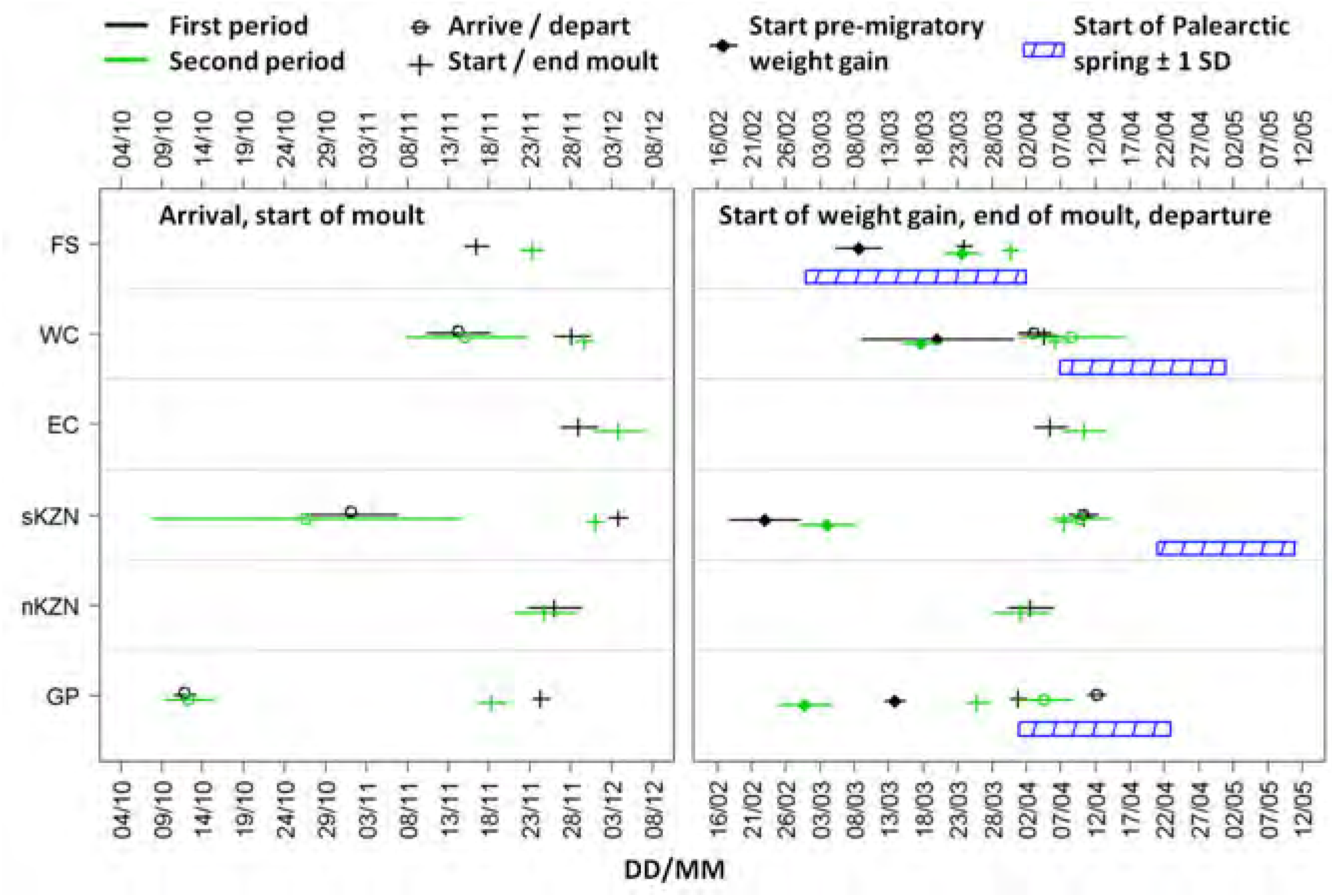

Figure 2. Calendar of estimated phenological changes in barn swallows at their South African non-breeding grounds in the 1990s and 2000s. Black lines: first period; green lines: second period. Horizontal lines: 95% confidence intervals. FS: Free State; WC: Western Cape; EC: Eastern Cape; sKZN: southern KwaZulu-Natal; nKZN: northern KwaZulu-Natal; GP: Gauteng. Migratory phenology based on Altwegg et al. (2012). Start of Palearctic spring estimates are weighted averages derived from Ahas *et al.* (2002) and the proportions potentially migrating to each Palearctic zone (Table 1), for the period 1951–1998. Moult estimates are from Chapter Five, and weight phenology estimates are from Chapter Six. The time periods are approximately matched between the zones and variables presented – first period: 1990s to early 2000s; second period: early to late 2000s (Chapters 5 and 6). See text for details about the methods and time periods.

Western and Eastern Cape

The Western Cape zone is home to birds from all parts of the breeding range (Table 1; Chapter Two), and the predicted shift in the start of Palearctic spring for the Western Cape, after extrapolating the weighted average (based on the period 1951–1998) into the period 1989–2009, was 3 days earlier (Table 2). Consistent with this, there were relatively small changes in barn swallow phenology in this zone: arrival and departure both shifted later over the study period, by one and five days respectively (Altwegg *et al*. 2012); mean start of moult shifted two days later (Chapter Five), and start of pre-migratory weight gain two days earlier (Chapter Six; Figure 2).

Arrival was latest in the Western Cape relative to the other South African zones (Altwegg *et al*. 2012). This probably reflects to some extent the extra migratory distance involved, with Cape Town located about 1200km south west of Gauteng and KwaZulu-Natal. The barn swallows that reach the Western Cape from Siberia probably migrate along the east coast of South Africa, passing through southern KwaZulu-Natal and the Eastern Cape, and presumably many stop in those two regions. Barn swallow phenology in the Eastern Cape shifted later over the period (Figure 2). The Eastern Cape is geographically between the Western Cape and southern KwaZulu-Natal, so the migratory patterns for the Eastern Cape were probably transitional between those for its neighbours (Chapter Two), but with more birds from Siberia than from the western Palearctic. The shift toward later start and end of moult in the Eastern Cape (Figure 2) is consistent with the effect of the delayed spring in Siberia (Ahas *et al.* 2002).

KwaZulu-Natal

The southern KwaZulu-Natal population consisted of birds from Siberia (54%) and the central Palearctic zone (40%) (Table 1; Chapter Two) – the predicted weighted average shift in the start of Palearctic spring for birds in the southern KwaZulu-Natal zone was two days earlier over the period 1989–2009, if one assumes that the average Palearctic spring trend also applied to this period (Table 2). From 1951–1998, in central and eastern Europe, mean start of spring shifted earlier by 13 days on average, whereas in Siberia the start of spring shifted later by five days on average (Ahas *et al.* 2002), or six days earlier and two days later respectively for the period 1989–2009 (Figure 1). The phenological shifts observed in southern KwaZulu-Natal are complex, with earlier arrival by six days (Altwegg *et al*. 2012) and earlier moult by three days (Chapter Five), pre-migratory weight gain nine days later (Chapter Six), and departure unchanged over the study period (Altwegg *et al.* 2012) (Figure 2). Hence it is difficult to draw firm conclusions for this zone.

Changes in northern KwaZulu-Natal (Chapter Five) were intermediate between those in southern KwaZulu-Natal and Gauteng, which is to be expected as that cohort was probably also a mixture of birds from central and eastern Europe and from Siberia. In southern KwaZulu-Natal there was an increase in barn swallow reporting rate of roughly 10% from 1987–1991 to 2007–2011 (Altwegg *et al.* 2012), suggesting that barn swallows became more abundant (or at least more visible) in this zone. The increase suggests that at least some of the breeding regions from which birds migrated to southern KwaZulu-Natal had increasing populations over the period.

Gauteng

Barn swallows in Gauteng originated mostly in the central Palearctic zone (81%; Table 1) where spring shifted earlier by a predicted six days from 1989–2009 (Figure 1). The shifts over the study period in moult (six days earlier; Chapter Five), start of weight gain (13 days earlier; Chapter Six) and departure (eight days earlier; Altwegg *et al*. 2012) were therefore entirely consistent with the predicted shift in start of spring in the central Palearctic zone. Arrival in Gauteng was, however, unchanged (Altwegg *et al.* 2012) – the fact that arrival in Gauteng did not change, whereas start of moult, start of pre-migratory weight gain, and departure all shifted earlier, supports the hypothesis that a longer European summer potentially encourages a longer breeding season. It seems likely that late breeding or late fledged birds cannot migrate early enough to arrive earlier at the non-breeding grounds. For this hypothesis to be verified, the earlier estimates of proportions having one, two and three broods (Møller 1991, 1994) would need to be updated.

Hypothesised responses of barn swallows to climate change

Several hypotheses have been raised about how climate changes could affect long-distance migrant birds, and I will discuss the relevance of these to barn swallows. First, because of the additional constraint of a long and costly migration, and because they spend different parts of the year in different places, long-distance migrant birds could be less capable of responding to changes in seasonality caused by climate changes than short-distance migrants or resident birds (Jonzén *et al.* 2006, Both *et al.* 2010, Knudsen *et al.* 2011, Saino *et al.* 2011). Second, birds can be affected by mistiming caused by changes in seasonal phenology, if they lack the phenotypic plasticity to respond fast enough; this applies both to resident and migratory birds (Visser *et al.* 1998, Visser *et al.* 2003, Both *et al.* 2009). Third, climate change can shift, expand or contract species' ranges through temperature and rainfall changes (Walther *et al.* 2002, Cunningham *et al.* 2015). Fourth, and associated with ranges shifts, climate change can lead to a reduction or increase in the migratory distance for some or all populations of a species (Robinson *et al.* 2009a, Ambrosini *et al.* 2011).

The phenological climate pattern in the Palearctic west of Siberia is that springs started earlier over the last few decades of the 20th century, whereas autumns did not change or became later, leading to a longer period during which conditions are suitable for breeding (Walther *et al.* 2002, Lemoine & Böhning-Gaese 2003, Root *et al.* 2003, Parmesan 2006, Knudsen *et al.* 2011). Migratory birds benefit from arriving and starting to breed as early as possible in the spring, as soon as conditions become warm enough (Alerstam 1990), hence the breeding season in the Palearctic west of Siberia has potentially become longer since the 1970s. Given that springs have shifted earlier in the western Palearctic, it is counter-intuitive that the mean start of moult in South Africa should shift later for birds migrating to the western Palearctic (by 12 days; Table 1). The lengthening summers in the western zone of the Palearctic could have enabled a greater proportion of barn swallows to extend their breeding season by raising a second or even a third brood, which would have previously occurred only in southern Europe – for example, 13% of pairs in Italy produced a third brood (Brichetti & Caffi 1992).

Parents that raised a third brood, and their third brood offspring, would leave the breeding grounds later. Their arrival and start of moult at the non-breeding grounds would then potentially shift later. This could cause these birds to delay departure, to have sufficient time to finish moulting at least the first eight primaries before departing. In northern Europe, the breeding season is too short for a third brood, although two broods are common – in Denmark 60% of pairs raised two broods (Møller 1994).

Later departure after breeding, migration and start of moult could then occur because the parents with extra broods must still recover condition after breeding, and in some places put on fuel reserves before departure (Rubolini *et al.* 2002). Further, the third–brood juveniles are nearly three months behind their second-brood offspring in development, so their non-breeding schedule would be correspondingly later – a single brood takes on average 46 days from egg laying to the end of parental care, and broods are separated by on average 47 days; two broods therefore take an average of 139 days, or 4.5 months, in total and three would require 232 days (7.6 months) (Møller 1991). To produce three broods, birds would have to start breeding during February, which puts them at risk of late-winter weather. Pairs that were able to start breeding in February would then finish breeding in late September or early October. There would presumably be a progressive increase in the number of pairs successfully raising an extra brood as the duration of the European barn swallow breeding season increased from year to year.

A further consequence of a longer breeding season would be to increase the spread of arrival dates and of the start dates of moult in South Africa. There was, however, apparently no change in spread of migratory arrival dates for the Western Cape, Gauteng and southern KwaZulu-Natal (Altwegg *et al.* 2012), and this was not tested for moult phenology (Chapter Five). However, any signal of an increase in spread of arrival dates in South Africa could have been masked by the high levels of migratory mixing in these South African zones (Chapter Two). Further, the patterns of change in Palearctic spring phenology were spatially complex (Ahas *et al.* 2002): springs started earlier, probably extending the breeding season, in the western Palearctic; in the central Palearctic, the pattern was mixed; and in

Siberia, start of Palearctic spring shifted later, thus possibly reducing the breeding season. The Free State, for which migratory arrival estimates are not available, was the only zone to have a clear majority of birds from the western Palearctic zone (Chapter Two); hence, it is likely to be the only zone where an increased spread of arrival dates would be detectable.

The shift towards earlier phenology in the central zone is expected, based on the earlier spring phenology in most of Europe. In far eastern Siberia, just east of the breeding range of the Palearctic barn swallow, springs shifted earlier and autumns shifted later in the last decades of the 20th century (Ananin & Sokolov 2009), potentially lengthening the breeding season for other long-distance migrants (including the Asian barn swallow subspecies, *H. r. tytleri*) (Turner 2006) in that region. However, the opposite trend occurred at the Ural mountains (Ahas *et al.* 2002) at the eastern edge of the breeding range of Palearctic barn swallows, hence in that region summers have possibly become shorter and the breeding season put under pressure. Barn swallows take on average just over 62 days from arrival to produce one brood – 16 days between pairing and laying, and a further 46 days until the end of fledging (Møller 1991). If one assumes about one week between arrival and pairing, a single brood takes about 69 days. As long as summers remain consistently longer than 70 days in Siberia, barn swallows could thus continue to breed in the region.

Impacts of climate change

Anthropogenic climate change and increasing levels of atmospheric CO_2 can, however, benefit some species some of the time. Northern Hemisphere phenological changes can benefit species, for example, by increasing the time period available for breeding (Menzel & Fabian 1999, Walther *et al.* 2002), enabling some species to increase their breeding output (Møller *et al.* 2008). Warmer conditions over the period 1950–2000 have been associated with increased tree and bush cover in Alaska (Sturme *et al.* 2001). In southern Africa, there has been extensive 'bush-encroachment' (increase of bush growth in grasslands) (Wigley *et al.* 2010, Sirami & Monadjem 2012, Peron & Altwegg 2015) which is thought to be caused by increased anthropogenic CO_2 in the atmosphere

(Midgley & Bond 2015), itself a primary cause of climate change (Vose *et al.* 2005). Bush encroachment in Swaziland from 1998 to 2008 was beneficial to some species – of the 106 bird species recorded in a protected area, 30% of species were found to expand their range, 27% to reduce it, and 42% remained stable (Sirami & Monadjem 2012). However, bush encroachment of reedbeds can change them into woody and dry habitats (Grygoruk *et al.* 2014), making them unsuitable for barn swallows and other species that depend on them. For example, bush encroachment (through the natural succession of reedbeds into shrubby land or forest) was associated with declines of bitterns *Botaurus stellaris* in the UK (Tyler *et al.* 1998), and of the great reed warbler *Acrocephalus arundinaceus* in the Netherlands (Graveland 1998). South African reedbeds should therefore be monitored for bush encroachment, and if necessary managed to maintain this habitat type.

In this thesis I have investigated changes in the timing of the life-cycle of barn swallows at their South African non-breeding grounds from 1986 to 2012, using the phenological calendar method (Ahas *et al.* 2000). The first objective was to describe changes in timing of the start of flight-feather moult and pre-migratory weight gain, to detect periods in the barn swallow life-cycle schedule where conflicts ('schedule conflicts') had developed or might develop if the trends continued – these conflicts arise when part of the life-cycle occurs earlier or later than it should, thereby overlapping with another part of the life-cycle. Such conflicts could have negative consequences for populations, although species with broad ranges could be well adapted to survive. For example, in a widely-distributed species such as the barn swallow one would not expect schedule conflicts to arise at the same rate or at the same time everywhere, because different populations, and even different individuals in breeding populations, have different life-cycle schedules.

Effects of changes at the breeding versus the non-breeding grounds

Northern Hemisphere climate changes have been identified as the key driver of phenological changes for long-distance migratory birds, having more impact than climate changes at the non-breeding grounds (Ockendon *et al.* 2013, Bussière *et al.* 2015). However, ecological conditions during migration and at the non-breeding grounds are important for long-distance migrants (van den Brink *et al.* 1997, Ockendon *et al.* 2012).

Between 1987 and 2010, climate change in South Africa was characterised by changes in temperature and rainfall patterns: temperatures increased in most of the western (winter-rainfall) and cenral (summer-rainfall) parts of South Africa, and parts of eastern South Africa (summer-rainfall); the Northern Cape became wetter and the southern Cape became drier; a wide coastal and mountainous belt, roughly extending through the eastern half of the Eastern Cape, KwaZulu-Natal, Mpumalanga and Limipopo and bordering Mozambique and Zimbabwe, became cooler and drier; the northern border with Botswana became cooler and wetter, and the northern border with Namibia became hotter and wetter (Cunningham *et al.* 2015). Such climatic changes could interact with other pressures facing long-distance migrants by, for example, causing range or distribution changes at the non-breeding grounds (Cunningham *et al.* 2015). Further, climatic changes at the non-breeding grounds could make it harder (or easier) for barn swallows to respond to climate changes at their breeding grounds. To understand the changes in barn swallow populations in South Africa, it is therefore important to consider range and distribution changes rather than just phenological changes (Cunningham *et al.* 2015). Barn swallows increased in abundance in large parts of South Africa between the first and second South African Bird Atlas Projects (SABAP), which ran from 1987–1991 (SABAP1) and 2007–2016 (SABAP2, which is ongoing). SABAP reporting rates give the proportion of SABAP checklists in which a species was recorded; other SABAP methods are described elsewhere (Harrison *et al.* 1997; sabap2.adu.org.za). Changes in abundance (and distribution) of a species can be inferred from changes in bird atlas reporting rates for that species (Hofmeyr *et al.* 2014). From visual inspection of the map of changes in reporting rates (Figure 3), it appears that barn swallows became on average more abundant (with higher reporting rates) in the eastern half of South Africa, in the Eastern Cape, in the southern Cape and in parts of the Free State. Reduced reporting rates and to a lesser extent 'disappearances' between the first and second SABAP projects were scattered throughout South Africa, but were concentrated in the eastern parts of the Eastern Cape, in the northern Free State, in the Northern Cape and particularly in the North West province. Some new ranges seem to have developed between the first and second SABAP project (blue cells, Figure 3). The new range along the east coast of Mozambique is particularly puzzling and worth exploring – there is no clear reason why, during SABAP1, barn swallows should have been present all along the east coast of South Africa, but absent along the coast of Mozambique. These geographically complex range and distribution changes are probably in response to fine-grained differences in climate change (Cunningham *et al.* 2015), and warrant further study.

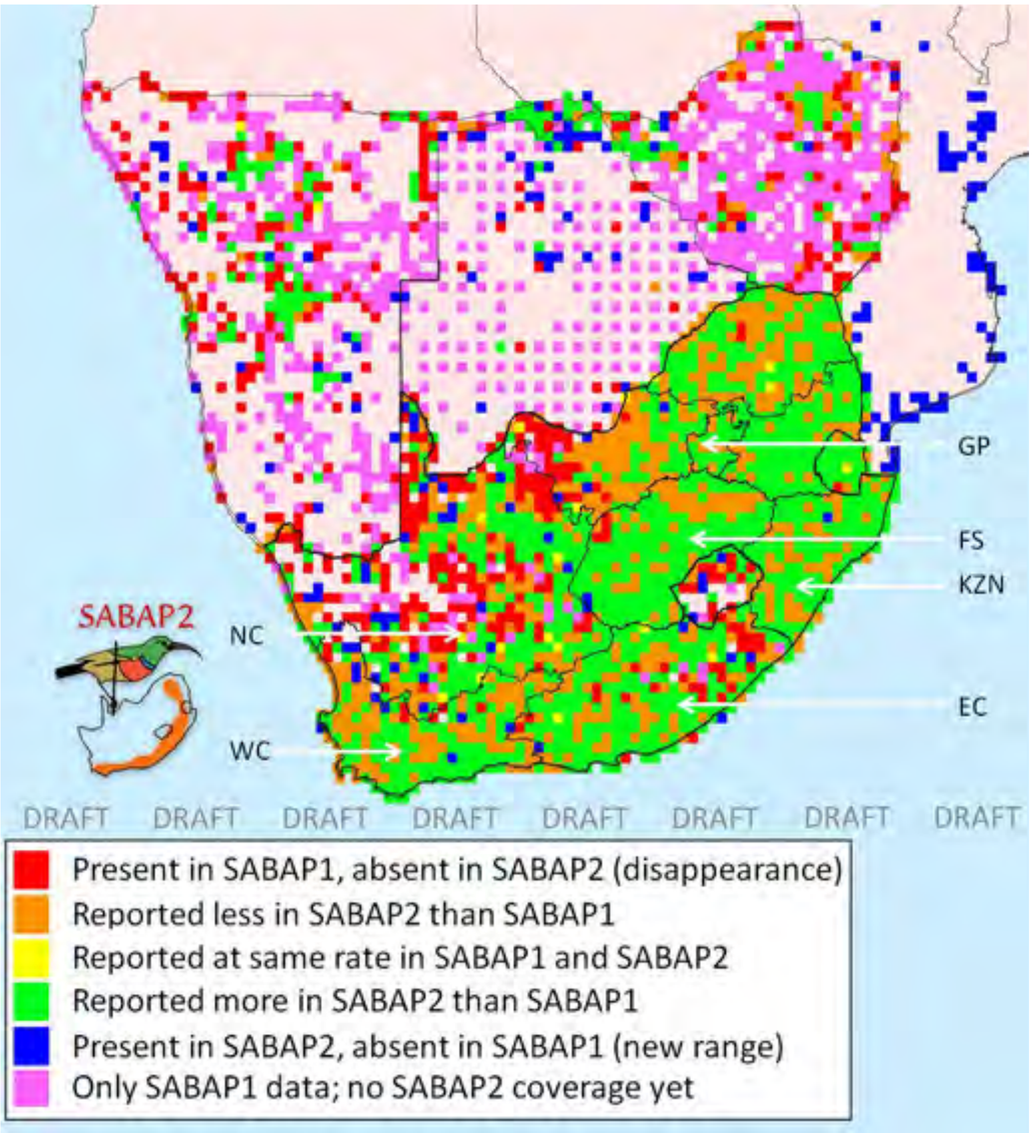

Figure 3. Barn swallow distribution and change in reporting rate in southern Africa, comparing the first (1987–1991) and second (2007–2016) South African Birds Atlas Projects (Animal Demography Unit 2016). SABAP2 is ongoing. Resolution is at the quarter degree level. Map generated on 23 March 2016. South African province boundaries are indicated, and provinces relevant to this discussion indicated by white arrows. WC: Western Cape; EC: Eastern Cape; NC: Northern Cape; KZN: KwaZulu-Natal; FS: Free State; GP: Gauteng.

Predictions and scenarios

This synthesis gives rise to several specific predictions for barns swallows in South Africa. Breeding in the Palearctic begins as soon as temperatures are suitably warm, and the schedules of migrants have evolved so that they arrive and start preparing to breed immediately, with no time wasted (Alerstam 1990). For barn swallows, it has been demonstrated that birds must arrive at the breeding grounds earlier if they are to start breeding earlier (Saino *et al.* 2004). Earlier arrival could be achieved in two ways, by shifting the northward migration earlier, or by reducing the migratory distance. Migrating faster would be feasible for barn swallows migrating southward, which involves long stop-overs, but not for the northward migration, which is already carried out probably as fast as possible (Turner 2006).

The end of the moult period overlaps with the departure from the non-breeding grounds, and many barn swallows migrate northward while completing the moult of the outer flight feather (Jenni & Winkler 1994). Hence, earlier departure could presumably occur only if moult and the start of pre-migratory weight gain also shifted earlier, and this was in fact observed in Gauteng. If the advancing trend in the start of European spring continues, the European summer could rapidly become long enough for a greater proportion of pairs to lay a second or third clutch. The cohort of birds raising an extra brood would then arrive relatively late in South Africa, and if Palearctic springs continued to shift earlier, would eventually be forced either to suspend moult early in order to maintain the early departure, or to rush moult. The former response would lead to birds migrating with worn outer flight feathers, and the latter to the production of poor-quality feathers (Vágási *et al.* 2012). Migrating with old or poor quality feathers would probably reduce an individual’s chance of surviving the northward migration; however, if the longer breeding season enabled an individual to increase its life-time reproductive output, even at the cost of a shorter life-span, these responses could be adaptive.

I predict that, if European summer continues to become longer, the mean dates of arrival, and following that, of moult and pre-migratory weight gain, will at some point begin to shift later everywhere in South Africa, while the mean departure date will continue to shift earlier, thus shortening the non-breeding period at both ends. The non-breeding season in South Africa could simply become too short – a full moult requires at least 130 days (four months; Chapter Five). This would lead to reduced barn swallow populations in South Africa, and therefore a shortening of the migratory distance. Such a conflict of the non-breeding stages seems to be developing in the Free State, and could already have developed in the Western Cape where the period of residence (140 days; Altwegg *et al*. 2012) is only just longer than the period required for moult. The situation observed in Gauteng was an earlier migratory departure, but no change in migratory arrival (Altwegg *et al.* 2012), earlier mean start of moult, and earlier mean start of pre-migratory weight gain – this suggests that the birds in Gauteng were not yet under pressure to remain longer at the breeding grounds. A possible explanation for this is that the breeding season in those parts of Europe where birds from Gauteng breed (mostly in Central and Eastern Europe, up to the Urals; Chapter Two) had not yet become long enough to enable many individuals to raise an extra brood. At some point, however, this could happen, if springs continue to become earlier throughout Europe.

Potential for successful adaptation

These findings suggest that changes in phenology at the breeding grounds have already begun to cause conflicts of timing between breeding, migration and moult, with various consequences. Individuals require phenotypic plasticity to respond directly to changes, by altering their life-cycle schedule (phenological plasticity), breeding, moulting or migration behaviour, migratory routes or destinations. Genetic variability and phenotypic plasticity are both required for adaptive responses through microevolution, and both processes are required to respond to rapid climate change (Gienapp *et al.* 2007). If the changes do not occur too rapidly, and enough individuals have the plasticity to adapt, those populations could survive the changes. Barn swallows have a short generation time, living on average two years (Turner 2006). It has been shown that the timing of migration arrival at the breeding grounds is to some extent heritable in barn swallows (Møller 2001). Further, the genetic polymorphism that enables such change in barn swallows has been described for the timing of moult (Saino *et al.* 2013). Barn swallows may therefore be well adapted to survive ongoing climate change through microevolution, both because of their adaptability and because they reproduce in their first year.

A potential and likely consequence of running out of time to moult at the non-breeding grounds is a range shift to non-breeding grounds nearer to the breeding grounds, leading to reduced migratory distance (Berthold 1995). The first way that this could occur is through individuals reducing their migratory distance, by choosing a different destination. If barn swallows are unable to change non-breeding destinations voluntarily, those experiencing the worst schedule conflict at the non-breeding grounds would be selected against, leading to a reduction in migratory distance. Whichever of these two mechanisms occured, it would lead to reduced populations further south. Much of southern Africa and the tropics are already used by barn swallows during the non-breeding season, so a northward range shift of the non-breeding range is possible from the perspective of available habitat. Migratory patterns resulting in different non-breeding grounds being used can change relatively fast (García-Pérez *et al.* 2013), so this is a feasible scenario. Phenotypic plasticity in the non-breeding destination choice has been demonstrated for Cory's shearwaters *Calonectris diomedea* (Dias *et al.* 2010). The signal of this scenario for barn swallows in South Africa would be decreased population sizes, or abandoned roosts, further south. This could explain the slight decrease in reporting rate in Gauteng between the first and second SABAP projects (Altwegg *et al.* 2012), as explained below.

It has in fact been reported that barn swallows reduced their migration distances in Africa, with their non-breeding grounds shifting progressively northward between 1921 and 2008, by between 350 and 950km over the period (Ambrosini *et al.* 2011). One might expect barn swallow reporting rates in South Africa to decline as a result of such a large northward shift. Consistent with this expectation, there was a 10% decrease in reporting rate for Gauteng from the 1990s to the 2000s, although contrary to it, there was no change in the Western Cape, and a slight increase in KwaZulu-Natal (Altwegg *et al.* 2012). Springs probably advanced more in the west of Europe, and less or not at all in the east, in the second half of the twentieth century (Ahas et al. 2002). One might therefore expect the proportion of birds raising an extra brood, and therefore compensating by shifting their non-breeding grounds northwards, to be larger in the west of Europe, and to decline to the east. Further, the signal in South Africa of this compensation would be strongest for regions where most of the birds come from the west of Europe. The decline in Gauteng might thus be explained by the large proportion of birds in Gauteng having their breeding grounds in the central Palearctic zone (Chapter 2; Table 1) – many of the birds in Gauteng might actually come from the west of the central Palearctic zone, where breeding seasons have become longer. In the light of the estimated northward shift of barn swallow non-breeding grounds (Ambrosini *et al.* 2011), the lack of any signal of this decreased in the Western Cape and southern KwaZulu-Natal (Altwegg *et al.* 2012) could be explained by the relatively low proportions of birds in these zones coming from the western Palearctic (Chapter 2; Table 1). Regardless of the fact that only a slight decrease in reporting rate was described, the reported shift northwards (Ambrosini *et al.* 2011) suggests barn swallows have the adaptive capacity to shift their non-breeding range in response to climate change.

Barn swallow populations in Europe were on average relatively stable during the last decades of the 20th century (Sanderson *et al.* 2006), or showed a moderate decrease (Walther *et al.* 2011). A potential reason that the decrease was not worse is the that breeding populations consisted of individuals that use widely separated non-breeding regions, and that the effects of the scheduling conflicts that I have described are somewhat averaged among breeding populations. As discussed in this synthesis, there were contradictory geographically variable changes in phenology in South Africa between the 1990s and 2000s, and the possibility exists that these trends will continue, in which case the most likely outcome is an eventual decrease in barn swallows that use the furthest southern reaches of their non-breeding range. Even if some genotypes are removed because of scheduling conflicts at the non-breeding grounds, others will remain.

Reduced migratory distances, and a tendency towards an increase in year-round residency at the breeding grounds, have been predicted to be key adaptive responses to climate change at the northern hemisphere breeding grounds (Berthold 1995, Morganti 2015). Further, such changes have been described. For example, eurasian blackcaps *Sylvia atricapilla* established new non-breeding grounds in Britain, closer to their breeding grounds in Central Europe, from the 1960s onwards (Berthold 1995). For short and medium-distance migrants, migration distances decreased in the second half of the twentieth century in 21 out of 24 species, and this change was associated with warmer winters in the Netherlands (Visser *et al.* 2009). And in three waterbird species (tufted duck Aythya fuligula, common goldeneye Bucephala clangula and goosander Mergus merganser), the non-breeding grounds in Europe shifted northwards, closer to their northern breeding grounds, between 1980 and 2010, a shift also linked to warmer winters at the breeding grounds (Lehikoinen *et al.* 2013). Barn swallows are already year-round residents in southern Spain (Cramp 1988), indicating that they are capable of becoming completely resident – the proportion of resident barn swallows might well thus increase as a result of climate change. Further, a northward shift of the non-breeding grounds of barn swallows in Africa has been reported (Ambrosini *et al.* 2011), indicating that these changes might already be underway.

Conclusions and recommendations

The barn swallow is globally distributed and abundant, so it provides an unparalleled opportunity to study the effects of climate change at a large scale, without the complications arising from inter-species comparisons. Barn swallows roost in high densities and are easily captured in large numbers, whereas solitary and less abundant birds are more difficult to capture, so the data are often sparse. To study phenological changes one needs large long-term data sets, with many records from each site or region. Using ad-hoc ringing of less abundant species it is difficult to generate long-term data sets with the spatial continuity and range necessary for this type of analysis. Climate change analysis is generally best done using a continuous time-series data, and hence requires regular and ongoing data collection, rather than a purely ad-hoc approach.

Citizen science data collection has enormous potential for climate monitoring, but some planning can help to ensure that the data are useful (Greenwood 2007). Planned bird ringing programmes and constant effort sites can be extremely successful. For example, the Bird Migration Research Station, University of Gdansk, Poland, manages a project called 'Operation Baltic'. This is an ongoing constant effort ringing programme, established more than five decades ago, with three ringing stations in the Baltic region that operate throughout summer with the help of volunteers. The project has generated more than 100 publications (e.g. Busse & Trocinska 1999, Nowakowski *et al.* 2014). Operation Baltic continues to collect biometric and demographic data according to the same strict sampling and measurement protocols that have been used for decades. Such data are invaluable in monitoring the effects of climate change on individuals and populations.

Similarly, bird atlas projects which receive their data from citizen scientists have strict protocols to standardise data collection: in the case of SABAP, the spatial unit is the quarter degree grid cell, a grid cell must be sampled for at least two hours, and every habitat type within the cell must be sampled (Harrison *et al.* 1997). SABAP data have generated numerous publications, many of which directly or indirectly relate to impacts of climate change, and this ongoing project continues to do so – to name a few examples: The Atlas of Southern African Birds , which provided baseline bird distributions (Harrison *et al.* 1997); estimates of climate-related phenological changes derived from reporting rates (Altwegg *et al.* 2012, Bussière *et al.* 2015); assessments of conservation area importance (Coetzee *et al.* 2009); range changes in relation to bush encroachment (Peron & Altwegg 2015); and population trend analysis revealing decreases of secretary bird *Sagittarius serpentarius* in South Africa (Hofmeyr *et al.* 2014).

This thesis highlights the value of barn swallow ringing data in particular for monitoring phenological changes in southern Africa, and its importance as part of the global climate change monitoring efforts. Barn swallows have been studied intensively in Europe, and have been the focus of several large citizen science projects, namely the Progetto Piccole Isole (Spina *et al.* 1993), the EURING Swallow

Project (Spina 1998), the EURING Autumn Swallow Roost Project (Coiffait *et al.* 2011) and the Botswana Swallow Project (van den Brink *et al.* 1997), and other smaller projects. In order for future barn swallow ringing in South Africa (and the rest of southern Africa) to have the most value for climate change monitoring, if would be useful if constant-effort ringing (Robinson *et al.* 2009b) were encouraged for barn swallows, and if the spatial gaps in the data set were reduced.

The abundance of many long-distance migrant species declined sharply in the late 20th century, possibly related to climate changes at the Palearctic breeding grounds; barn swallows, however, did not represent a particular cause for concern (BirdLife International 2012), although their populations could have changed subsequently. Their continued presence in South Africa will depend on climate changes throughout their range, as well as the specific possibility of range contraction northwards as a consequence of Palearctic climate changes. For many southern African people living near river or wetlands that have reed-beds, they are regarded as heralds of spring and their arrival is keenly anticipated, and thousands of people every year visit the massive swallow roost at Mount Moreland in KwaZulu-Natal. Healthy barn swallow populations indicate that there are healthy reed-beds and insect populations, and that the local climate is suitable for them. Barn swallow monitoring in South Africa, through ringing and bird atlas monitoring, therefore also serves an important conservation purposes – to detect short-term changes in populations that reflect local disturbances by humans, and longer-term effects of local climate changes.

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Appendix A. List of known contributors of barn swallow ringing data to the SAFRING data base and therefore to this thesis. Presented in acknowledgement of their involvement and contribution.

Adie, H
Aiston, G
Ally, E
Anderson, M D
Andersson, S
Archibald, T
Badenhorst, C
Bantjes, H
Barnard, P
Becker, P D
Bentley, L
Bernitz, H
Bernitz, Z
Berruti, A
Blaber, S
Bonnevie, B
Boon, R
Boorman, M
Botha, A J
Bousfield, N
Bouwman, H
Bowker, M
Bowland, A
Braby, R
Bradley, G
Braine, S
Brensing, D
Brewster, CA
Bridgeford, P
Broekhuysen, G
Brooks, A
Brooks, J
Brown, A R
Brown, M
Bunning, L J
Buttress, J
Cairnsross, C J
Chalton, D
Chenaux-Respond, R
Claassen, J J
Clinning, S
Cochran, P G
Coetzee, P
Conner, M
Conradie, F
Cooper, J
Couto, J T
Cox, D
Craig, A J F
Cyrus, D P
Dalziel, D
Dalziel, J
D'Arcy, P
Day, D
de Beer, S J
de Klerk, H
de Klerk, W
de Kock, C
de Swardt, D H
Dearlove, P
Deetlefs, D
Dixon, K
Douwes, M
Dowsett, R J
Drygal, E
du Plooy, C
du Plooy, F
du Plooy, J F
du Plooy, L
Du Plooy, S
Durr, M
Durrant, M
Edwards, K Z
Egen, G
Eiselen, G T S
Elliott, C C H
Ellis, R N
Ellmer, A
Engelbrecht, G D
Erasmus, R
Evans, S W
Fagan, M J
Fleming, T
Foggin, B
Ford, M A
Francis, S
Franke, U
Fraser, D
Fraser, L
Fraser, M
Furno, J R
Geyer, L
Geyser, R
Gibbs, D
Ginn, P
Grieve, G
Grobler, G P J
Groenewald, M
Hagens, Q
Hanmer, D
Hanmer, D
Harebottle, D M
Harwin, RM
Harwood, J
Heath-Stubbs, G
Heinrich, D
Herholdt, J J
Heritage, B
Herremans, M
Hewitt, A
Heymans, J A
Hofmeyr, J H
Holtshausen, G
Hopcroft, C
Hulley, P.E
Hunter, C
Jackson,
Jackson, C
Jansen van Rensburg, G J
Jarvis, M J
Johannsmeier, M F
Johnson, D N
Johnson, J
Jones, P J
Kemp, A
Kilian, C
Kirk, M P
Klages, N T W
Kleynhans, D H
Kok, J D S
Kolberg, H F
Kolberg, H
Kreft, K
la Hausse de la Louvière, P
Lane, S
Law, B
Lawes, M
Lawson, W
Lee, A
Leonard, P
Lewis, M C
Liversidge, R
Lockwood, G
Lodder, J
Lodder, J
Loon, R
Lowden-Stoole
Ludwig, D
Macleod, J
Malherbe, E
Mangold, W
Manson, C
Marais, E
Marais, M L
Marais, R
Markus, M B
Marshall, A
Martens, E
Martin, A
Martin, A P
Martin, C G C
McCall, M I
McLean, S
Medland, R D
Meller, I
Mendelsohn, H P
Mendelsohn, J
Milton, I V

Appendix A continued.

Mines, B
Monadjem, A
Morgan, B
Mousley, G
Muller, H
Mundy, P J
Nel (Poferl), M
Nel, A
Nel, C
Nel, T
Nelson, K
Neser, W
Niemand, A
Nilsson, P
Nuttall, R J
Oatley, T B
O'Connor, M
Odendaal, T
Oosthuizen, J
Opperman, G
Osborne, T
Oschadleus, H D
Palmer, M G
Parker, M
Parker, R H
Paterson, J
Peters, J
Pfister, H P
Philip, D A
Pickles, A
Pickles, I
Piper, S E
Potgieter, E M
Potgieter, M
Pretorius, R
Pringle, J S
Raijmakers, A P L
Raijmakers, J M H
Raijmakers, S
Ranger, G
Raum, M
Reed, R
Remisiewicz, M
Roberts, L
Roberts, M
Roberts, T
Robertson, T
Robertson, T
Robinson, R C S
Robson, J E
Rochfort, N B
Rohloff, P
Roos, C J
Roxburgh, L
Schaefer, D
Schaum, G A
Schmidt, R K
Schmitt, M B
Scholtz, G
Schultz, A
Schultz, D
Schultz, S J
Scott, W A
Silks, L
Slotar, M
Smit, S
Snyman, J
Solomon, D
Steyn, P
Stojakovic, D
Stutterheim, C J
Symes, C
Taylor, B
Taylor, M
Teifel, R E
Theron, G
Thomson, R L
Thornton, P A
Tree, A J
Tucker, A
Tyler, S J
Underhill, G
Underhill, L G
van de Ven, T
van den Brink, B
van der Merwe, J P
van der Merwe, S
van Eeden, P
van Huysteen, J
van Niekerk, D J
van Pletsen, E G
van Rooyen, N D
van Stuyvenberg, D
van Stuyvenberg, K
van Stuyvenberg, S
van Zyl, MP
Vaughan, J
Viljoen, G
Visagie, R
Wakelin, J
Waltner, M
Ward, V
White, D F
Williams, A
Williams, C
Williams, D M
Williams, L A
Williams, N
Wilson, G H
Wilson, H
Wilson, M
Winterbottom, J M
Wirminghaus, O
Wolfaardt, A
Wood, C J
Wright, C A