THE NON-BREEDING ECOLOGY OF COMMON WHITETHROATS *CURRUCA COMMUNIS* IN CENTRAL NIGERIA

Claudia Tapia Harris

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews

2022

Identifiers to use to cite or link to this thesis:

DOI: https://doi.org/10.17630/sta/402
http://hdl.handle.net/10023/27400

Candidate's declaration

I, Claudia Tapia Harris, do hereby certify that this thesis, submitted for the degree of PhD, which is approximately 67,000 words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for any degree. I confirm that any appendices included in my thesis contain only material permitted by the 'Assessment of Postgraduate Research Students' policy.

I was admitted as a research student at the University of St Andrews in September 2017.

I received funding from an organisation or institution and have acknowledged the funder(s) in the full text of my thesis.

Date: 25/05/2022

Supervisor's declaration

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of PhD in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree. I confirm that any appendices included in the thesis contain only material permitted by the 'Assessment of Postgraduate Research Students' policy.

Date: 25/02/2022

Permission for publication

In submitting this thesis to the University of St Andrews we understand that we are giving permission for it to be made available for use in accordance with the regulations of the University Library for the time being in force, subject to any copyright vested in the work not being affected thereby. We also understand, unless exempt by an award of an embargo as requested below, that the title and the abstract will be published, and that a copy of the work may be made and supplied to any bona fide library or research worker, that this thesis will be electronically accessible for personal or research use and that the library has the right to migrate this thesis into new electronic forms as required to ensure continued access to the thesis.

I, Claudia Tapia Harris, confirm that my thesis does not contain any third-party material that requires copyright clearance.

The following is an agreed request by candidate and supervisor regarding the publication of this thesis:

Printed copy

Embargo on all of print copy for a period of 1 year on the following ground(s):

- Publication would preclude future publication

Supporting statement for printed embargo request

I intend to submit this work for publication in academic journals.

Electronic copy

Embargo on all of electronic copy for a period of 1 year on the following ground(s):

- Publication would preclude future publication

Supporting statement for electronic embargo request

I intend to submit this work for publication in academic journals.

Title and Abstract

- I agree to the title and abstract being published.

Date: 25/05/2022

Date: 25/05/2022

Underpinning Research Data or Digital Outputs

Candidate's declaration

I, Claudia Tapia Harris, understand that by declaring that I have original research data or digital outputs, I should make every effort in meeting the University's and research funders' requirements on the deposit and sharing of research data or research digital outputs.

Date: 25/05/2022

Permission for publication of underpinning research data or digital outputs

We understand that for any original research data or digital outputs which are deposited, we are giving permission for them to be made available for use in accordance with the requirements of the University and research funders, for the time being in force.

We also understand that the title and the description will be published, and that the underpinning research data or digital outputs will be electronically accessible for use in accordance with the license specified at the point of deposit, unless exempt by award of an embargo as requested below.

The following is an agreed request by candidate and supervisor regarding the publication of underpinning research data or digital outputs:

Embargo on all of electronic files for a period of 3 years on the following ground(s):

- Publication would preclude future publication

Supporting statement for embargo request

Publication of manuscripts from thesis data and analyses still pending

Date: 25/05/2022

Date: 25/05/2022

University of St Andrews

School of Biology Ethics Committee

22ND November 2017

Project Title:	Non-breeding ecology of Palearctic migrant birds wintering in Africa
Researchers Name(s):	Will Cresswell and Claudia Harris
Supervisor(s):	Professor Will Cresswell
Biology SEC Ref:	SEC17028

Thank you for submitting your application which was considered by the Biology School Ethics Committee on the 22nd November. The following documents were reviewed:

1. Animal Ethics Form 04/10/2017

The School of Biology Ethics Committee approves this study from an ethical point of view.

Approval is given for five years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the condition that local permits are obtained prior to the project starting, and also on the understanding that the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching published in Animal Behaviour, 2003, 65, 249-255, are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs School Ethics Committee
Dr Tamara Lawson (Home Office Liaison Officer)

SEC Convenor, CBD, Dyers Brae House, Greenside Place, St Andrews, Fife KY16 9TH, Scotland
Email: bioethics@st-andrews.ac.uk Tel: 01334 462054
The University of St Andrews is a charity registered in Scotland: No SC013532

UNIVERSITY OF ST ANDREWS ANIMAL ETHICS FORM

University
of
St Andrews

Application for change(s):
A School Ethics Committee Form

1. Details of Researcher

a) Title (e.g. Mr, Dr etc.): Miss

b) Full name: Claudia Tapia Harris

c) Contact telephone number: 0793 357 9949

e) Title of project: The non-breeding ecology of Common Whitethroats (*Sylvia communis*) and Nightingales (*Luscinia megarhynchos*) in Central Nigeria

2. Proposed change(s)

Please summarise below the changes for which you are applying:

On the 22nd of November, 2017 (by email confirmation), I was approved the use of mist nets and spring traps on up to 100 individuals of 6 species and the use of radio tags on up to 25 individuals per species.

The motive of this new Ethics Application is to request permission to:

- Eliminate study species: We had originally suggested working with potentially six species; Yellow Wagtails (*Motacilla flava*), Tree Pipits (*Anthus trivialis*), Common Whitethroats (*Sylvia communis*), Pied Flycatchers (*Ficedula hypoleuca*), Whinchats (*Saxicola rubetra*) and Nightingales (*Luscinia megarhynchos*). After my first fieldwork session (from Nov, 2017 to April, 2018), it became clear that I was not going to be able to work with all six proposed species for logistical reasons. Instead, I will work exclusively with the Common Whitethroat and Nightingale: the numbers of individual birds studied will remain roughly the same but these will now be of two – not six – species.
- Increase sample size: We would like to increase the amount of Common Whitethroat individuals to be captured, banded, processed and followed, to up to 700 individuals during the totality of the study. This winter I captured 212 Common Whitethroats.
- Increase amount of radio tags: We would like to increase the amount of radio tagged Common Whitethroats from 25 to up to 100 individuals per year.
- Use of geolocators: We would like to deploy up to 40 geolocators on Common Whitethroats in order to determine general annual migration information such as migratory routes, breeding, wintering and stopover locations, connectivity, speed and duration.

Ethical implications:

UNIVERSITY OF ST ANDREWS ANIMAL ETHICS FORM

- The ethical implications remain the same from my previously proposed work but instead of working with six species, we are now focusing on two; the Nightingale and the Common Whitethroat, especially the latter. Conservation wise, the Common Whitethroat is an abundant species throughout the study area, whose populations are increasing, and are of low conservation concern. We believe that the use of radio tags and geolocators will not have any major effects on individuals or on the population, and thus consider this study to be of low impact.

3. Declaration by the Supervisor

I have read the amended application and the Guidelines (Animal Behaviour 83 (2012): 301-309) and also have approved the amended project, with consideration for the balance between risk and the value of the research.

I enclose my original SEC Animal Ethics Form with the proposed amendments included and highlighted (in yellow).

Signature .... Date 01/08/18...............

4. SEC Approval

Signature:

Name in BLOCK CAPITALS: PATRICK MILLER Date: 27/08/2018

Para M y P,

quienes siempre han estado y siempre estarán.

(Ahora sí, la última)

Abstract

Identifying what drives or prevents long-distance migrants from responding to environmental changes requires a complete understanding of the ecology and behaviour of individuals throughout their annual cycle. The non-breeding period represents a significant part of an Afro-Palearctic migratory bird's life; what occurs during this period influences an individual's survival and future reproductive success. I studied factors that influence the population dynamics of Common Whitethroats *Curruca communis* during three non-breeding periods in Nigeria (2017 – 2020). First, I collected and analysed data from six geolocators deployed in 2019 to understand how non-breeding and breeding sites are connected. Second, I used data collected from >300 colour-ringed individuals and daily resightings to understand site persistence, within- and between-years site fidelity, fine-scale spatial movements, and habitat preference and availability. Lastly, I used daily resighting and long-term ringing data to calculate annual and overwinter survival rates. Results indicate that Whitethroats bred across eastern Europe, suggesting a somewhat high migratory spread defined by a north-eastern flight pattern, and a predominantly intermittent migratory strategy. All birds undertook a loop migration and stopped at a first non-breeding site in the Sahel. At core wintering grounds Whitethroats showed a great degree of individual variation regarding temporal and spatial behaviour: individuals exhibited different residency periods (from 1 – 165 days), a high degree of within- and between-years site fidelity, and many individuals established small home ranges with little significant variation through time, age, sex, and residency, despite habitat changing through the winter. Shrubs were identified as the preferred main vegetation type. High overwinter survival rates and a potential generalist strategy during the wintering period all strongly indicate that this period is likely a low-mortality period for Whitethroats. This study highlights the importance of conserving suitable habitats for Whitethroats over a very large area in both the breeding and non-breeding grounds, particularly the Sahel region, an important refuelling and stationary site.

Acknowledgements

This thesis would not have been possible without the help of many, many people. Over the course of these 4+ years I have been moving between three continents, feeling what it was like to be a transcontinental migratory bird, with its pros and cons. In each place, however, I felt welcomed and supported, and I consider myself lucky of having been surrounded by such beautiful people.

I would first like to thank my supervisor Will Cresswell whose patience and guidance have been crucial throughout this process. Since I sent him an email, out of nowhere, right up until now he has been kind and supportive. He has been a good mentor, pushing me into the right direction when needed and always encouraging me to do better. I am very grateful to have been a part of your group and for all your support along the way, especially during tough times. This whole process not only made me a better scientist but also a better person.

A special thank you to Ian Hartley and Graeme Ruxton for serving as members of my thesis committee. Not only was the *viva* an enjoyable moment with insightful discussion, but your comments and suggestions have helped to greatly improve this work and the manuscripts that arose from it.

I am extremely grateful to all the staff and students of APLORI who made this an interesting and fun experience. A special thank you to Manu, Yahkat, Marcus “admin” and all APLORI staff for the logistical support and for facilitating my stay in the Institute. Thanks to Ulf and Theophine for all the support. This thesis could not have been completed without the help of everybody who accompanied me to the field and collected data. I am especially grateful to have had an amazing field assistant, and *aboki*, Arin. Thank you for all your help, advice, and friendship (and hausa/izere lessons). *Na gode* to all my APLORI *abokis* and *abokianas*.

A special thank you to the people from Laminga and the Afizere community without whose permission I would not have been able to do any fieldwork.

Over in St Andrews, I am grateful for everybody in the CBD who made it a fun place to work at. Thanks to Lianne and Dave for the logistical and technical support. Special thanks to the discord group and the best pub quiz crew ever (no thanks to me). I am also grateful for the basketball crew, whose good vibes were felt inside and out of the court. Thanks to my flatmates who later became my family.

I am forever grateful to those friends that have been present for a long period of my life and who are always with me.

A special thank you to Ron, my happy coincidence, who not only read this thesis and gave me amazing suggestions but has been an important support over the last few months. There are no words to describe how grateful I am to have met you.

And lastly, I am eternally grateful to my family. Words will never be able to express my gratitude.

Funding

This work was supported by the National Council for Science and Technology (CONACyT, Mexico) through scholarship number 472286.

Fieldwork costs for the PhD were paid for by the University of St Andrews Postgraduate Research Fieldwork Bursary, the Russell Trust travel award, but mostly by the AP Leventis Conservation Foundation.

Research Data/Digital Outputs access statement

Research data underpinning this thesis are available at: https://doi.org/10.17630/259bb40c-4d4c-4247-b522-ebd0f42ee51e.

Table of Contents

List of Figures

List of Tables

Chapter 1. A general introduction to the ecology of long-distance migrants focusing on the non-breeding period of Afro-Palearctic birds

1.1 General introduction to bird migration

Migration, the regular seasonal movement from breeding grounds to wintering grounds and back, year after year (Berthold, 1993; Newton, 2010), is an adaptation that has evolved independently among many animals (*i.e*. birds, mammals, fish, reptiles, amphibians) in order to survive in a world of constant resource fluctuations (Alerstam, 1990; Berthold, 1993; Newton, 2010). Of all animals, birds have the most extensive and well-developed migration patterns (Alerstam, 1990): they can be found in nearly all habitats across the world, fly for thousands of kilometres, and cross extreme ecological barriers. Every year, approximately half of the world's bird species undertake some type of migratory movement (Berthold, 1993). These migrations can be as short as hundreds of metres up a mountainside and back, or a journey spanning the whole globe, of tens of thousands of kilometres. For this reason, migrants are typically separated according to distances travelled: (1) short-distance migrants, *i.e*. birds that make over-land journeys within continents, and (2) long-distance migrants, those that carry out intercontinental journeys (Newton, 2010). By way of contrast, non-migratory (or "resident birds"), remain year-round in a single location and move short distances as a means for foraging and dispersal.

Long-distance migration occurs mainly in species that live in highly seasonal environments, where resource peaks occur at a predictable time of the year (Alerstam et al., 2003). Therefore, breeding occurs at high latitudes each spring and summer, when days are long and food is abundant, and is followed by migration to the tropics to avoid shorter days and cold unproductive winters (Alerstam, 1990; Newton, 2010). Though being a migrant enhances survival and reproduction by taking advantage of ephemeral resources throughout the year, it demands a challenging and complex lifestyle. For example, to cope with the long journey, migrants have developed certain physical and physiological adaptations that differentiate them from residents, such as a highly developed hippocampus (to increase spatial memory), the ability to change the gut structure and digestive capacity, smaller bodies and longer and more pointed wings to reduce air resistance during flight, and the ability to accumulate significant fat reserves (Mönkkönen, 1992; Winkler & Leisler, 1992; Berthold, 1993). Even though they facilitate migration, all of these adaptations incur costs. Migrants also require high energy levels to complete the migratory journey twice a year and need to occupy different habitats, modify diets according to available resources, exist within different communities, cross hostile terrains, fill distinct niches, cope with inter- and intra-specific competition, and, above all, must coordinate migration with other life-history traits such as breeding and moulting (Biber & Salathé, 1991; Alerstam et al., 2003; Newton, 2010). For long-distance migration to offer an evolutionary advantage, survival and reproduction have to increase when moving between locations compared to remaining at the same place throughout the year, outweighing the benefits of residency and shorter distance movements (Biber & Salathé, 1991; Zúñiga et al., 2017).

A migrant's survival is influenced by conditions at breeding and wintering grounds as well as along migratory routes (Berthold & Terrill, 1991; Walther & Pirsig, 2017). Research in general population dynamics, as well as how, where, and why long-distance migrants die, is therefore important for recognising and mitigating threats that occur throughout the annual cycle, and for identifying conservation priorities, especially in light of recent global population declines (Sanderson et al., 2006; Marra et al., 2015). Challenges arise when each species or population responds differently to changes: some may be affected mainly by conditions at breeding or wintering grounds, whilst for others, conditions in one region may influence reproductive success and/or survival in the other (Sheehan & Sanderson, 2012; Bairlein, 2016). Conservation of these organisms requires large spatial and temporal scales, fundamental knowledge of the functioning of intercontinental systems such as the Palearctic-Afrotropical migratory system and, above all, transnational research collaborations (Berthold & Terrill, 1991; Sheehan & Sanderson, 2012).

1.2 The Afro-Palearctic system

Even though bird migration occurs all over the world, three broad and overlapping migratory systems are defined: (1) the Nearctic-Neotropical – movement between the Americas, (2) the East Asian-Australasian – movement between East Asia and Oceania, and (3) the Palearctic-Afrotropical system – movement between Europe/West Asia and Africa (Kirby et al., 2008; Newton, 2010). These systems are by no means closed and permit broad categorisation of species with geographically similar migratory routes and potential evolutionary similarities. This thesis will focus mainly on the Afro-Palearctic system, although the problems, trade-offs, and characteristics of this system are likely to apply to any avian migratory system.

Billions of individuals across over 200 species migrate every year from Eurasia to spend the northern winter in sub-Saharan Africa (Moreau, 1972; Fry, 1992; Hahn et al., 2009; Zwarts et al., 2009); 64 of these are passerines, and winter exclusively in West Africa (Morel & Morel, 1992). In the Palearctic system, migration may have evolved in response to climate becoming increasingly seasonal, cold, and arid (around 30 mya; Finlayson, 2011). Aridity has especially shaped migration in this region by creating savannahs, deserts, and seasonal wetlands for birds to exploit (Finlayson, 2011). The origin of migration, however, is still open to debate. Two main theories are proposed: (1) that migration evolved in tropical species (in Africa) when they started to breed at higher latitudes to take advantage of seasonal bursts of resources, the “southern origin model”, or (2) that migration evolved from high latitude breeding grounds (Europe and Asia) when individuals gradually shifted their winter ranges southwards to escape from deteriorating habitats, the “northern origin model” (Cox, 1985; Safriel, 1995; Bell, 2000; Rappole & Jones, 2002; Salewski & Bruderer, 2007; Bruderer & Salewski, 2008; Finlayson, 2011). Perhaps both theories, or a combination of both, could be true. Regardless of origin however, habitats, climate, and migration have been changing and evolving through time, thus species that could switch from residency to migration and back are the ones that historically fared best (Finlayson, 2011). Species and populations with high dispersal capacities (*i.e*. traits that decrease the cost of dispersal and increase colonisation abilities) will have benefitted from and therefore evolved migratory behaviours (Salewski & Bruderer, 2007). Hence, migration may be a continuous adaptation according to seasonality in the breeding areas, no matter whether it originated from Europe/Asia or Africa (Bruderer & Salewski, 2008).

Afro-Palearctic migrants undergo one of the most hazardous migrations in the world: individuals breeding in western and central Europe cross the Mediterranean Sea and the Sahara Desert. Individuals breeding north and northeast of the eastern Mediterranean, however, are faced with even harsher conditions as they fly over the Black and Caspian Sea, across the deserts of southwest Asia, and through high mountain ranges (Moreau, 1952, 1972; Newton, 2008). The harshness of these habitats – low probability of finding food and/or land, strong winds, and high risk of dehydration – make this journey a crucial and dangerous stage of their life (Safriel, 1995; Sandercock & Jaramillo, 2002; Strandberg et al., 2010; Halupka et al., 2017). Africa is roughly three times larger than Europe, yet once in Africa, migrants arrive at a geographical area less than half the size of their breeding grounds (Jones, 1995; Newton, 1995). Conditions in Africa are different from those at breeding grounds: when in Africa, individuals experience shorter days, longer nights, warmer climates, higher mobility, and birds are free from breeding-related stresses. This results in approximately 30% less maintenance in Africa compared to when at breeding grounds (Moreau, 1972). The non-breeding period in Africa is also longer than that of the breeding period, yet relatively little is known about their time in Africa. It is therefore important to understand what environmental and habitat changes occur throughout this period that may be affecting a migrant’s decisions and survival strategies.

Ecological conditions in Africa are usually determined much more by the alternation of wet and dry seasons (*i.e*. precipitation) than by absolute temperature, so vegetation varies predominantly according to the amount of rain and the relative duration of the seasons (Moreau, 1972; Salewski & Jones, 2006). Sub-Saharan Africa experiences a great degree of seasonal change and a habitat's optimal conditions may be short-lived (Morel, 1973; Jones, 1995). Rains fall in the Sahel region between July and September and, as one progresses further south, rainfall occurs for longer periods until reaching the equator, where rain is constant throughout the year. Crossing the equator, a mirror-image pattern is observed (Moreau, 1952; Morel, 1973; Jones, 1995). In most places, especially south of the Sahara in western Africa, a single rainy season is followed by months of drought, while in East Africa there is a more marked double peak in rainfall, resulting in two wet seasons separated by two dry seasons whose relative timing and durations vary from place to place. Because the severity of the dry season increases the further one is from the equator, the vegetation zones also mirror each other. In the region of year-round rainfall rainforests prevail and as one moves away from the equator the predominant habitats become guinea savannas, followed by mixed broad-leaved/*Acacia* woodlands (the Sudan zone in the northern tropics), and increasingly arid *Acacia* savannahs (the Sahel in the northern tropics) until the Deserts are reached (the Sahara in the northern tropics). The region of two wet and dry seasons in East Africa supports a complex mixture of different savannah types (Moreau, 1972; Newton, 2010; Wangai et al., 2016).

Most Afro-Palearctic migrants spend the non-breeding period above the equator, in the Sudan and Sahel regions, even though habitats like rainforests and guinea savannahs have constant resources throughout the year (Moreau, 1972; Morel, 1973; Jones, 1995). Higher latitudes are closer to the breeding grounds, minimising migration distances (La Sorte & Fink, 2017; Rotics et al., 2017), but given their position above the equator, the regions have a dry season and high temperatures during the northern winter when migrants are present. This means that on arrival, although migrants find abundant food (*e.g*. seeds and insects) because the wet season has just finished, they leave when resources are limited and competition for them is high (Alerstam et al., 2003; Salewski & Jones, 2006). There are a few reasons why south of the Sahara is a hotspot for migrants: (1) seasonality, where the abrupt alternation of dry and wet seasons results in a sharp seasonal increase in plants and invertebrates that resident birds alone cannot exploit, (2) an absence of potential competitors, particularly of Afrotropical and resident birds, and (3) the fact that during the dry season, there are trees at every stage of leaf, flower and fruit production that also support high insect abundance (Moreau, 1972; Morel, 1973; Jones, 1995).

1.3 Recent declines and potential causes

Many migratory bird species are in rapid global decline (Sanderson et al., 2006; Laaksonen & Lehikoinen, 2013; Vickery et al., 2014; Bairlein, 2016; Soykan et al., 2016) and long-distance migrants seem to be at more risk than short-distance migrants and residents (Berthold et al., 1998; Sanderson et al., 2006; Heldbjerg & Fox, 2008; Thaxter et al., 2010; Vickery et al., 2014). Pinpointing where these declines occur, however, is difficult. Large spatial-scale movements carried out by migrants mean that the limiting factors may be operating from the breeding, wintering, or stopover sites, or from an interaction occurring between the sites (Morrison et al., 2013). Vickery and collaborators (2014) suggest that the main causes of these declines are the following (*n.b*. they are not mutually exclusive, and effects could be species-, population- and site-specific):

- *Changes at the breeding grounds*: Over the past few decades, the increase in agricultural lands, the homogenisation of the landscape due to monocultures, the drainage of water bodies for irrigation, and the intensification of crop management (*e.g*. increase of fertilisers, pesticides, grazing) have reduced the number of suitable habitats for breeding, nesting and foraging of birds in Europe (Chamberlain et al., 2000; Donald et al., 2001; Vickery et al., 2004; Hewson & Noble, 2009; Thaxter et al., 2010), especially woodland specialists (Fuller et al., 2007; Gregory et al., 2007; Hewson & Noble, 2009). Additionally, warmer winters within Europe may enhance survival and advance the breeding period of short-distance migrants and residents, increasing competition and disadvantaging long-distance migrants (Sanderson et al., 2006).
- *Changes at the non-breeding grounds*: Africa has undergone many landscape changes through both environmental and anthropogenic causes. Rainfall in this region decreased dramatically during the late 1960s causing severe population declines in Common Whitethroats *Curruca communis* and Sedge Warblers *Acrocephalus schoenobaenus*, amongst other species (Winstanley et al., 1974; Peach et al., 1991). Since then, annual fluctuations in migratory birds' survival rates have been related to rainfall in the wintering and stopover sites in this region (Baillie & Peach, 1992; Boano et al., 2004; Robinson et al., 2008; Halupka et al., 2017). Furthermore, the increase in human and livestock populations in the Sahel has impoverished grasslands, accentuated desertification, and decreased suitable sites for birds to exploit (Jones et al., 1996; Hewson & Noble, 2009; Laaksonen & Lehikoinen, 2013; Walther, 2016).
- *Climate change*: Long-distance migratory birds are especially susceptible to climate changes. The drop in mean average annual rainfall has also generated an expansion of both the Sahara Desert

and the Sahel zone and has decreased wetlands in the region, increasing migration-related stress (Zwarts et al., 2009; Newton, 2010), and possible expansion or reduction of species' geographical ranges (Barbet-Massin et al., 2009). If breeding areas expand north and wintering grounds remain constant, an increase in energy during migration would negatively impact populations (Doswald et al., 2009; Vickery et al., 2014). Climatic change may also disrupt the synchrony of bird-prey dynamics: the arrival dates at European breeding sites may no longer occur during key phenological events of spring (*e.g*. flowering and fruiting of plants, emergence of insects), leading to a mismatch between the timing of a migrants reproduction and its main food supply (Both et al., 2006).

- *Other factors*: There are many other factors that, on a smaller scale, are affecting Afro-Palearctic migrants such as hunting, especially in the Mediterranean region, and increases in collisions with buildings encountered during migration (McCulloch et al., 1992; Alerstam et al., 2003; Vickery et al., 2014; Bairlein, 2016).

1.4 The complexity of the annual cycle and the implications for conservation

The study of long-distance migrants has mainly been divided into breeding (Mason, 1995; Haas, 1998; Tsiakiris et al., 2009; Mallord et al., 2016), migration (Hedenström & Alerstam, 1997; Catry et al., 2004; Arizaga et al., 2008; Maggini & Bairlein, 2011; Ouwehand et al., 2016), and wintering periods (Barshep et al., 2012; Blackburn & Cresswell, 2015, 2016a; Thorup et al., 2019). This division occurs due to limitations in following individuals throughout the year and each study only solves a small piece of the puzzle, because these periods are intricately linked (Marra et al., 1998; Webster et al., 2002). To fully understand the biology and ecology of any animal, one must appreciate its full annual cycle and understand how each event during each period influences events of subsequent phases. Each stage can also influence the next temporally (*i.e*. by carry-over effects; Ockendon et al., 2013), or spatially (*i.e*. by means of migratory connectivity; Webster & Marra, 2005; Hahn et al., 2009; Finch et al., 2017). Studying a species' full annual cycle is important for understanding how populations of migratory animals are limited throughout the year (Martin et al., 2007; Tøttrup et al., 2012; Klaassen et al., 2014; Marra et al., 2015; Briedis et al., 2019). Moreover, how stages are linked, and how flexible birds are in exploiting resources (*i.e*. whether they are specialists or generalists) is crucial for predicting how a population will respond to future climate changes and has important implications for their conservation (Lerche-Jørgensen et al., 2019).

Events within one stage of the migratory bird's annual cycle may affect events in subsequent stages (Webster et al., 2002; Rockwell et al., 2017). Not finding suitable habitat at the stationary wintering grounds, for example, could have a significant negative impact on an individual's body condition, decreasing its probability of surviving the winter, which will in turn influence spring migration departure dates and consequently arrival dates at the breeding grounds. Proper timing is of critical importance in migratory species and key in securing their fitness because individuals need to time their arrival when resources are most plentiful: not before they are available, and not when they are soon to disappear (Cotton, 2003; Visser & Both, 2005; Møller et al., 2008).

The ecology and conservation of migratory birds are significantly affected by how different breeding populations spread and mix during the non-breeding season (migratory spread). This will, in turn, affect a species' response to changing environmental pressures (Webster et al., 2002; Cresswell, 2014). Species with low migratory spread (or strong migratory connectivity, when most individuals from a breeding population have the same non-breeding grounds) are less likely to adapt to shifting habitats and be less resilient to global changes than species with higher migratory spread (or weak migratory connectivity, when individuals from same breeding population spread over several non-breeding areas and mix with individuals from other populations; Webster & Marra, 2005; Cresswell, 2014). In addition, high migratory spread means that changes occurring in one non-breeding site have minor effects on breeding populations because few individuals in any one population spend the non-breeding season in the same location (Cresswell, 2014; Gilroy et al., 2016; Finch et al., 2017).

How birds overcome these challenges and the strategy they exercise in selecting and using non-breeding habitats is highly related to the degree of specialism in a species' habitat requirements. In other words, whether they are generalists, *i.e*. feed on a variety of resources and thrive in a range of habitats, or specialists, *i.e*. feed on limited resources and have stricter habitat requirements. Each strategy reflects a trade-off between the capacity to exploit a variety of environmental conditions and the ability to use each one (Julliard et al., 2006). More specialised species can use resources more efficiently but have lower dispersal abilities, are more strongly regulated by intraspecific competition, and are constrained to certain habitats, whilst generalists are less restrictive of their habitat requirements, can exploit a variety of resources, can survive in suboptimal habitats and are more likely to cope with habitat changes both within and between non-breeding seasons (Salewski et al., 2002; Julliard et al., 2006). Therefore, specialism is a good strategy for unchanging and predictable conditions while generalism is a good strategy for changing and unpredictable conditions.

Overall, Afro-Palearctic migrants seem to be generalists during the non-breeding season, even to a similar degree as their Afrotropical resident counterparts (Ivande & Cresswell, 2016), and thus occupy a wide variety of habitats, both natural and human-modified (Salewski & Jones, 2006). Once at the non-breeding grounds, however, and even when individuals are generalists, there is a trade-off between finding optimal high-quality habitats and reducing the costs of moving. As the dry season progresses, habitats deteriorate, so individuals can either opt to remain at a low-quality habitat that could potentially lead to death or a decrease in fitness, or risk moving to another unfamiliar site, which increases risks through further migration. Under this scenario, generalists could probably decide to remain at suboptimal habitats, facing higher competition as the season progresses, but avoiding the risk of moving and discovering new terrain, whilst specialists would have to find other sites with their specific requirements, assuming an increased risk of predation due to movement and initial unfamiliarity with a new site.

Until recently, there was no technology available for tracking individuals throughout their full annual cycle. It is not surprising, therefore, that most of the research undertaken on these birds has been during their breeding season and at high latitudes (*e.g*. in North America and Europe; Holmes, 2007; Morrison et al., 2013). For a long time, information regarding the non-breeding season, a period during which birds spend >60% of the year, was lacking and mainly anecdotal. Fortunately, the recent development of novel techniques that allow tracking individual movements throughout the year and an increase in scientific efforts carried out at the wintering grounds have slowly allowed scientists to unravel and to start to understand the non-breeding ecology period.

1.5 The non-breeding period

The non-breeding period, which includes both the active migration and the stationary wintering periods, is crucial in limiting migrant populations.

1.5.1 Active migration

During migratory periods, birds are affected by events and conditions that occur during the migratory flight and at stopover sites. Migrating implies flying thousands of kilometres, crossing extreme ecological barriers, and overcoming diverse threats along the way. Even though the migratory period is the shortest stage of the annual cycle (~3 months), it seems that migratory songbird mortality rates may be up to 15 times higher during migration than during stationary periods (Sillett & Holmes, 2002; Klaassen et al., 2014). Not only is migration energetically costly, but many levels of unpredictability make this a high mortality period. The ideal migratory strategy would be to travel the shortest distance possible under favourable conditions. Certain decisions, therefore, influence the success of migration, making it a good trade-off for future survival and breeding success. Decisions such as what migratory routes to take, what speed to fly at, whether to stop to refuel or not, and if so, where and for how long to remain at a stopover, the timing of departure and arrival dates, and how to correct for wind patterns and cope with non-ideal weather conditions are all key in undertaking a successful migration.

When crossing ecological barriers such as the Sahara Desert, migrants encounter harsh environmental conditions for over 2000 km (Hahn et al., 2009; Strandberg et al., 2010; Klaassen et al., 2014; Blackburn et al., 2019). To cope with these conditions, birds opt for one of two strategies: (1) a non-stop journey, where individuals accumulate enough body reserves to carry out a long, quick flight, crossing both the Mediterranean Sea and the Sahara Desert in one journey (large fuel reserves but longer flights), or (2) an intermittent flight, where individuals break their journey into sections, usually flying at night, resting and refuelling during the day (small fuel reserves but shorter flights; Moreau, 1972; Newton, 2010; Alerstam, 2011). The first strategy decreases migration time and exposure to threats but requires high body reserves (mostly fat) before starting the journey. On the other hand, an intermittent flight strategy increases exposure to threats, mainly at stopover sites, but fuel-use and recovery rates are more efficient. Fat is the optimal and most efficient flight fuel (Alerstam, 1990; Berthold, 1993; Klaassen, 1996) and some individuals as much as double their weight prior to or during migration (Ottosson et al. 2005; Nwaogu & Cresswell 2015). However, an increase in weight also increases air resistance and general flight costs per unit of distance travelled, which in turn increases the risk of predation and injury, and decreases foraging efficiency (Alerstam, 1990; Klaassen, 1996). There is a trade-off, therefore, between fuel accumulation rates and the duration of migration and its associated risks. Even though birds may vary their strategy at different stages of their journey depending on feeding opportunities in different parts of the route, most passerines seem to migrate using the intermittent flight strategy (Bairlein, 1988; Schmaljohann et al., 2007).

The intermittent strategy requires birds to stop along the way to refuel, rest, and shelter (Berthold & Terrill, 1991; Schmaljohann et al., 2007; Maggini & Bairlein, 2011), thus conditions at these sites are crucial for migrating successfully and for overall survival (Kirby et al., 2008; Hewson et al., 2016; Halupka et al., 2017). Birds can spend up to 85% of the migration period at stopover sites to store or replenish fuel for the next flight (Hedenström & Alerstam, 1997; Schmaljohann et al., 2012). Some individuals descend into the desert or oases during the day to shelter and rest, and continue their flight during the night, while others stop for longer periods to refuel (Bairlein, 1988; Berthold & Terrill, 1991), including setting up and defending territories (Bibby & Green, 1980). Thus, the quality of the site will determine the amount of fuel stored (refuelling rates) and the duration spent at them, which in turn will determine the number of stopover sites that need to be visited and arrival dates at the breeding and wintering grounds (Arizaga et al., 2008; Halupka et al., 2017). Stopover sites, however, are not without risk: a large number of individuals and species gather and increase inter- and intra-specific competition, predation, and exchange of pathogens and parasites (Flegg, 2004). Birds are also likely to arrive at unfamiliar sites, potentially arriving at suboptimal habitats that may not meet their needs and must adopt certain foraging behaviours according to what resources, often seasonal, are available at the time. Composition and quality of stopover sites differ seasonally and annually (Pearson & Lack, 1992), adding to the uncertainty. Thus, stopping at several sites is costly and dangerous, suggesting that individuals should reduce the number of stopovers visited, and should remain for as short as possible a time, just enough to rest and replenish the necessary fuel loads to survive and account for unpredictability in weather conditions *en route* and quality of subsequent stopover sites.

Stochastic events such as weather conditions also have a strong impact on mortality and significantly influence migration (Richardson, 1990). Most birds, especially smaller ones, are more likely to migrate when skies are clear, tailwinds are present and wind speeds are low (Newton, 2010). Most migrants can adjust their flight altitudes to take advantage of prevailing winds. Those individuals that fly during high winds, storms, or any extreme weather events, however, cannot compensate and readjust their flight, and risk getting lost and arriving at low-quality sites, compromising survival (Piersma & Van de Sant, 1992; Erni et al., 2005). In addition, hunting and the presence of structures birds may collide into (*i.e*. buildings, wind turbines) increase migration risk during this period (McCulloch et al., 1992; Kirby et al., 2008; Bairlein, 2016).

Migrants also show flexibility to environmental variations. In sub-Saharan Africa, the non-breeding season coincides with the dry season, so as time passes, habitats deteriorate (Alerstam et al., 2003). This means that at the beginning of autumn, the end of the wet season, the Sahel is an optimal habitat that is highly vegetated, where insects are abundant and northward winds prevail (Biebach et al., 2000). During spring, however, winds are against them, habitats are more limited, and the Desert is drier and more extensive (Zwarts et al., 2009). To cope with the significant changes in productivity and resource availability throughout the year, and to take advantage of the seasonal differences in wind pattern (*i.e*. speed and direction), many Afro-Palearctic migrants often follow different routes during spring and autumn (termed “loop migration”; Pearson & Lack, 1992; Lemke et al., 2013; Koleček et al., 2016;

Lerche-Jørgensen et al., 2017; Briedis et al., 2018; Burgess et al., 2020). Loop migrations reduce overall migration duration and increase migration speed, despite increasing distance. How flights are carried out also depends on seasonality.

Arrival and departure times to and from breeding and non-breeding stationary sites are also important and help shape migration. In spring, birds need to arrive early to obtain higher quality territories and mates, without arriving too early when weather is unfavorable and resources are still lacking (Kokko, 1999; Drent et al., 2003). In autumn, however, birds are less time-constrained, as late arrival at the non-breeding grounds has fewer fitness consequences (McNamara et al., 1998). Because of this, spring migration is expected to be shorter and faster (Yohannes et al., 2009; Schmaljohann et al., 2012; Stach et al., 2016), and species with later departure rates tend to migrate faster than early migrating species (Yohannes et al., 2009).

All these differences can be highly influenced by the age and sex of individuals, mainly due to differences in breeding pressures, preceding events in the annual cycle, body size, and dominance. These in turn can further accentuate seasonal differences. The main factor regarding age is the level of experience: in autumn, first-years are undertaking their first migration, so migrate without specific knowledge of non-breeding locations. Departure times during this period vary, with examples of adults leaving before first-years (McKinnon et al., 2014; Schmaljohann et al., 2018) and vice versa (Blackburn et al., 2019). First-years also tend to have slower and longer overall migration (McKinnon et al., 2014): they may spend longer at stopover sites or may require visiting more of them. They are also more likely to arrive at lower quality stopover sites due to the stochastic nature of first migrations for example (Cresswell, 2014) because they are less likely to correct for wind drift (Thorup et al., 2003; McKinnon et al., 2014) and more likely to be displaced. Arriving at a lower quality site means first-years are then less able to compete for resources and have lower rates of energy accumulation. However, individuals develop and improve migratory behaviour rapidly, so much so that, by spring, there is not much difference between age cohorts (Schmaljohann et al., 2018; Blackburn et al., 2019). Migration differences between females and males also occur and can be due to the different roles of the sexes during breeding, and dominance (Kokko et al., 2006; Briedis et al., 2019). In species that pair up at the breeding areas, males need to arrive first to establish territories at the most suitable habitats (Briedis et al., 2019). This means that males should start spring migration earlier or migrate faster and shorter distances, or a combination of all these factors, though males have a strong advantage while competing for food at stopover sites and could also refuel faster.

1.5.2 Stationary periods

Afro-Palearctic migrants spend approximately three months of the year at their breeding grounds, three months actively migrating, and the remaining six months at the “stationary” non-breeding grounds. The decisions undertaken and behaviours exhibited during this period will have significant effects on population dynamics and the overall fitness of migrants. Here, individuals are experiencing shorter nights and warmer days and are relieved of constraints imposed by breeding and migration pressures. Individuals then direct energy on recovering from the long journey, surviving through the season, and preparing for the return to the breeding grounds, prioritising and optimising short-term maintenance. Survival then relies on finding sufficient resources, as well as escaping predation, parasites, and diseases (Alerstam et al., 2003). The quality of the site an individual reaches, how long it remains there for, whether it returns to it in subsequent years, and how it adapts to strong seasonal changes will all determine the success and survival of the period.

The decision as to whether to remain at or move from a site is extremely important in a region as seasonally changeable as Africa. For many years there was a largely evidence-free assumption that small migrants tended to move across Africa, tracking changing seasonal conditions in a generally itinerant way (Moreau, 1972; Jones, 1995). More recently, evidence has emerged that this behaviour is strongly species- and population-specific (Bulluck et al., 2019), with some species visiting several different sites (Catry et al., 2003; Hedenström et al., 1993; Salewski et al., 2002; Thorup et al., 2019), others spending longer periods at fewer sites (Salewski et al., 2002; Kristensen et al., 2013; Ouwehand et al., 2016; Thorup et al., 2019) or, in some cases, species doing both (Cuadrado, 1995; Senar & Borras, 2004; Belda et al., 2007). There are inherent risks both to moving during the winter and remaining in the same area. Itinerant individuals might have an advantage in tracking ephemeral resources over a large area and are likely to move as environmental conditions change with the progression of the winter season (Newton, 2004; Ruiz-Gutierrez et al., 2016). As habitats deteriorate, movement to more southerly and mesic sites could be a good way to secure enough resources to survive the period. On the other hand, remaining at one specific site and maintaining a territory during the non-breeding period could confer advantages in terms of local knowledge such as foraging locations, competitor densities, resource fluctuations, and predators (Brown & Long, 2006; Catry et al., 2004; Latta & Faaborg, 2001; Lind & Cresswell, 2006). It could also increase the value of a site (Piper, 2011) and avoid high costs and unpredictability associated with moving long distances (Warkentin & Hernández, 1996; Cresswell, 2014). More recently, evidence suggests that the use of multiple wintering sites for prolonged periods may be more common than previously thought (Fraser et al., 2012; Lemke et al., 2013; Koleček et al., 2016; Burgess et al., 2020).

During stationary periods many migrants, regardless of their residency period, may restrict their activities to small areas that secure and contain all necessary resources (*i.e*. home ranges) and/or establish and defend territories. During the breeding season, territories are established to secure resources, attract a mate, defend chicks and nests and raise the young (Greenwood & Harvey, 1982). Remaining within a small home range during the non-breeding period, however, or during a part of it, is beneficial in terms of obtaining local knowledge regarding foraging locations, resource fluctuation, and competitor and predator densities (Brown & Long, 2006; Catry et al., 2004; Latta & Faaborg, 2001; Lind & Cresswell, 2006), and is a good strategy to ensure food availability throughout the period and for subsequent years (Greenberg, 1986; Kelsey, 1989; Cuadrado, 1995; Rolando, 2002; Zwarts et al., 2009). Territoriality is also species-specific (Salewski et al., 2002).

Contemporary studies have shown that many Afro-Palearctic show a relatively high degree of between-year site fidelity, where individuals return to the same wintering sites year after year, regardless of the duration they spent at them previously. This is especially true of territorial individuals (Cuadrado, 1992; Salewski et al., 2000; Koronkiewicz et al., 2006; Cresswell et al., 2009; Blackburn & Cresswell, 2016b; Thorup et al., 2019). The decision to come back to the same site/territory is highly linked to their previous experience: if the site previously provided the resources necessary for survival, then individuals are more likely to return to it (Cuadrado, 1992; Cresswell, 2014). The degree of return rates, however, also varies greatly by individuals and species: whilst some species show high return rates year after year, others seem to have a more nomadic strategy, changing non-breeding locations from one year to another (Herrera & Rodriguez, 1979; Kelsey, 1989; Catry et al., 2003; Somershoe et al., 2009; Blackburn & Cresswell, 2016b; Thorup et al., 2019). Familiarity with these sites confers the same advantages as longer residency patterns, especially regarding knowledge of local and fluctuating food sources, competitor densities, and location of refuges.

To survive the non-breeding winter period, during which environmental conditions and individual body conditions fluctuate, spatiotemporal decisions must be made accordingly. At arrival, individuals have poor body condition. At this time, habitats are productive and finding suitable habitats to recover is not difficult. As winter progresses, individuals increasingly focus on establishing and defending territories, or moving amongst sites to maintain a stable body condition and have just the right amount of energy to carry out basic activities, especially foraging and avoiding predators and/or unfavourable weather (Cuadrado, 1995; Salewski et al., 2002; Blackburn & Cresswell, 2015; Williams et al., 2016; Thorup et al., 2019). At the end of this period, individuals must increase foraging intensity to prepare for spring migration, during which time individuals will substantially increase their body condition accordingly (Vickery et al., 1999; Ottosson et al., 2005; Risely et al., 2015).

Age and sex differences also become apparent during the stationary periods. Given that selection of appropriate winter home ranges affects overall survival, some species exhibit dominance-based habitat occupancy, where habitats with optimal resources are occupied by behaviourally dominant birds (mainly larger and more experienced individuals, *i.e*. adults and/or males) and subdominant individuals (smaller and inexperienced individuals, *i.e*. first-years and/or females) are forced to occupy lower-quality habitats or adopt a non-territorial strategy (Hutto, 1980; Marra & Holmes, 2001; Mazerolle & Hobson, 2004; Brown & Long, 2006). Home range sizes and degree of residency (or mobility) are also influenced by age and/or sex. Finally, the decision as to where to winter will also depend on experience: first-years, which lack knowledge of small and medium scale locations of where to arrive, will reach the non-breeding ground stochastically and must look for a suitable wintering area. Some will find a site and remain at it until migration, while others will continue their search elsewhere, many of them arriving at less suitable sites or even discovering new unknown suitable habitats (Cresswell, 2014). Lower quality sites would inevitably require higher energy expenditure to maintain the same net energy intake (Brown & Long, 2006).

1.5.3 Carry-over effects

Stationary periods and migratory periods are not independent of each other. Consequently, carry-over effects – where conditions or decisions at one stage affect later stages – are important to understand. In addition, timing conflicts can arise because the time spent on activities undertaken in one stage reduce the options in other stages.

A classic example of a carry-over effect is the phenological mismatch due to climate change. Long-distance migrants are especially susceptible to mistiming in the face of climate change because of the temporal and spatial complexity of their annual cycle. Climate change is not regular throughout the globe and different organisms do not respond to it at the same pace (IPCC, 2014). It has been well documented that climate change can generate phenological mismatch between migratory birds and their prey if both respond differently (Cotton, 2003; Lemoine & Böhning-Gaese, 2003; Both et al., 2006; Visser et al., 2006; Saino et al., 2010; Vickery et al., 2014; Bairlein, 2016; Mayor et al., 2017). The increase in winter and spring temperatures in the Northern Hemisphere have advanced spring phenological events, such as flowering and fruiting in plants and emergence of insects (Menzel et al., 2006). Birds wintering in Africa may be constrained by conditions there or encountered during traveling and may not receive the new phenological cues of their breeding areas. Arriving too early or too late at the breeding grounds is likely to generate strong fitness consequences (Visser et al., 2006; Saino et al., 2010).

Another classic example of a timing conflict is moult scheduling. The moult, or renewal of feathers, is an energetically demanding process and thus, should not overlap with other high energy-consuming activities such as breeding and migration (Berthold, 1996; Salewski et al., 2004; de la Hera et al., 2010). Poor feather quality reduces the ability to evade predators and increases the metabolic demands of flight by reducing flight performance. Moulting is, therefore, essential for survival. The Palearctic passerine migrants are well known for moulting at the breeding grounds, but information is scarce for many species that moult in the African non-breeding grounds, either shortly before spring migration (prebreeding moult) or after autumn migration (postbreeding moult). When and how species moult reflects the allocation of energy and time to different activities during the annual cycle and thus, affects general population dynamics, as well as migration and wintering strategies (Waldenström & Ottosson, 2002; Salewski et al., 2004; de la Hera et al., 2010).

1.6 Study species: The Common Whitethroat *Curruca communis*

The Common Whitethroat *Curruca communis* is a widely distributed Afro-Palearctic migrant. It breeds throughout most of Europe and North Africa and across to western central Asia, as far as central Siberia, and spends the non-breeding season in sub-Saharan Africa, from Senegal to Ethiopia and south to South Africa (Cramp, 1992; Walther et al., 2010; Escandell & García, 2011). Four subspecies are classified: (1) *C.c. communis* breeds in Europe and north-west Africa and winters mainly in West and central Africa, (2) C.*c. volgensis* breeds between south-eastern European Russia and western Siberia and potentially winters in north-central and eastern Africa, (3) *C.c. icterops* breeds between Turkey and Turkmenistan and winters in eastern and southern Africa, and (4) *C.c. rubicola* breeds in Asian mountains and Mongolia and winters in eastern and southern Africa (Aymí & Gargallo, 2021).

Individuals breed in a wide variety of landscapes, mostly in open areas with scrubs and bushes. Males establish small territories in March/April and defend them by song and threat display (Urban et al., 1997). Whitethroats are essentially monogamous, and the pair-bond only lasts for the breeding season. Egg-laying (from four to five) starts in May/June, but precise timing varies with altitude. Incubation lasts from nine to 14 days, both parents care for the young from eight to 15 days and until they become independent from 15 to 20 days after fledgling. Some populations, mostly southern, may double brood (Urban et al., 1997). After breeding, by June/July, all populations migrate to winter in sub-Saharan

Africa. Whitethroats have been suggested, on one hand, to fly from one stopover site to the next, accumulating just the necessary fat to do so (Ellegren & Fransson, 1992; Schaub & Jenni, 2000; Escandell & García, 2011; Jenni-Eiermann et al., 2011), and on the other hand, to have sufficient fat reserves to be able to fly across the Sahara Desert and the Mediterranean Sea without the need to refuel (Ottosson et al., 2001). During the non-breeding period, they inhabit scattered scrub and thickets, bushes at oases, open woodland with good shrub cover, and gardens (Urban et al., 1997). During spring migration, mixed Sahelian woodlands act as important habitats for Whitethroats compared to woodlands of lower diversity and tree density, rangelands, and farmlands (Vickery et al., 1999). While diet is mainly insectivorous, fruit consumption strongly increases outwith breeding grounds (Aymí & Gargallo, 2021). Whitethroats have been shown to have diverse moulting strategies (*i.e*. complete post-breeding, complete pre-breeding and interrupted) that could be population-specific depending on their breeding grounds (Waldenström & Ottosson, 2002).

Whitethroats underwent a large population decline in the mid-1960s. In Europe, they were abundant and widely distributed until 1968, and from then until 1973 many populations declined by over 60% (Winstanley et al., 1974). These declines were associated with a shortage of food, water, and shelter availability in their African grounds caused by extreme drought conditions in the Sahel (Winstanley et al., 1974; Hjort & Lindholm, 1978; Baillie & Peach, 1992; Newton, 2004). Even though Whitethroat population trends are currently increasing (BirdLife International, 2015), populations have yet to fully recover (Zwarts et al., 2009). This highlights how dependent Whitethroats are upon conditions at the non-breeding grounds and emphasises the importance of understanding the ecology and what factors limit populations during this period. Whitethroat numbers may be limited by habitat quality or availability at the non-breeding grounds, but the non-breeding habitat requirements, and complete annual cycle ecology, are still poorly known (Baillie & Peach, 1992). Whitethroats are one of the most studied migrants in the Sahel region, yet this represents fewer than ten studies and there is still a lack of information on several aspects of the species' ecology in the non-breeding season.

For many years, recaptures and sporadic resightings were the only source of knowledge regarding large-scale movement of small birds and all bird movements in Africa. However, the development of smaller and cheaper tracking devices over the years has helped fill in the gaps of knowledge related to bird migration, as individual birds can now be tracked throughout the entirety of their life cycle. Arguably, one of the best methods to estimate accurate survival rates is the use of global-scale remote-tracking systems to track individuals live and with great precision (*e.g*. Klaassen et al., 2014; Cheng et al., 2019;

Sergio et al., 2019) but this technology is still not available for small songbirds. Currently, small light-level geolocators are the only option for tracking long-distance movements of small passerine birds (Bridge et al., 2011): they record light intensity at regular time intervals that can be used to infer solar positions, that, in turn, can calculate geographical locations (Stach et al., 2012; Bridge et al., 2013). The main disadvantages of these devices are the need to recapture individuals to download the data, and that the resolution is low. Nevertheless, they reveal new information regarding migration routes, stopover locations, and breeding and non-breeding grounds and are a great tool for the study of migration, even when sample sizes are small (McKinnon et al., 2013).

1.7 Nigeria as an ideal study site

Nigeria was elected as our study site for three main reasons. First, it possesses one of the highest bird species richness in the world, from 861 to 883 species, of which 170 are long-distance migrants (Elgood et al., 1994). Second, with over 200 million people, Nigeria is currently the most populated country in Africa and the seventh most populated country in the world. It has alarmingly high land-use change, habitat loss, and deforestation rates, mainly due to population growth and expansion. Many other West African countries are following their example, experiencing high population growth and environmental degradation, and thus, Nigeria may reflect their possible future. Understanding the importance of Nigeria as a wintering ground for Afro-Palearctic migrants, and how human activities affect (or do not affect) them will allow us to propose appropriate conservation measures to avoid future Afro-Palearctic population declines at a country and regional West African level. Thirdly and finally, the A.P. Leventis Ornithological Research Institute (APLORI) provides good logistical support to carry out extensive fieldwork research in an organised environment (Chapter 2).

1.8 Thesis outline

Populations of long-distance migrants are declining. Their complex annual cycle and the gap in knowledge from the non-breeding grounds make it difficult to pinpoint where the problems lie and to understand why they occur. Although migratory strategies vary significantly between species and many times even between populations, they still share numerous similarities. Studying and understanding the annual cycle of a single migratory species could therefore help propose and direct conservation efforts of other similar migrant species.

Even though Whitethroats are, as a species, increasing and listed as “least concern” according to the IUCN Red List (BirdLife International, 2019), populations have yet to recover from the devastating crash after the 1960s Sahel drought (Winstanley et al., 1974; Zwarts et al., 2009). Identifying what drives or prevents long-distance migrants from responding to environmental change requires a complete understanding of the ecology and behaviour throughout the annual cycle. The non-breeding period is a poorly studied stage of many long-distance migrants, and even if Whitethroats are well studied at their breeding grounds and some data are available from their non-breeding grounds, results from this thesis will be important. They will generate information about how flexible Whitethroats and other migrant species are in the face of climate and habitat changes, and what conservation efforts should be undertaken to maintain their rate of population increase, either by identifying limiting factors operating on their non-breeding grounds or discounting the non-breeding area as a point of concern. Furthermore, by identifying and understanding the annual cycle of a migrant that is *not* declining, it can help pinpoint what strategies are likely to work for other migrants. Whitethroats are demonstrably susceptible to changes in conditions in Africa, thus knowledge of the ecology at the non-breeding grounds is crucial in understanding their recovery and, potentially, preventing future declines.

The main aim of the thesis is to study factors that influence the population dynamics of Whitethroats – a common and fairly typical Afro-Palearctic migrant – during the non-breeding period in Nigeria and to understand the connections between breeding and non-breeding grounds. The specific aims of this project are to study habitat use, survival rates, site fidelity, and residency patterns of Whitethroats during three wintering seasons in Jos, Nigeria (2017–2020), and to determine and identify migratory routes and specific stopover and breeding sites. To our knowledge, this is the first study to research Whitethroat ecology, at a very fine scale, for the entirety of the non-breeding season.

During this thesis, I first work at a large scale to describe the migratory routes and strategies of six individuals (Chapter 3). I then focus on a main non-breeding site in Nigeria and describe spatiotemporal behaviours and decisions carried out during the non-breeding period at very fine scales (Chapters 4 and 5) and finally, I explore whether the non-breeding period is a high-mortality period for the species, or not (Chapter 6). By exploring many aspects of their biology, I will identify whether Whitethroats are generalists and how susceptible they may be to changes in environmental and habitat conditions.

- In **Chapter 2**, I briefly describe conditions at the A.P. Leventis Ornithological Research Institute (APLORI), our **study site**, and explain the field **methods** used for data collection for all empirical chapters. All chapters, however, have their corresponding methods section. I also give a brief statement regarding the **ethics** of handling birds in the wild.

- In **Chapter 3**, I present the complete **annual cycle** of a handful of Whitethroats obtained by deploying geolocators. Here, I describe migratory routes, identify breeding grounds and key stopover sites, the degree of migratory spread, and discuss different migratory strategies. This study is the first to ever attach **geolocators** on Whitethroats and to track individuals for the entirety of the annual cycle. How populations mix and what sites are important is essential for identifying where migrants are the most threatened/susceptible.
- In **Chapter 4**, I explore **detection** rates, **residency** patterns, and the degree to which individuals return to the same site across years, and the differences between individuals of different age and sex categories. Knowledge of how long individuals use different sites, as well as the degree of **between-year site fidelity**, is crucial for estimating true survival rates, as well as identifying hotspots to protect the range of habitats used by all individuals throughout the non-breeding period.
- In **Chapter 5**, I explore fine-scale **spatial movements**, **habitat preference**, **predictors** of home range sizes, and **time allocation** to daily activities. I also explore whether there are differences amongst age and sex groups. This information is crucial in understanding how flexible Whitethroats are during the non-breeding period and how they cope with deteriorating conditions by the end of the non-breeding period.
- In **Chapter 6**, I calculate annual and overwinter **survival** rates to explore whether the wintering stage is the limiting part of the annual cycle. I also explore the influence of age and sex on survival. By detecting where higher mortality rates occur, and whether there are differences in survival amongst individuals, conservation efforts can be better directed.
- Lastly, in **Chapter 7**, I summarise and discuss the **implications of my results** by integrating the full annual cycle to understand the role of the non-breeding period in the population dynamics of Whitethroats. I also discuss the overall **conservation implications** of these findings on Whitethroats and other migrants. I then highlight the **novel contributions** and **limitations** that occurred throughout this work and suggest improvements and topics for **future research**. I finalise this section with a short **conclusion**.

All chapters are written as stand-alone research documents, with an integral relevant introduction, methods, results, and discussion section for ease of future publication in peer-reviewed journals.

Chapter 2. General methods

This research took place over three consecutive winters (hereby referred to as year1, year2, and year3), from November 2017 to March 2020. Each fieldwork season had the following, specific aims:

- **Year1** (13 November 2017 – 14 April 2018): The purpose of this season was to try to understand and familiarise myself with the study site and the species, and to locate the best areas and habitats within which to work with Whitethroats. During the first half of the season, the focus was on capturing and colour-ringing as many individuals as possible. For the second half, mist-netting efforts decreased and resighting individuals became the main aim.
- **Year2 (**18 September 2018 – 13 April 2019): This season was the longest and busiest. Mist-netting and resighting were undertaken constantly throughout the period. Additionally, radio tags and geolocators were deployed, and vegetation sampling and focal observations were carried out.
- **Year3** (8 November 2019 – 12 March 2020): During this season the main aim was to locate and recapture individuals with geolocators, thus mist-netting and resightings were undertaken throughout. Fortunately, the COVID-19 pandemic did not affect data collection.

In this chapter, I describe the study site, and outline the general methods used during the study that broadly apply across most chapters. I also give a brief statement regarding the ethics of handling birds in the wild. Specific methods are described in detail within their relevant chapters.

2.1 Study site

This study was carried out in a guinea savannah on the Jos Plateau, central Nigeria in West Africa (09°52’N, 08°58’E, 1250 masl; Fig. 2.1a). This region experiences single pronounced wet and dry seasons (Figs. 2.1e and f) lasting six months each, from May to October and November to April, respectively. Afro-Palearctic migrants are present from the end of the wet season (August – September) and depart during the final months of the dry season; the last migrants leave as late as May (Nwaogu & Cresswell, 2016). Study sites are located within the Amurum Forest Reserve, a ~120 ha conservation area, and in open scrublands surrounding it. All sites are located close to and within the A.P. Leventis Ornithological Research Institute (APLORI). The Reserve consists of four main habitat types: regenerating guinea savannah woodland, gallery forest, rocky outcrops, and farmland (Nwaogu & Cresswell, 2016); work was undertaken in all but the rocky outcrops. However, work was mostly undertaken in the open croplands/scrublands surrounding it. These lands consist of scattered bushes and grasses and are sites that have different degrees of anthropogenic activities such as farming (*e.g*. tomato, cucumber, pepper, maize, sweet potato), livestock grazing (cows and goats), tin mining and fires, intensities of which vary throughout the dry season (Hulme & Cresswell, 2012) but are greatest in intensity by the end of the season. These sites, in particular, represent typical African dynamic habitats, where anthropogenic activities are constant and continuously changing throughout the year. Given that not all year1 sites were optimal Whitethroat habitats, efforts in years 2 and 3 efforts were concentrated in sites with higher Whitethroat densities (Figs. 2.1b, c, and d). For statistical purposes, we grouped study sites into three location categories: (1) Crops, which consisted of open croplands/scrublands surrounding the Reserve, (2) Forest, study sites mostly located well within the protected Reserve, mostly in guinea savannah woodland habitats, and (3) Reserve, sites located within the edges of the Reserve, mostly savannah habitats but with a higher degree of human activity interactions compared to the 'Forest'.

The study site seems to be an important non-breeding site for Whitethroats as they are one of the most common Afro-Palearctic migrants to winter there. Furthermore, the study site is located close to the southernmost part of the species' distribution in West Africa, which increases the probability of capturing and working with winter resident birds and of excluding passage birds, which would only be seen when ringed. This makes our study site an ideal place to study Whitethroats throughout their non-breeding season. Furthermore, APLORI is a secure and friendly environment, presenting a perfect opportunity to undertake research in an otherwise difficult region to work at.

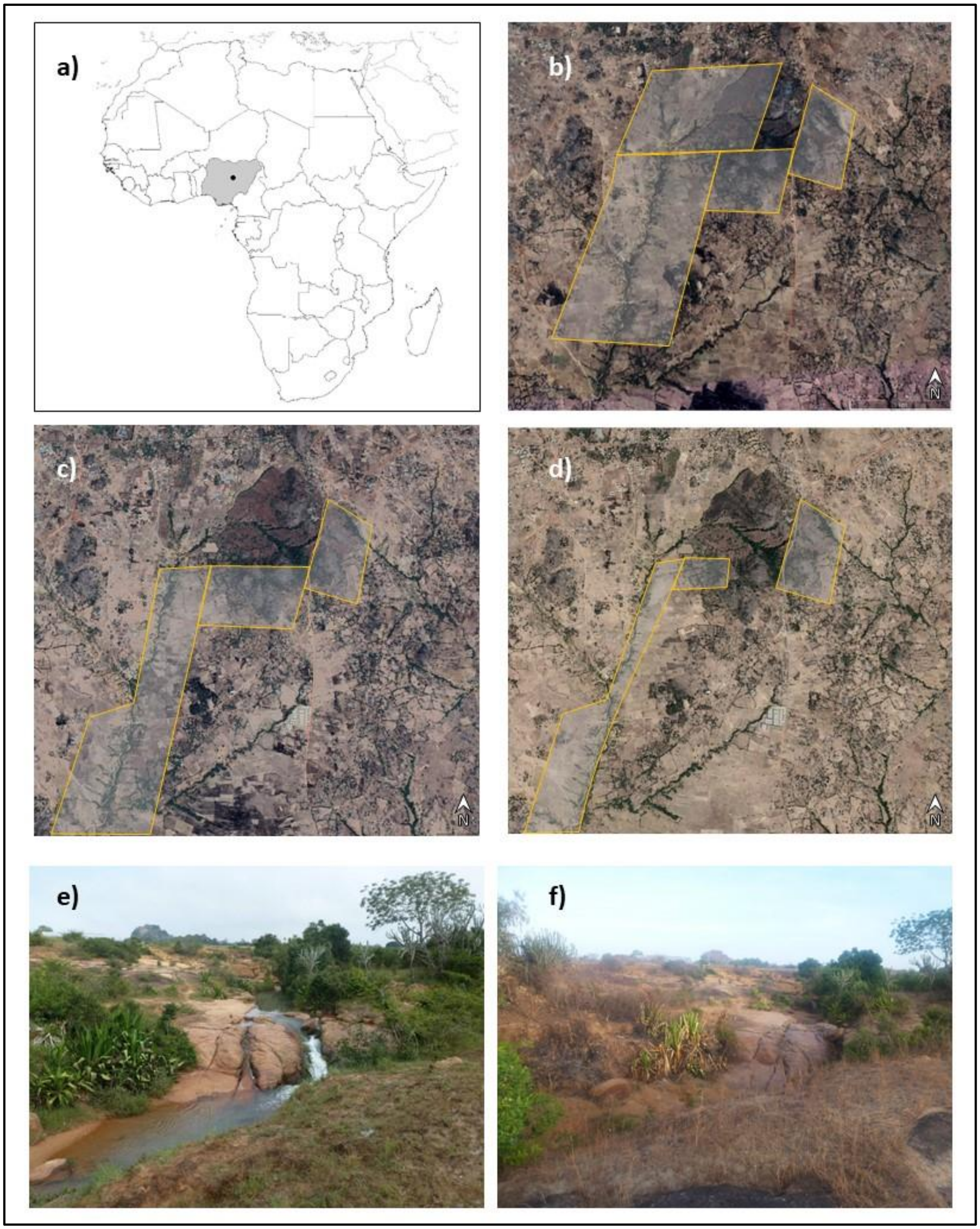


Figure 2.1. Study site. Location of study site within Nigeria, West Africa (a), rough delineation of study plots in year1 (b), year2 (c), and year3 (d), and an example of the landscape at the beginning (September; e) and end (March; f) of the year2 field season. Base maps of figures b, c, and d were downloaded from Google Earth™ in November 2021 and were taken on 10 January 2018, 22 January 2019, and 9 January 2021, respectively (imagery could not be obtained from January 2020).

2.2 Mist-netting

Birds were captured using 9m x 2.5m 5-shelf (16 x 16mm mesh) mist nets; 12m and 18m length nets were also used. During year1 nets were set up between 14 November 2017 and 23 February 2018 (average = four nets per day open for 2h 50m), from Monday to Saturday between ~0630 and 1030 hrs (totalling 70 visits). In year2 nets were set up from 25 October 2018 to 10 April 2019 (average = 4.5 nets per day for 3h 24m) during 60 days between 0600 and 1030 hrs and 1550 and 1830 hrs (totalling 69 visits). In year3, netting was targeted towards geolocated birds (Chapter 3), so the net effort was lower than in previous years. Between 12 November 2019 and 13 February 2020, mist nets were used for 23 days for an average of 2h 2m.

Overall, sites that appeared to have higher Whitethroat densities were netted more frequently. Conspecific playback was used to attract birds and to avoid non-targeted species. All captured Whitethroat individuals were sexed as either female, male or unknown, and aged as either first-year, adult, or unknown (Svensson, 1992). Biometric information (weight, tarsus, and maximum wing length) was measured for all individuals. Visible fat scores (scale of 0–8, based on the European Science Foundation system), pectoral muscle (0–3, based on the APLORI's ringing guide and Redfern & Clark, 2001), and the stage of the head and body moult (0–3) were estimated for most individuals. Each individual was given a unique combination of coloured leg rings (three colour rings and an additional SAFRING metal ring) for posterior identification. In total we colour-ringed 212 individuals in year1 (additional 32 recapture events), 115 individuals in year2 (additional 28 recapture events), and ten in year3 (additional 11 recapture events). Capture locations were recorded with a Garmin eTrex10™ GPS.

2.3 Resightings

Resightings were carried out during all three fieldwork seasons. Resightings consisted of revisiting all sites where birds were previously caught and/or seen. Ringed individuals were commonly sought out at least once a week between sunrise and ~1030 hrs and/or between ~1500 and sunset. Once an individual was detected we proceeded to identify its complete colour combination using binoculars. GPS points were recorded with a Garmin eTrex10™ GPS where individuals were first detected. Due to the skittish and shy behaviour of Whitethroats, conspecific playback had to be used. In some cases, individuals were first detected and playback was then used to help reveal the complete colour-combination. In most cases, however, when there were no signs of activity (*e.g*. movement, calling), playback was used before detection. This did not seem to induce any significant movement in individuals; only on one occasion during the three seasons did a single individual follow the playback for > 10m. Therefore, playback was mainly used for attracting individuals for proper ring colour-combination identification and we believe that most recorded GPS points reflect unbiased locations where the individuals would be without any interaction with observers. We tried to spend the same effort resighting all individuals, but we acknowledge that this may not have been always the case.

2.4 Radio tag deployment

Between 25 October and 28 November 2018, 11 individuals were fitted with "LifeTags™", a 0.45 g solar-powered and battery-free radio transmitter from Cellular Tracking Technologies™. Tags were attached to the bird's back using an elastic leg-loop harness following Rappole & Tipton (1991). Devices weighed, on average, 0.51 g with the leg-loop harness, corresponding to ~3.4% (3.2–3.8%) of an individual's body mass. Harnesses were attached to the radio tags before fieldwork. It took approximately three minutes to fit the devices onto each bird. As individuals were fitted with radio tags, an effort was made to seek them out at least twice a week after tag deployment until 8 December 2019. All birds were observed for at least three days after deployment. When an individual was detected, efforts were made to observe and corroborate the bird's colour combinations. GPS coordinates were recorded where individuals were first seen or heard or when detection was strong. To determine whether radio tags had any negative effect on individuals, the residency period (number of days between when individuals were caught and the last time individuals were detected) and return rates (proportion of individuals that returned the following non-breeding period) was compared between 11 radio-tagged individuals and 11 randomly selected control birds, ringed during the same period. No significant differences were found for either the residency periods ($F_{(1,20)} = 0.05$, $p = 0.82$) nor return rates ($\chi^2 = 0.26$, df = 1, $p = 0.61$) between tagged and control individuals. These results suggest that tagged birds and non-tagged birds show similar winter behaviour and overwinter survival and that these particular radio tags do not represent any significant threat to individuals.

Technical issues occurred, however. We felt that the receiving signals were not as strong as we thought they would be. This could be attributed to: (1) harsh harmattans (cool dry winds coming from the Sahara Desert that create dense clouds of dust) and/or (2) because Whitethroats tend to hide inside dense bushes. A combination of both may have meant that the tags were not getting the necessary solar energy to work ideally. Combined with the extra work for this project, it was decided that the use of these radio tags should be stopped. Nevertheless, even though these tags were only used for a short period, valuable information was obtained to confirm visual detection probabilities and territory and habitat use for some birds.

2.5 Ethics statement

The purpose of this study was to comprehend why migratory species are undergoing strong population declines and to understand how individuals behave in the wild, especially during the non-breeding period. It was therefore in everybody's interest – mine and the animals – to apply methods that would have a minimal effect on the studied individuals. Even though no official licenses were required to carry out this study in Nigeria, we consider that it is of crucial importance to prioritise the safety and welfare of all captured birds. As a result, all methods used throughout this research (*i.e*. during captures, colour-ringing, radio tagging, and geolocator deployment) were based on animal welfare guidelines issued by the Association for the Study of Animal Behaviour (ASAB, 2020) and the British Trust for Ornithology (BTO) and were approved by the School of Biology Ethics Committee of the University of St. Andrews on 22 November 2017 and 28 October 2018 (approval letters are shown at the beginning of this thesis).

For further, detailed information regarding ethical concerns, see Appendix 1.

Chapter 3. Common Whitethroats have a somewhat high migratory spread and multiple non-breeding sites as revealed by geolocators

3.1 Abstract

Understanding general migration characteristics and how breeding and non-breeding sites are connected is crucial for successfully predicting the response of long-distance migratory bird populations to recent global changes. The development of miniaturised light-level geolocators for small passerine birds has revealed general annual migration information for some long-distance migrants, but this information is still lacking for many species. This study is the first to ever attach geolocators on Common Whitethroats *Curruca communis*, an Afro-Palearctic migrant. Six individuals were successfully tracked from non-breeding grounds in central Nigeria: five were tracked throughout the annual cycle and one until it reached its breeding grounds. Most individuals commenced spring migration at the beginning of April. All birds followed a north-easterly direction, through central Europe. Most individuals flew to Algeria, Libya, or Tunisia with stopovers prior to crossing the Mediterranean Sea. Individuals arrived at their breeding grounds in May. Breeding sites were located across eastern Europe, on average, 729 km apart and covering an area of 425,000 km^2 (~4.2% of the total area of Europe) where they remained for, on average, 81 days. Departures from breeding grounds took place between late July and early August. All individuals flew in a south-westerly direction. There is some evidence of loop migration: four individuals moved in a clockwise direction, and one in an anticlockwise direction. The number of stationary days, number of days spent flying, longest staging period, and number of stopovers did not vary between spring and autumn migrations. Spring migration, however, was faster and longer and took overall less time than autumn migration. All individuals occupied two important non-breeding sites; they arrived at the first site, in the Sahel, during the end of September and remained for at least 50 days. The area of the convex polygon during this period was similar to that covered during the breeding season (~360,000 km^2). Birds arrived at the second and main non-breeding grounds in November where they remained until spring migration. We suggest that, while Whitethroats can cross the Sahara Desert and Mediterranean Sea in one single flight, they are likely to refuel before and after crossing them, highlighting the importance of stopover sites for the conservation of the species. Whitethroats also have a somewhat high migratory spread defined by a north-eastern flight pattern and use the Sahel as an important refuelling and stationary site.

3.2 Introduction

The conservation of long-distance migratory bird species is of great concern and poses complex problems as they move around large spatial scales — spanning between continents — through various habitats, environmental conditions, and anthropogenic pressures. Populations of these species are therefore vulnerable to any changes at their breeding and non-breeding grounds, as well as along migratory routes (Berthold & Terrill, 1991; Walther & Pirsig, 2017) and their survival is dependent on the conservation of all of these sites.

How different breeding populations spread and mix during the non-breeding season (*i.e*. migratory spread) has important effects on the ecology and conservation of migratory birds, and will affect a species' response to changing environmental pressures (Webster et al., 2002; Cresswell, 2014). Species with low migratory spread (or strong migratory connectivity, when most individuals from a breeding population have the same non-breeding grounds) are less likely to adapt to shifting habitats and can be less resilient to global changes than species with higher migratory spread (or weak migratory connectivity, when individuals from same breeding population spread over several non-breeding areas and mix with individuals from other populations; Webster & Marra, 2005; Cresswell, 2014). Furthermore, high migratory spread means that changes occurring at one non-breeding site have minor effects on breeding populations because few individuals in any population spend the non-breeding season in the same location (Cresswell, 2014; Gilroy et al., 2016; Finch et al., 2017). Measuring migratory spread is difficult as it requires tracking many individuals, and intra-African movements can further complicate this, as the degree of migratory spread with respect to the breeding grounds changes over the non-breeding season as birds change sites (McKinnon et al., 2013).

Key to identifying where, when, and how population declines occur is in understanding the routes individuals take from the breeding grounds to the non-breeding grounds and back. When crossing ecological barriers such as the Sahara Desert, migrants encounter harsh environmental conditions for over 2000 km (Tøttrup et al., 2008; Hahn et al., 2009; Strandberg et al., 2010; Åkesson et al., 2012; Klaassen et al., 2014; Blackburn et al., 2019). To cope with these conditions, birds opt for one of two strategies: (1) a non-stop journey, where individuals accumulate enough body reserves to carry out a long, quick flight, crossing both the Mediterranean Sea and the Sahara Desert in one journey (large fuel reserves but longer flights), or (2) an intermittent flight, where individuals break their journey into sections, usually flying at night, resting and refuelling during the day (small fuel reserves but shorter flights; Moreau, 1972; Newton, 2008; Alerstam, 2011). A non-stop strategy decreases migration time and exposure to threats but requires high body reserves (mostly fat) before starting the journey, while an intermittent flight increases exposure to threats, mainly at stopover sites, but fuel-use and recovery rates are more efficient. Both strategies may be utilised by a single species dependent on whether they are crossing barriers or more favourable continental areas, and the degree to which these strategies are used may vary individually (Blackburn et al., 2019). Moreover, what strategy is performed not only varies between species and individuals, but is also strongly dependent on weather conditions (*e.g.* wind speed and direction; Erni et al., 2005), habitat quality, and energy stores (Jenni-Eiermann et al., 2011).

Even though birds may vary their strategy at different stages of their journey depending on feeding opportunities in different parts of the route, most Afro-Palearctic passerines seem to migrate using the intermittent flight strategy (Bairlein, 1988; Schmaljohann et al., 2007; Adamík et al., 2016) and refuel at suitable habitats (Schmaljohann et al., 2007; Eraud et al., 2013; Adamík et al., 2016). Prolonged stopovers have been linked to strategic stops along the routes in areas with abundant food resources (Jones, 1995; Newton, 2008; Stach et al., 2012), especially prior to crossing ecological barriers (Salewski et al., 2002; Ottosson et al., 2005), but could also reflect low refuelling rates (Newton, 2008). The quality of these stopovers will determine the amount of fuel an individual stores (refuelling rates) and the duration spent at them, which will in turn determine the number of necessary stopover sites, arrival dates at the breeding and non-breeding grounds, migration success and overall survival (Arizaga et al., 2008; Halupka et al., 2017).

The composition and quality of stopover sites differ seasonally and annually (Pearson & Lack, 1992). In many regions of Africa there is a very pronounced wet and dry season, so habitats change considerably throughout the year. For example, in autumn, the Sahelian zone of Sudan is green and productive while eastern Ethiopia and Somalia are hot and dry, whereas in spring, conditions are reversed (Pearson & Lack, 1992). The difference in migratory strategies, between a single or intermittent flight, then also reflects how species overcome seasonal changes and how flexible they can be regarding the number of stopovers used and the time spent at them. Individuals are expected to adjust departure decisions and behaviours with respect to constraints that may have important fitness consequences, such as early arrival at the breeding ground compared to the relative unimportance of the time of arrival at the non-breeding grounds. There is evidence that long-distance migrants can adjust migratory behaviour *en route* in response to environmental variation at stopover sites to avoid predators, optimise fuel deposition and other annual life-history events (Ahola et al., 2004; Newton, 2008; La Sorte & Fink, 2017).

Large scale migration routes may also indicate behavioural flexibility to environmental variation. To cope with the significant changes in productivity and resource availability throughout the year, and to take advantage of the seasonal differences in wind pattern (*i.e*. speed and direction), many Afro-Palearctic migrants often follow different routes during spring and autumn (termed “loop migration”; Pearson & Lack, 1992; Lemke et al., 2013; Koleček et al., 2016; Lerche-Jørgensen et al., 2017; Briedis et al., 2018; Burgess et al., 2020). Loop migration reduces overall migration duration and increases migration speed, despite increasing distance. The direction of the loop seems to vary by species, as some travel in a clockwise direction (autumn migration has a more westerly direction than spring; *e.g*. Stach et al., 2016; Jacobsen et al., 2017), while others travel in an anticlockwise direction (autumn migration has a more easterly direction than spring; *e.g*. Tøttrup et al., 2012; Kristensen et al., 2013; Ouwehand et al., 2016; Briedis et al., 2018; Burgess et al., 2020).

Besides seasonal differences in stopover sites and migratory routes, other important aspects of migration may vary between spring and autumn. Arrival and departure times from breeding and non-breeding sites are of critical importance for an individual’s fitness and helps determine migration duration across seasons: individuals need to time their arrival when resources are most plentiful, not before they are available, and not when they are soon to disappear (Cotton, 2003; Visser & Both, 2005; Møller et al., 2008). In spring, for example, birds need to arrive early to obtain higher quality territories and mates but must avoid arriving too early when weather is unfavourable and resources are still lacking (Kokko, 1999; Drent et al., 2003). In autumn, however, birds are less time-constrained, as late arrival at the non-breeding grounds has fewer fitness consequences (McNamara et al., 1998). As a result, spring migration is expected to be quicker and faster (Yohannes et al., 2009; Schmaljohann et al., 2012; Stach et al., 2016), and species with later departure rates tend to migrate faster than species that migrate earlier (Yohannes et al., 2009).

All these differences can be highly influenced by the age and sex of individuals, mainly due to differences in breeding pressures, preceding events in the annual cycle, body size, and dominance. These in turn can further accentuate seasonal differences. The main factor regarding age is the level of experience: in autumn, first-years are undertaking their first migration, so migrate without specific knowledge of non-breeding locations. Departure times during this period vary, with examples of adults leaving before first-years (McKinnon et al., 2014; Schmaljohann et al., 2018) and vice versa (Blackburn et al., 2019). First-years also tend to undertake slower and longer overall migration (McKinnon et al., 2014): they may spend longer at stopover sites or may require visiting more of them. They are also more likely to arrive at lower quality stopover sites due to the stochastic nature of first migrations (Cresswell, 2014) because they are for example less likely to correct for wind drift (Thorup et al., 2003; McKinnon et al., 2014) and more likely to therefore be displaced. Arriving at a lower quality site means first-years are then less able to compete for resources and have lower rates of energy accumulation. However, individuals develop and improve migratory behaviour rapidly, so much so that, by spring, there is not much difference between age cohorts (Schmaljohann et al., 2018; Blackburn et al., 2019). Migration differences between females and males also occur and can be due to the different roles of the sexes during breeding, and dominance (Kokko et al., 2006; Briedis et al., 2019). In species that pair up at the breeding areas, males need to arrive first to establish territories at the most suitable habitats (Briedis et al., 2019).

Sub-Saharan Africa, where most migrants spend the non-breeding season, experiences a great degree of seasonal change. Rains fall in the Sahel region between July and September and, as one progresses further south, rainfall occurs for longer periods until reaching the equator, where rain is constant throughout the year. Crossing the equator, a mirror-image pattern is observed (Moreau, 1952; Morel, 1973; Jones, 1995). In most places, especially south of the Sahara in western Africa, a single rainy season is followed by months of drought. Thus, the decision of whether to remain at or move from a site is extremely important in a region as seasonally changeable as Africa. For many years there was a largely evidence-free assumption that small migrants tended to move across Africa, tracking changing seasonal conditions in a generally itinerant way (Moreau, 1972; Jones, 1995). More recently, evidence has emerged that this behaviour is strongly species- and population-specific (Bulluck et al., 2019), with some species visiting several different sites (Hedenström et al., 1993; Salewski et al., 2002; Catry et al., 2003; Thorup et al., 2019) and others spending longer periods at fewer sites (Salewski et al., 2002; Kristensen et al., 2013; Ouwehand et al., 2016; Thorup et al., 2019) or, in some cases, species doing both. More recent evidence suggests that the use of multiple wintering sites for prolonged periods (where individuals seem to remain for longer periods than needed for refuelling) may be more common than previously thought (Fraser et al., 2012; Lemke et al., 2013; Koleček et al., 2016; Burgess et al., 2020). These prolonged stationary periods could be a result of variance in seasonal food and habitat availability due to rainfall patterns rather than temperature (Winstanley et al., 1974; Pearson & Lack, 1992; Jones, 1995; Newton, 2008; Stach et al., 2016).

Breeding population trends of several species have been highly correlated with rainfall and the Normalized Difference Vegetation Index (NDVI) of non-breeding grounds (Winstanley et al., 1974;

Zwarts et al., 2009; Ockendon et al., 2014). A clear example of this is the Common Whitethroat *Curruca communis*. In Europe, it was abundant and widely distributed until 1968, but from then until 1973 many populations declined over 60% (Winstanley et al., 1974) due to shortage of food, water and shelter availability in their African grounds caused by extreme drought conditions in the Sahel (Winstanley et al., 1974; Hjort & Lindholm, 1978; Baillie & Peach, 1992; Newton, 2004).

Understanding the implications of migratory spread, and migration timing and routes requires detailed knowledge of where breeding birds go during the non-breeding season and vice versa. For many years, recaptures and sporadic resightings were the only source of knowledge regarding the large-scale movement of small birds and all bird movements in Africa. However, the development of smaller and cheaper tracking devices over the years has helped fill in gaps of knowledge related to bird migration, as individual birds can now be tracked throughout the entirety of their life cycle.

Small light-level geolocators are currently the only option for tracking long-distance movements of small passerine birds (Bridge et al., 2011). These devices can weigh <1 g and are relatively cheap compared to other similar devices (Bridge et al., 2011). These devices record light intensity at regular time intervals. The data collected can then be used to infer solar positions that, in turn, can allow one to calculate geographical locations (Stach et al., 2012; Bridge et al., 2013). The main disadvantages of these devices are the need to recapture individuals to download the data and the low resolution of the geographical positions due to variations in sun elevation angle secondary to variations in topography and/or individual behaviour. Nevertheless, geolocators reveal new information regarding migration routes, stopover locations and breeding and non-breeding grounds of specific individuals, making them a great tool for the study of migration, even when sample sizes are small (McKinnon et al., 2013). They have so far been placed on many small birds such as Wood Thrushes *Hylocichla mustelina* (Stutchbury et al., 2009; McKinnon et al., 2014), Purple Martins *Progne subis* (Stutchbury et al., 2009), Thrush Nightingales *Luscinia luscinia* (Stach et al., 2012), Whinchats *Saxicola rubetra* (Blackburn et al., 2017; Burgess et al., 2020), Reed Warblers *Acrocephalus scirpaceus* (Koleček et al., 2016), Common Nightingales *Luscinia megarhynchos* (Hahn et al., 2013; Emmenegger et al., 2014), Eurasian Hoopoes *Upupa epops* (Bächler et al., 2010), and Willow Warblers *Phylloscopus trochilus* (Lerche-Jørgensen et al., 2017). Blackburn and collaborators (2016) showed that tags that varied between 2.5 and 5.3% of the Whinchats' body mass did not affect apparent survival, but effects are species-dependent and their use should be treated with caution (Costantini & Møller, 2013).

Many migratory species have been tracked at their breeding grounds (Schmaljohann et al., 2012; Ouwehand et al., 2016; Lerche-Jørgensen et al., 2017; Xenophontos et al., 2017; Burgess et al., 2020) but very few at non-breeding grounds (Seavy et al., 2012; Stanley et al., 2012; Hallworth et al., 2015; Blackburn et al., 2017). By deploying geolocators at non-breeding sites on species that are territorial during this period, data regarding migratory spread can be collected more accurately because latitude estimation is more accurate towards the poles, and birds are more likely to be stationary during the breeding period (McKinnon et al., 2013). Such studies also give insight into non-breeding habitat quality and the breeding origins of birds sharing the same non-breeding sites (McKinnon et al., 2014).

The Whitethroat is a widely distributed Afro-Palearctic migrant that breeds from the Arctic Circle to Morocco, and from Ireland to central Siberia, and spends the non-breeding season in sub-Saharan Africa, from Senegal to Ethiopia and south to South Africa along the eastern coast (Cramp, 1992; Walther et al., 2010; BirdLife International, 2019). It has been suggested that individuals hop from one stopover to the next, accumulating just the necessary fat to do so (Schaub & Jenni, 2000; Escandell & García, 2011; Jenni-Eiermann et al., 2011), but can also fly across the Sahara Desert and the Mediterranean Sea without refuelling (Ottosson et al., 2001). Data obtained through ring recoveries from 150 individuals, mostly during migration, indicate that more western breeding populations spend the non-breeding period in western Africa (Zwarts et al., 2009), while more eastern breeding populations spend it in central and eastern Africa (these findings are supported by Escandell & García, 2011; Waldenström & Ottosson, 2002), but there is still much information lacking regarding general migration details such as migratory spread, important stopover sites, routes and timing.

3.3 Aims

The general aim of this chapter is to describe migratory routes and strategies of Whitethroats for the first time and to establish a broad overview of the complete annual cycle of individuals that spend the non-breeding season in central Nigeria. The specific aims and corresponding predictions are the following:

1) To identify the breeding grounds of individuals that spend the non-breeding season in a small area in central Nigeria and to determine the degree of migratory spread of the species. We expect individuals to breed in a large area throughout central, northern, and eastern Europe (*i.e*. high migratory spread). These will be in a broad north-easterly direction from the non-breeding grounds.

2) To identify key stopover sites and their temporal use along the journey. We expect few short-duration stopovers where individuals accumulate enough fuel to reach the subsequent stopovers and long distances between stopovers. We also expect a difference in the time an individual spends at each stopover site: we predict that individuals will have longer stationary periods before and after crossing major ecological barriers, especially before crossing the Sahara Desert, where *Salvadora persica* berries are present and available.
3) To evaluate whether there are strong differences between spring and autumn migration with respect to routes and timing. We expect spring migration to be faster, as birds leave APLORI in April and need to arrive quickly at the breeding grounds to set up territories. Loop migration is a common pattern within the Afro-Palearctic migratory system, so we expect Whitethroats to also undertake this.
4) To understand Whitethroats' movement within the African continent, as well as to identify whether individuals have multiple non-breeding sites. Some Whitethroats will likely have more than one non-breeding site used sequentially during this period, as has been found in other long-distance migratory passerine species that spend the non-breeding season close to the Sahel region.

3.4 Methods

3.4.1 Geolocator deployment

Between 28 January 2019 and 23 March 2019, 60 individuals (35 adults, 24 first-years, and one of unknown age; Table 3.1) were fitted with light-level geolocators. Forty individuals were fitted with "ML6740" geolocators (~0.51g, 5 mm light-stalk positioned at a 45° fixed angle; British Antarctic Survey), ten with "FL6B57" geolocators (~0.40 g, 5 mm light-stalk; Biotrack) and ten with "FL6057" geolocators (~0.37 g, no light-stalk; Biotrack). Geolocators were attached to the bird's back using an elastic leg-loop harness as described by Rappole & Tipton (1991). Harnesses were attached to the geolocators before fieldwork. It took approximately three minutes to fit a device on a bird. On average, devices weighed 0.5 g (including harness), corresponding to ~3.7% of birds body mass (Table 3.1), lower than the suggested 5% body-mass rule (Kenward, 2001). To estimate the effects these tags had on birds, 60 individuals were captured, handled and colour-ringed during the same period but were not fitted with geolocators (Table 3.1).

Table 3.1. Geolocator data. Mean weight and SE of each geolocator model with and without harness, and the number of control birds and individuals fitted with each geolocator model according to age and sex (F = female, M = male, U = unknown). The numbers in parenthesis indicate the number of individuals that were recovered and/or seen the following year. Photographs below show the different geolocator models fitted on individuals using an elastic leg-loop harness following Rappole and Tipton (1991).

Model	**Weight without harness (g)**	**Weight with harness (g)**	**% of body weight**	**Adult**			**First-year**			**Unk age**	**Total**
				F	M	U	F	M	U		
ML6740	0.51 ± 0.03	0.57 ± 0.03	4.0 ± 0.6	13	10	0	0	3	13	1	40 (6)
FL6B57	0.40 ± 0.01	0.45 ± 0.02	3.2 ± 0.3	1	6	0	0	0	3	0	10 (1)
FL6057	0.37 ± 0.01	0.43 ± 0.01	3.1 ± 0.4	3	1	1	1	3	1	0	10 (0)
	Geolocated birds			**17** (4)	**17** (3)	**1** (0)	**1** (0)	**6** (0)	**17** (0)	**1** (0)	**60** (7)
	Control birds			**8** (1)	**15** (3)	**6** (1)	**1** (1)	**4** (0)	**23** (3)	**3** (0)	**60** (9)

3.4.2 Recovery

Individuals were sought out the following non-breeding season (November 2019–March 2020). When identified, individuals were captured, geolocators were removed by cutting the harness and birds were released unharmed. Seven geolocators were recovered (six "ML6740" and one "FL6B57"). Data were obtained from six "ML6740" devices; five with complete annual-cycle information (three females, two males) and one with partial information corresponding to spring migration (a female whose battery ran out on 10 June 2019, after arriving at its breeding ground). No data could be obtained from the "FL6B57". All individuals were adults when geolocators were deployed. Of the 60 colour-ringed control birds, nine were seen the following season (five adults and four first-years). Chi-square tests (χ^2) were used to compare return rates between control and geolocated birds and between birds with different geolocator models.

3.4.3 Data analyses

Geolocator data

Raw geolocator data were analysed using the "BASTrak" software. Light-level data were linearly corrected for clock drift using "Decompressor". The program "TransEdit2" was used to obtain daily sunrises and sunsets using a single light threshold value of two. To eliminate false twilights due to vegetation or weather shading, the "minimum dark period" filter was used. Data were then visually inspected to ensure that only two positions were obtained each day. Every detected sunrise and sunset was scored as follows: 9 if position seemed correct, 7 if it was ±15 days from the equinoxes (20 March and 23 September), 5 if the value seemed to be very different from previous/latter values and 0 when the value was considered wrong. When positions scored 5 or 0, new values were obtained by averaging the sunrise/sunset of the day before and after.

Further analyses were analysed using R version 3.6.3 (R Core Team, 2020). Sunrise and sunset data were filtered with the "*loessFilter*" function from the "*GeoLight*" package (version 2.0.0), which validates twilights and identifies possible shading events (caused by topography, weather, vegetation, behaviour, etc.), and thus are considered erroneous (by identifying outliers that were greater than three times the interquartile range; Lisovski & Hahn, 2012). We visually inspected results and manually eliminated those false coordinates that were 20 min different from prior and latter values during stationary periods. This step removed 0–7.4% of locations (mean = 2.5%).

The sun-elevation angle (SEA) was obtained from the known non-breeding location over the period we were certain the bird remained at the site, except for individual 094, where we used a two-week period after deployment for calibration (resightings were carried out throughout the season), using the "*getElevation*" function. All SEAs were between -3.5 and -4.2; (median and mean = -3.85). Because it is impossible to know the conditions outside of the non-breeding grounds, six sets of SEAs were used to estimate latitudes in these locations: (1) the exact SEA provided by the "*getElevation*" function, (2) SEA = -2, (3) SEA = -3, (4) SEA = -4 (median and mean SEA from all five individuals), and (5) SEA = -5. We used the individual SEA that best located our known non-breeding site (APLORI), which varied according to each individual (ranging from -3 to -4.2) and these SEA values were used throughout the annual cycle. Note that breeding sites were similar when using all five possible SEA values.

Stationary and migratory periods were determined with the "*changeLight*" function, setting the minimal stopover period to three days and the quantile probability threshold to 0.95 (Lisovski & Hahn, 2012). We then used the "*mergeSites*" function to combine consecutive sites separated by 150 km, which are likely to be at the same site but that the function separates due to errors in the twilight times. All twilight values were converted to geographic coordinates using the "*coord*" function.

Latitude is derived from the length of the day, and longitude from the absolute time of local noon and midnight on a given date. Latitude is difficult to estimate around the equinox periods, when the difference in day and night length is minimal, so they should be taken with caution around a period of 14 days before and after the equinoxes. Data from these days were therefore excluded from further analyses. Given that birds are still at the non-breeding grounds during the spring equinox, this only affected results from the autumn migration. We used the most direct route when connecting points, which could lead to an underestimation of the distance travelled. We averaged the latitude and longitude for each identified stationary period (stopover sites as well as breeding and non-breeding grounds) and calculated the duration as the length of time (in days) birds remained at them.

Each individual's data were run with different SEAs, and "*mergeSites*" settings (with 50, 100, and 200 km). Data were also compared with visual inspection of changes in twilight times, latitude and longitude. We believe that the set of parameters we finally selected reasonably describes the migratory routes of our species but varying these parameters does not greatly change the biological or statistical significance of the results. As very few devices were retrieved, due to low statistical power, we cannot make any inferences regarding sex differences.

Breeding grounds

General linear models (GLMs) were performed to explore whether the distance between APLORI and the breeding grounds was dependent on the number of stopovers, duration of spring migration, departure date, and the mean duration of stopovers.

Stopovers

GLMs were performed to compare the duration of first stopovers with other stopovers and with the duration of stopovers according to their geographic location. For the latter, geographic locations were divided as follows: In spring, (1) "pre-Sahara/Sahel", which corresponded to stopovers occurring close to the non-breeding grounds, prior to the Sahara Desert, (2) pre-Mediterranean, stopovers located in northern Africa, and (3) Europe, stopovers in Europe prior to arriving at the breeding grounds. In autumn, (1) Europe, stopovers in Europe after the breeding period, (2) pre-Mediterranean, stopovers in southern Europe, prior to crossing the Mediterranean Sea), and (3) post-Mediterranean, stopovers in North Africa. GLMs were also performed to understand the relation between the number of stopovers and departure dates.

Differences between spring and autumn migration

Paired *t*-tests were carried out to explore whether stationary days, total days of flying, distance travelled (km), longest stationary period (days) and the number of stopovers varied between spring and autumn migration. GLMs were also used to compare arrival and departure dates with the duration of both migrations and the correlation between arrival and departure dates.

Additionally, a Generalised Linear Mixed Model with individuals as a random effect was performed to analyse whether the total duration of migration, as well as the start date of migrations, was different between spring and autumn migration (total migration duration ~ start date + season + (1|individual)) using the "*lmer*" function of the R package "*lme4*" (Bates et al., 2015). The final model did not consider an interaction as it was not significant.

Non-breeding grounds

GLMs were used to test whether the time spent at the first non-breeding grounds was dependent on the departure date from the breeding grounds, the distance between both sites, and autumn migration duration. GLMs were also used to determine the relationship between environmental factors (*i.e*. mean NDVI and mean rainfall at first non-breeding grounds during October and November 2019) with the duration spent at the first non-breeding grounds, and with departure dates from them.

3.5 Results

3.5.1 Geolocated vs controls

Return rates were similar between all geolocated individuals and controls (geolocated *n* = 7/60, 11.7%; controls *n* = 9/60, 15%; χ^2 = 0.3, df = 1, *p* = .60) and between geolocated and control adult birds (geolocated *n* = 7/35, 20%; controls *n* = 5/29, 17.2%; χ^2 = 0.08, df = 1, *p* = .78). Although we did not detect any first-year geolocated bird the following year, there was no statistical difference between return rates of geolocated and control first-year individuals (geolocated *n* = 0/24, 0%; controls *n* = 4/29, 13.8%; Fisher's Exact Test *p* = .12). Birds that carried geolocators model "ML" seemed to have higher return rates (*n* = 6/40, 15%) than those carrying "FL" geolocators (*n* = 1/20, 5%), but this difference was not statistically significant (Fisher's Exact Test *p* = .41) and could be because they were fitted on late-season birds (mid/end March), most likely birds on passage with lower probabilities of being seen or captured the following season. The mean weight of recovered geolocated birds was similar to controls captured during the same period (geolocated = 14.05 g, controls = 14.4 g; two sample *t*-test: *t* = 0.8, df = 9.5, *p* = .43).

3.5.2 Breeding grounds

Individuals arrived at their breeding grounds between 7 May and 25 May (Appendix 3.1). These sites were located across eastern Europe, between Slovakia and eastern Russia (between 48°–58°N and 18°–33°E; Fig. 3.1). Breeding grounds were, on average, 729 km from each other, covering an area of 425,300 km^2 (~4.2% of the total area of Europe) where they remained for, on average, 81 days (range = 53–116 days). The mean minimum distance between breeding grounds and first non-breeding grounds was 4,300 km (range = 3,978–4,939 km; Fig. 3.1), while the mean minimum distance between breeding grounds and APLORI was 5,151 km (range = 4,377–5,713 km).

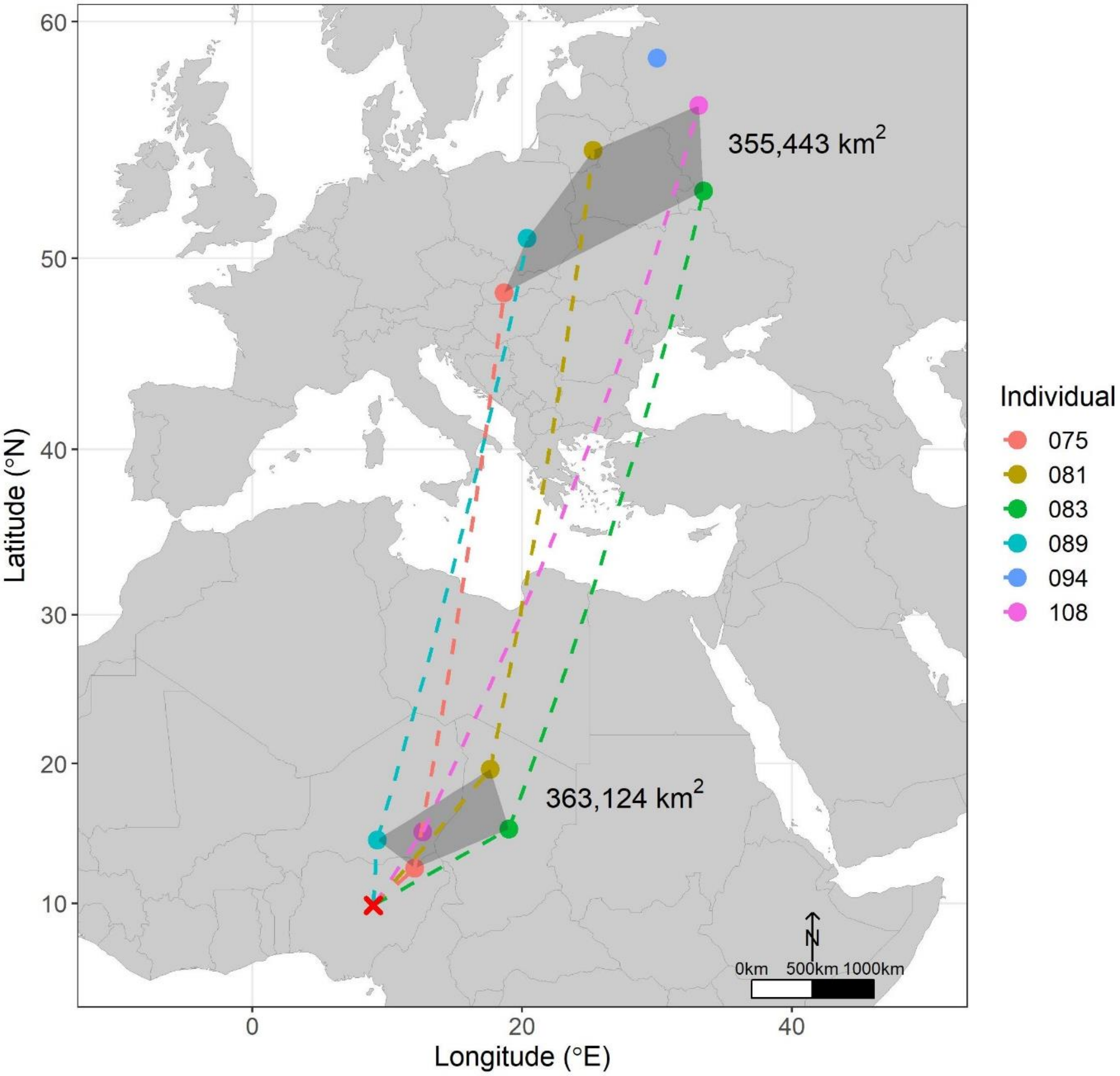


Figure 3.1. Area utilised during the breeding season and at first non-breeding grounds. Each colour is a different individual. Grey convex polygons represent the connection of outer locations. Lines connect breeding sites with respective first non-breeding sites and first non-breeding sites with APLORI (represented with a red cross). Because there was no data regarding the first non-breeding site of individual 094, this individual was excluded from both area estimates.

Statistical power is naturally limited in all cases but the distance travelled between APLORI and the breeding grounds during spring (km flown by each individual) did not correlate with the number of stopovers ($F_{(1,4)} = 0.6$, $p = 0.50$), duration of spring migration ($F_{(1,4)} = 0.04$, $p = 0.85$), departure date from APLORI ($F_{(1,4)} = 0.7$, $p = 0.45$) or mean duration of stopovers ($F_{(1,4)} = 0.3$, $p = 0.61$). Similar results were obtained during autumn migration when comparing the distance between the breeding grounds and the first non-breeding grounds with the number of stopovers ($F_{(1,3)} = 2.8$, $p = 0.19$), duration of autumn migration ($F_{(1,3)} = 1.4$, $p = 0.32$), departure dates from breeding grounds ($F_{(1,3)} = 2.3$, $p = 0.23$) or mean duration of stopovers ($F_{(1,3)} = 0.3$, $p = 0.87$).

3.5.3 Stopovers

The number of stopovers was similar during both migrations (mean spring: 2.8; mean autumn: 2.6; Table 3.2, Appendix 3.1). In spring, the duration of the first stopover was significantly longer compared to the following stopovers (paired *t*-test: $t = 5$, df = 4, $p = 0.008$). Similar results were obtained in autumn (paired *t*-test: $t = 2.8$, df = 3, $p = 0.07$). When comparing the duration of stopovers according to their geographic location in spring, birds showed longer stopover periods at the pre-Sahara/Sahel locations compared to sites in the pre-Mediterranean and Europe ($F_{(2,14)} = 7.0$, $p = 0.008$; Fig. 3.2). In autumn, however, the duration spent at stopovers did not vary according to geographic location ($F_{(2,10)} = 1.2$, $p = 0.35$; Fig. 3.2).

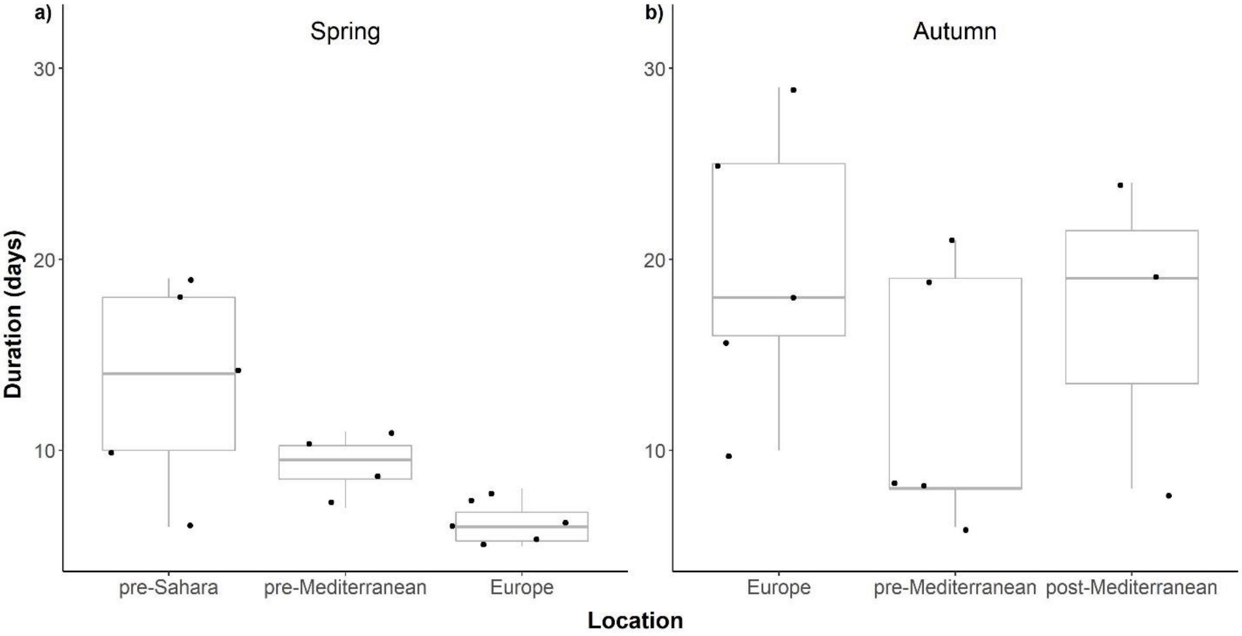


Figure 3.2. Days spent at stopovers located in different geographic locations during spring (a) and autumn (b) migrations.

Statistical power is again limited but the number of stopovers during autumn migration was strongly related to departure date from the breeding grounds ($F_{(1,3)} = 149.8$, $p = 0.001$; Fig. 3.3): individuals that departed earlier from breeding grounds had more stopovers than later-departing individuals. A similar trend was found during spring migration ($F_{(1,4)} = 4.5$, $p = 0.1$; Fig. 3.3), individuals that departed earlier had more stopovers, though this was not significant.

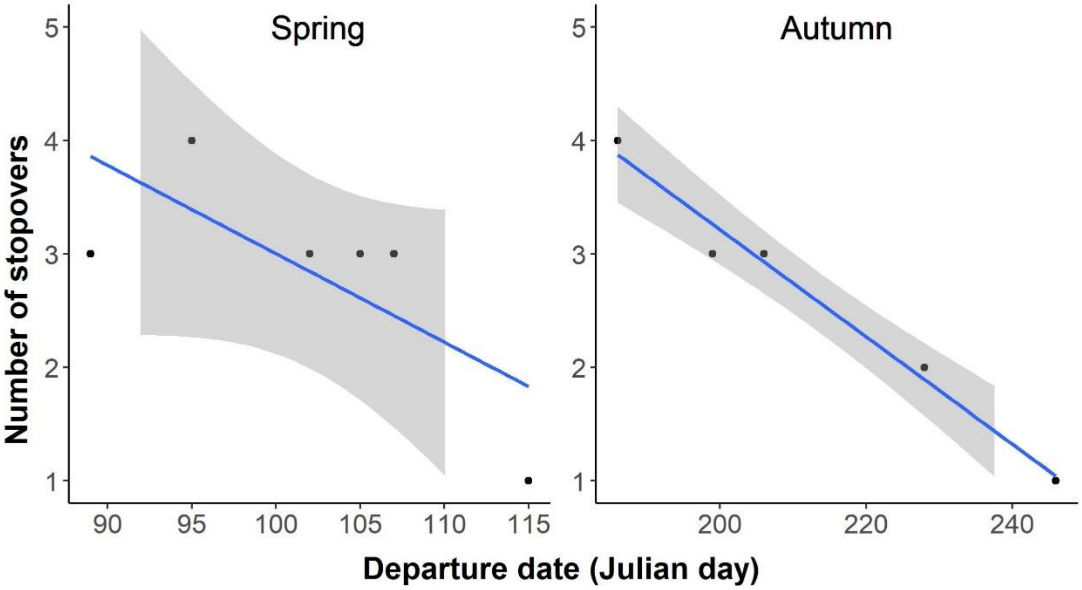


Figure 3.3. The number of stopovers in relation to spring and autumn departure dates. Julian day 1 = 1 January 2019.

3.5.4 Spring and autumn migration

Spring migration (*n* = 6)

Birds left Nigeria between 30 March and 25 April and spent, on average, 33 days (range = 12–51 days) migrating until they reached the breeding grounds (Fig. 3.4, Table 3.2, Appendices 3.1 and 3.2). Four out of six individuals flew northwardly to Algeria, Libya, or Tunisia and had a stopover site before crossing the Mediterranean Sea (Fig. 3.5). The remaining two flew in a north-easterly direction, where one stopped in Libya and another flew directly to Albania. All individuals had a stopover site at least once in southern Europe before reaching the final breeding site across eastern Europe (between Slovakia and Russia) in May (Fig. 3.5). The mean distance travelled during this period was 5,524 km (range = 4,446–6,132 km) at a mean rate of 785 km/day (range = 412–1,148 km/day). The mean number of stopover sites was 2.8 (range = 1–4 sites), where birds remained a mean of 9 days (range = 3–19 days). The mean longest staging period of each individual was 12.7 days (range = 5–19 days; Table 3.2, Appendix 3.1).

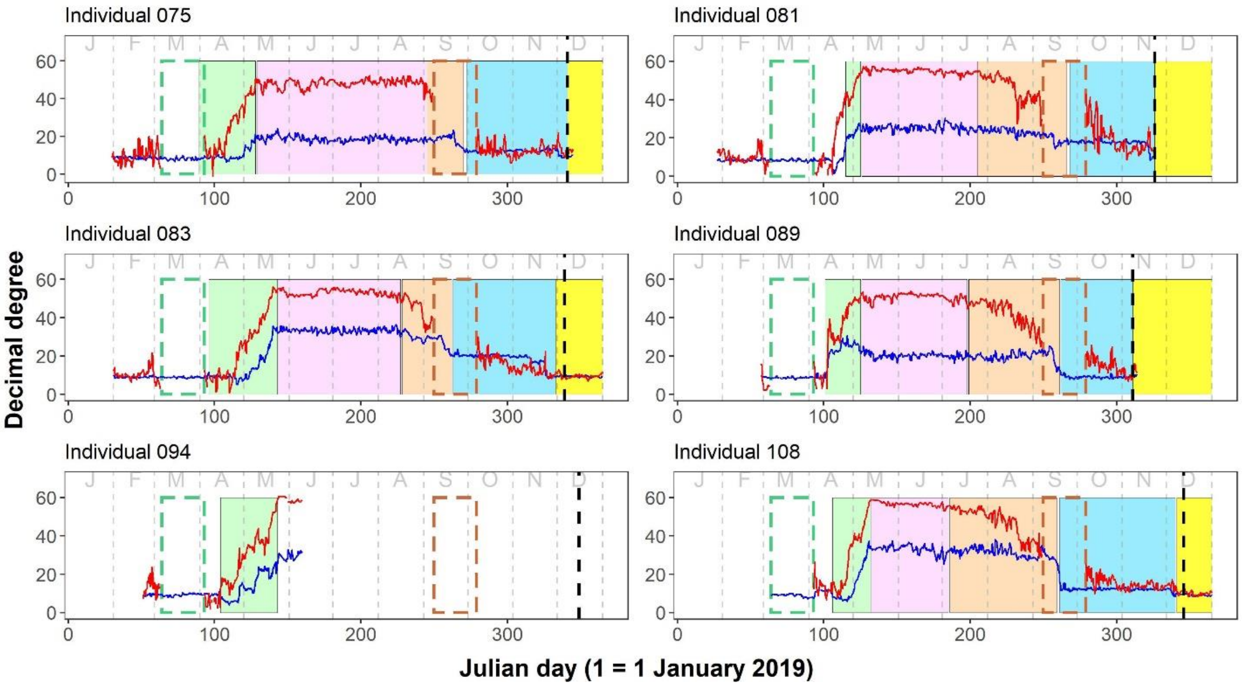


Figure 3.4. Migration phenology. Duration of spring migration (green square), breeding season (pink square) and autumn migration (orange square), and time spent at the first non-breeding site (blue square), and APLORI (yellow square; note that it ends on 31 December 2019 and does not reflect when individuals left the area). Annual latitudes (red line) and longitudes (blue line) of individuals. Hollow squares represent equinoxes ± 14 days (green = spring, orange = autumn). The black dotted line represents the day that the individual was first detected in APLORI.

Autumn migration (*n* = 5)

Individuals departed the breeding sites between 5 July and 3 September (Fig. 3.4, Table 3.2, Appendices 3.1 and 3.2). They took, on average, 53 days (range = 26–75 days) to reach the first non-breeding grounds in the Sahel region. Four individuals returned following a more easterly route than their spring migration. Of those individuals, two bred in Russia – the most easterly breeders – and returned via the Black Sea in a more pronounced south-westerly direction, stopping in Turkey before crossing the Mediterranean Sea (Fig. 3.5). The remaining two flew southwards and stopped before the Mediterranean Sea. The remaining individual, came back in an anticlockwise direction, returning via Greece (Fig. 3.5). Most individuals left the breeding grounds and stopped in a more southerly site for between 10 and 29 days (mean = 20.6 days). The mean distance travelled during this period was 4,415 km (range = 4,023–5,221 km) at a mean speed of 574 km/day (mean range = 212–873 km/day; Table 3.2, Appendix 3.1). The mean number of stopover sites was 2.6 (range = 1–4 sites), with individuals remaining a mean of 15 days (range = 6–29 days) at each. The mean longest staging period exhibited by each individual was 20.8 days (range = 10–29 days; Table 3.2, Appendix 3.1).

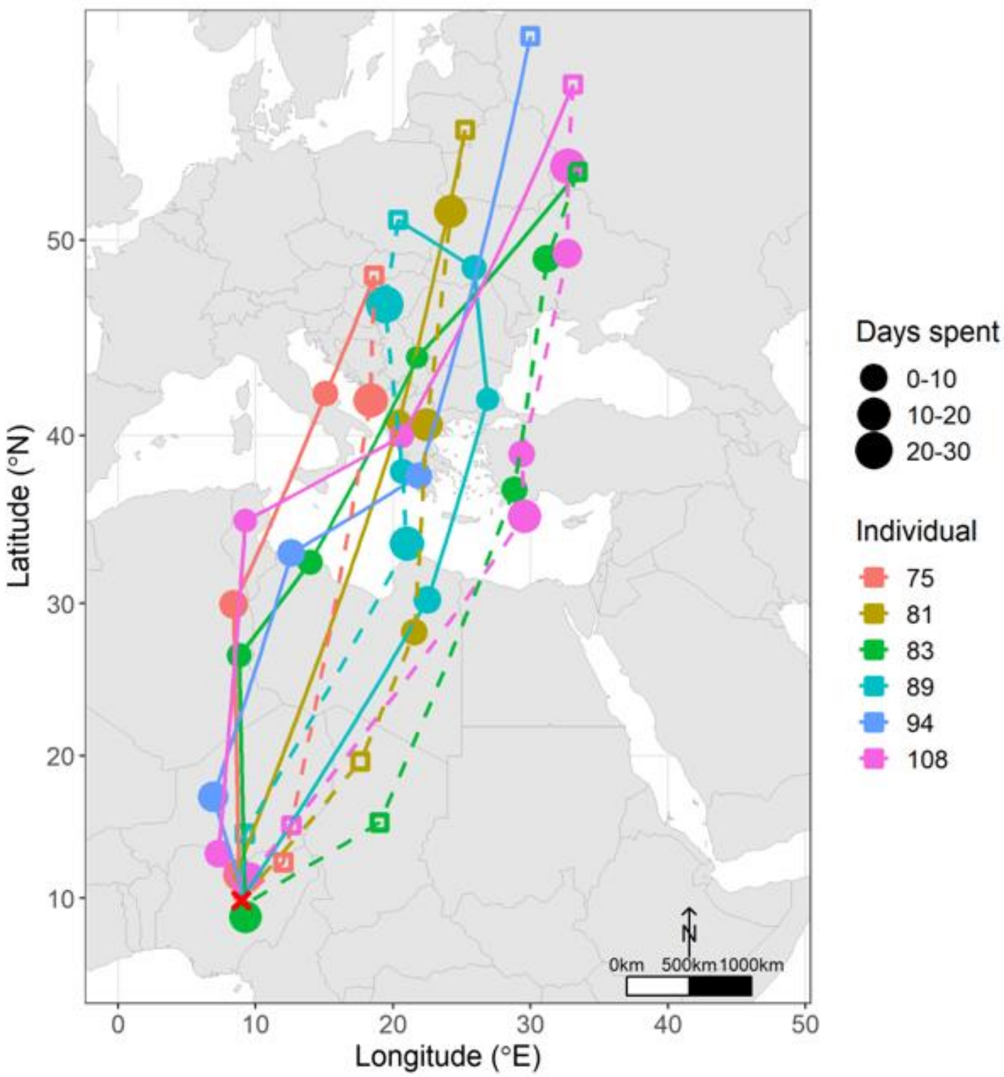


Figure 3.5. Migratory routes of Common Whitethroats wintering in Nigeria. Migratory routes of Whitethroats wintering in Nigeria. The size of the circle represents time spent at stopover sites. Different colours are different individuals. Lines represent the most direct route from one site to the next during spring (continuous line) and autumn (dashed line) migration. APLORI is represented by its logo. Squares represent breeding grounds (in Europe) and the first non-breeding grounds (in Africa).

Spring vs autumn migration

Paired *t*-tests showed no statistical differences in the mean number of stationary days, total days flying, longest staging period, or the number of stopover sites between spring and autumn migration (Table 3.2). However, distance travelled was significantly longer and speed was faster during spring migration (Table 3.2).

Table 3.2. Information regarding spring and autumn migrations. Results from paired *t*-tests. All data from individual 094 was excluded. * are statistically significant values *p*<0.5.

	Autumn		**Spring**		
	Mean	*SD*	*Mean*	*SD*	*Statistical results*
Stationary (days)	42.2	22.3	23.4	13.4	t = 1.3, df = 4, p = 0.27
Flying (days)	11	7.4	7.6	3.7	t = 1.4, df = 4, p = 0.22
Longest staging period (days)	20.8	7.2	12.4	5.9	t = 1.7, df = 4, p = 0.18
Distance (km)	4,415	487	5,524	619	t = -5.3, df = 4, p = 0.006*
Mean rate (km/day)	574	324	785	268	t = -2.9, df = 4, p = 0.04*
Number of stopovers	2.6	1.1	2.8	1	t = -0.3, df = 4, p = 0.82

Autumn migration was overall longer (in terms of time) than spring migration (Table 3.3). Similarly, there was a strong negative linear effect between departure of the breeding and main non-breeding grounds and duration of migration; birds that started migration earlier carried out longer migrations, especially during autumn (Table 3.3). Arrival dates did not correlate with departure dates in either spring (r = -0.2, t = -0.4, df = 4, p = 0.68) or autumn (r = 0.7, t = 1.9, df = 3, p = 0.15).

Table 3.3. Results from a Generalised Linear Mixed Model of migration duration. Formula: total migration duration ~ departure date + season + (1|individual).

Variable	**Estimate**	**Std. Error**	***t*-value**	***p*-value**
(Intercept)	125.7	15.4	8.2	<0.001
Start of migration	-0.9	0.2	-6.2	<0.001
Season (spring/autumn)	121.5	16.9	7.2	<0.001

3.5.5 Two non-breeding sites

All individuals (n = 5) had a first non-breeding site before arriving at APLORI. Individuals arrived at these sites between 18 and 29 September (Fig. 3.3, Appendices 3.1 and 3.2). Sites were located in the Sahel region, in Niger, Chad and northern Nigeria (between 12°–20°N and 9°–19°E; Figs. 3.1 and 3.4). These were, on average, 686 km from each other, covering an area of 363,100 km^2. Here birds remained, on average, for 65 days (range = 50–78 days). The mean direct distance between first non-breeding grounds and APLORI was 875 km (range = 450–1,431 km). When considering only the five birds for whom we have information regarding their full annual cycle, we found that the area utilised during this period was similar to the area covered during the breeding season (355,400 km^2; Fig. 3.1). All individuals potentially flew directly to APLORI, the last non-breeding site, between 7 November and 12 December and all remained there until, at least, 10 February (daily visual *in situ* observations were carried out throughout the season).

No obvious phenological or environmental change predictors of the duration spent at the first non-breeding site were found, but statistical power was very low (Table 3.4). No significant relation was found between departure date from the first non-breeding grounds and November mean precipitation ($F_{(1,3)}$ = 0.05, p = 0.84).

Table 3.4. Phenological and environmental predictors of duration at first non-breeding grounds. * = October and November mean precipitation of non-breeding grounds.

Variable	Estimate	Std. Error	*t*-value	*p*-value
Intercept	-17.70	36.80	-0.5	0.7
Duration autumn migration	-0.30	0.20	-1.2	0.4
Distance from breeding grounds	0.02	0.01	2.4	0.3
Mean precipitation*	-0.10	0.10	-1.3	0.4

3.6 Discussion

Here we describe, for the first time, the complete annual cycle of a small sample of Whitethroats. Our results show that individuals that spend the non-breeding period in central Nigeria breed across a large area of eastern Europe, indicating a somewhat high migratory spread. We found that during spring, individuals spend more time at stopovers located in the Sahel, before crossing the Sahara Desert. Individuals that commence migration earlier have a longer migration and, during autumn migration, have more stopovers. Spring migration does not differ significantly from autumn migration with respect to the number of staging days, flying days, longest staging period, and number of stopovers. In spring, however, though distances are longer, migration is undertaken faster. Birds also carry out a loop migration: four individuals exhibited a clockwise direction and one an anticlockwise direction. There is clear evidence to show that Whitethroats have a first non-breeding site in the Sahel region prior to arriving at APLORI, where they spent the remainder of the non-breeding period until the start of spring migration. We found no obvious phenological or environmental change predictors of the duration spent at the first non-breeding sites. The total area occupied during this period was similar to that occupied during the breeding season, *i.e*. a relatively high migratory spread between non-breeding sites. In this section, we will discuss: (1) the effects of geolocators on birds, (2) the degree of migratory spread of Whitethroats, (3) migratory strategies and how this compares with other Afro-Palearctic passerine species, (4) differences between spring and autumn migration, (4) movements and spatial use across the

African continent, and (5) what this new information can tell us regarding the status of the species and implications for its conservation.

It is important first to highlight that geolocator position data are associated with possible errors (Lisovski et al., 2012) and that, by implication, exact coordinates must be interpreted with caution. However, we expect that the degree of error is equal throughout individuals and seasons, thus making data comparable between birds and between spring and autumn migration (although the latter needs to be interpreted with more caution, as it coincides with the autumn equinox). We also consider that the level of geographic accuracy is enough for robust large-scale interpretations and to visualise general migratory patterns.

3.6.1 Effects of geolocators on birds

Geolocators have become an increasingly useful tool for the general study of migration and have great potential to address important conservation problems when we consider that the recent population declines of long-distance migrants are often associated with changes in routes and phenology (Both et al., 2006; Hewson et al., 2016). However, the impact that the tags have on individuals remains open to debate and appears inconsistent (Bridge et al., 2013; Costantini & Møller, 2013; Brlík et al., 2020), and the degree of these effects strongly depend on the study species, attachment methods and device weights. In this study, we found no clear differences in the return rates of geolocated and control adult birds. However, we did not recover or see any birds that were tagged in their first year of age. This could either be because of a direct effect from geolocators (although weight was similar between adult geolocated and first-year geolocated birds during deployment; first-years $n = 26$, mean = 26.8 g, SE = 3.1 and adults $n = 35$, mean = 24.1 g, SE = 2.5; $t = -0.7$, df = 52.6, $p = 0.5$), or due to lower site fidelity rates of first-year birds (Chapter 4).

Despite “FL” models being lighter than the “ML” models, we only recovered one “FL” device. This could be because we deployed them later in the season (mid/end March) and were most likely attached to passage birds, decreasing the probabilities of seeing or capturing them the following season. Except for a small patch of dry skin seen in the back of one individual, no visual harm was detected on birds while retrieving geolocators. Overall our evidence, although of limited statistical power, does not suggest that tagging had a strong negative effect on the survival of this species in this particular area and is consistent with results from other studies (Blackburn et al., 2016; van Wijk et al., 2016; Cooper et al., 2017; Xenophontos et al., 2017). Blackburn and collaborators (2016), for example, showed that geolocators that varied between 2.5 and 5.3% of Whinchats’ body mass did not affect apparent survival.

Effects, however, seem to be species-dependent and the use of geolocators should be treated with caution (Costantini & Møller, 2013; McKinnon & Love, 2018; Brlík et al., 2020).

3.6.2 Migratory spread

The location of Whitethroats' breeding grounds revealed by geolocators is in line with our prediction and with previous knowledge gained through years of ring recoveries: Nigerian individuals fly in a north-easterly/south-westerly direction during migration, and breed in a large area throughout central, northern, and eastern Europe (Waldenström & Ottosson, 2002; Zwarts et al., 2009; Escandell & García, 2011). These results are also consistent with "EURING's" long-term ringing database (Fig. 3.6) and with the recapture of a Nigerian-ringed individual in Poland in 2000[1].

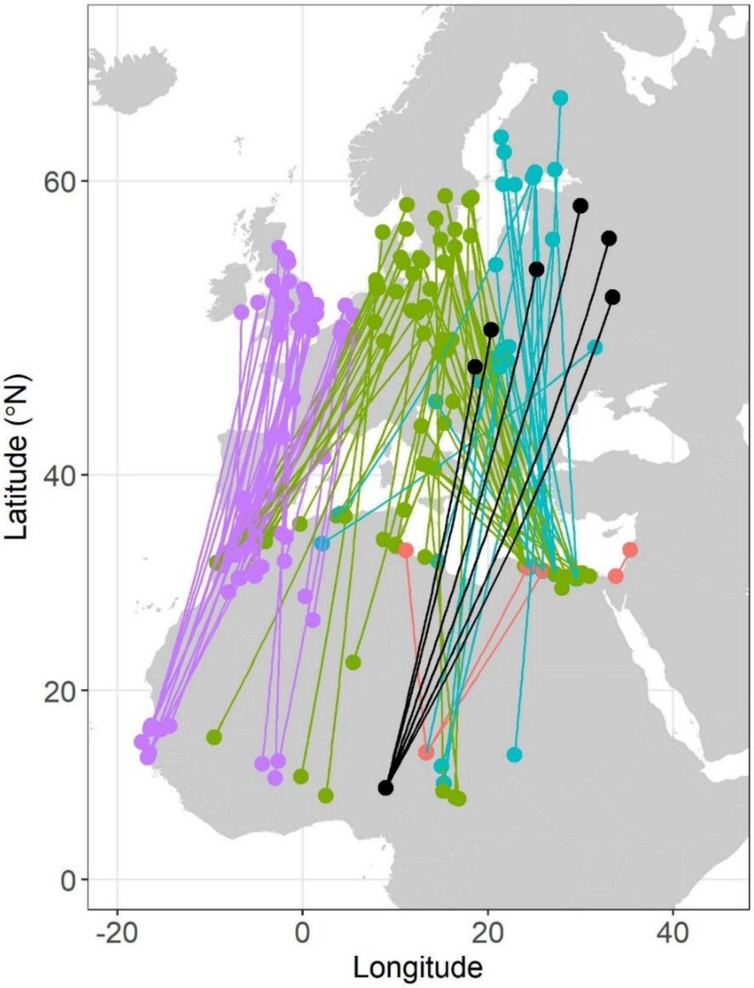


Figure 3.6. Map showing 131 Common Whitethroats detected in both Europe and Africa. Most data have been collected through "EURING". Dots represent sites where individuals were ringed and/or recaptured. Colours

---

[1] Information obtained from Dr. Magdalena Remisiewicz, University of Gdańsk, Poland.

were arbitrarily set to represent the location where birds were ringed: eastern Europe (purple), central Europe (green), western Europe (blue), and Africa (red). Black dots and lines represent data collected through this study. All North-African locations are highly likely to be stopover sites and should not represent important stationary non-breeding locations.

These results show a high degree of migratory spread consistent with the general pattern from other studies, where individuals from different breeding populations tend to mix during the non-breeding season (Finch et al., 2017). Individuals from a small three km^2 main non-breeding site bred between Slovakia and Russia and occupied a first non-breeding site between Nigeria and Chad, in a roughly similarly sized area (~360,000 km^2). The degree of migratory spread has important effects on the ecology and conservation of migratory birds and will affect a species' response to changing environmental pressures (Webster et al., 2002). On one hand, a population that relies on few non-breeding sites (low spread) is expected to have stronger local adaptations (*e.g*. food, predators, climate) and a higher vulnerability if there were to be any changes at those particular sites (Gilroy et al., 2016). On the other hand, populations showing a high spread should have generalist-associated traits and greater potential to track shifting habitats and be more resilient to these changes (Webster et al., 2002; Cresswell, 2014; Finch et al., 2017). However, high spread implies high inter-population mixing at the non-breeding grounds, so changes occurring there would have "small" effects on many breeding populations (Finch et al., 2017). Many Afro-Palearctic migrants have shown different degrees of migratory spread, ranging from extremely high spread (*e.g*. Eurasian Hoopoe, Bächler et al., 2010; Common Redstart *Phoenicurus phoenicurus*, Kristensen et al., 2013; Great Reed Warbler *Acrocephalus arundinaceus*, Lemke et al., 2013; Barn Swallow *Hirundo rustica*, Liechti et al., 2015; Whinchat, Blackburn et al., 2017; Burgess et al., 2020; Willow Warbler, Lerche-Jørgensen et al., 2017), to moderate spread (*e.g*. Turtle Dove *Streptopelia turtur*, Eraud et al., 2013; Reed Warbler, Koleček et al., 2016; Cyprus Wheatear *Oenanthe cypriaca*, Xenophontos et al., 2017), and low spread (*e.g*. Northern Wheatear *Oenanthe oenanthe*, Schmaljohann et al., 2012; Common Nightingale, Hahn et al., 2013; Pied Flycatcher *Ficedula hypoleuca*, Ouwehand et al., 2016).

We believe that Whitethroats have a somewhat moderate migratory spread defined by a north-eastern flight pattern, so changes in the central sub-Saharan African non-breeding grounds will have a severe effect on a subset of individuals from specific European breeding populations (*e.g*. Polish, Belarussian, Lithuanian, western Russian), but due to the large distribution of Whitethroats, the most western and eastern populations may not be as severely affected (Koleček et al., 2016).

3.6.3 Migratory strategy and seasonal migration differences

Migratory strategy

Whitethroats have been suggested, on the one hand, to fly from one stopover to the next, accumulating just the necessary fat in order to do so (Ellegren & Fransson, 1992; Schaub & Jenni, 2000; Escandell & García, 2011; Jenni-Eiermann et al., 2011), and on the other, to be able to fly across the Sahara Desert and Mediterranean Sea without the need to refuel (Ottosson et al., 2001). Here we found that birds have few stopovers prior to arriving at the breeding/non-breeding grounds. Except for one individual that probably crossed the Sahara and the Mediterranean Sea in a single non-stop flight (in the sense that it had no stopovers of greater than three days), all individuals stopped in North Africa, after the Sahara crossing, during spring migration. The exceptional bird happened to be the last individual to leave the non-breeding site (bird 081 left APLORI on 25 April), thus it was a late, faster travelling bird under more time constraints than earlier departing individuals. During the autumn equinox, there is much more uncertainty regarding barrier crossing due to the difficulties of tracking during the equinox, but evidence suggests that Whitethroats fly to a first non-breeding site, several hundred kilometres further north than the main non-breeding site at APLORI, and it seems possible that they carried out a single non-stop flight from Europe without any major stopovers to get there. This is not surprising as, during the end of summer, resources are likely to still be available throughout the route and long stopovers may not be necessary.

Our results suggest that while Whitethroats are able to carry out both strategies, they prefer to undertake an intermittent flight to restore their body condition prior to and after crossing a major barrier (Eraud et al., 2013). In extreme situations where they are strongly constrained by time, however, they can cross both the Sahara Desert and Mediterranean Sea in a single flight, as proposed by Ottosson et al., 2001, and as carried out by a high proportion of Whinchats also tracked from APLORI (Blackburn et al., 2019). It is important to state that, when analysing geolocator data, we defined a stopover as a site where birds spent at least three days. The latter, together with geolocator limitations (low resolution of the locations in time and latitude inaccuracy; Lisovski et al., 2012), does not allow us to fully understand small-scale spatiotemporal movements. Prolonged stopovers have been linked to strategic stops along routes in areas with abundant food resources (Jones, 1995; Stach et al., 2012). We found that individuals left the non-breeding territories to fatten up in a site further north, in the Sahel close to the southern limit of the Sahara Desert, prior to crossing the desert. Individuals were observed remaining there longer than the subsequent spring stopovers. This region, therefore, represents an important site during spring migration and could be due to the presence and availability of *Salvadora* *persica* berries, which are an important resource for pre-migratory fattening for the species (Moreau, 1972; Stoate & Moreby, 1995; Wilson & Cresswell, 2006).

Spring *vs* autumn migration

Total migration duration among birds depends strongly on environmental conditions and fuel deposition rates (Alerstam et al., 2003), and selection pressures differ according to seasonality (Newton, 2008). Many studies have found important seasonal differences between migration characteristics. We did not find any strong differences between spring and autumn migration regarding number of stationary days, number of days spent flying, longest staging period and number of stopovers, but found that the total duration of spring migration, despite it being shorter than autumn migration, was much faster, lasting 12 to 51 days, while autumn migration took between 26 and 75 days. These results support the optimal migration theory: the timing of migration is more critical in spring than in autumn. Birds exhibit overall quicker migrations during spring (Tøttrup et al., 2012) in order to ensure timely arrival at the breeding grounds to occupy and establish better territories and to find higher-quality mates (Drent et al., 2003; Yohannes et al., 2009), while arriving later at the non-breeding grounds has fewer fitness consequences (McNamara et al., 1998).

We suspect that departure dates are also of key importance for survival. Individuals departing earlier had more stopovers and longer migrations in both spring and autumn. Individuals need to balance and plan arrival dates in such a manner that they do not arrive *too* early, when weather is unfavourable and peak resource availability is yet to occur, but must still attempt to arrive earlier than others – especially when arriving at the breeding grounds (Kokko, 1999; Drent et al., 2003)

3.6.4 Loop migration

The use of different migratory routes during autumn and spring migration is a common strategy for several Afro-Palearctic migrants. Loop migration patterns (clockwise when birds take a more easterly route in autumn, anticlockwise when reversed) likely emerge from a combination of adaptations to dominant wind systems, ecological barriers, spatiotemporal distribution of resources and suitable habitats and historical aspects of the species' distribution (Briedis et al., 2018). Loop migrations reduce overall migration duration, mitigate the risk of running out of fuel and increase migration speed, despite increasing distance travelled overall. In Mauritania, a higher number of Whitethroats were trapped during spring than autumn, suggesting a different migratory route between seasons (Herremans, 2003), and supporting our findings.

The direction of the loop seems to vary substantially according to the location, population and species and might be related to a combination of wind direction and food availability (Alerstam, 1990; Pearson & Lack, 1992; Tøttrup et al., 2012; Lemke et al., 2013; Koleček et al., 2016). A few species exhibit a clockwise direction (*e.g*. Turtle Doves, Eraud et al., 2013, Common Cuckoo *Cuculus canorus*, Willemoes et al., 2014), but most seem to show an anticlockwise direction (*e.g*. Red-Backed Shrike *Lanius collurio*, Tøttrup et al., 2012; Willow Warblers, Lerche-Jørgensen et al., 2017; Barn Swallows, Briedis et al., 2018; Whinchats, Burgess et al., 2020) or both (*e.g*. Northern Wheatears, Schmaljohann et al., 2012, Great Reed Warblers, Horns et al., 2016; Koleček et al., 2016).

In this study, we found intraspecific variation, as four of our tracked individuals showed a clockwise loop migration and one in an anticlockwise direction. The odd one out did not show any obvious difference in its breeding location. Schmaljohann et al. (2012) also found differences in the direction of loop migration in Northern Wheatears that spend the non-breeding season in central and western Africa. If winds were the strongest predictor in the direction of the loop, we would expect all individuals or similar species that are in roughly the same areas to have the same loop direction. Our results suggest that there are other selective pressures determining loop direction, but larger sample sizes are needed to test this.

3.6.5 Migration rate

Whitethroats covered >4,000 km, and actively migrated for a mean of 9.3 days (± 5.2 SD), leading to an estimated mean migration rate of 690 km/day (± 277 SD; distance/flying duration), considerably higher than reports from other Whitethroats (<250 km/day; Fransson, 1995; Yohannes et al., 2009). Assuming birds fly continuously through the day and night, the mean minimum flight speed is 29 km/h. Because of low geolocator resolution, this method does not allow the detection of short stops (<three days), so we expect this speed to be an underestimation of real mean flight speed. Typical flight speeds of migrating passerines the size of Whitethroats has been measured in the field as a mean of 45 km/h, potentially much higher with wind assistance (Bruderer & Boldt, 2001; Xenophontos et al., 2017). Whitethroats could therefore fly just overnight and rest and/or refuel during much of the day.

3.6.6 Intra-African space use

There is a continuum of residency and some ambiguity as to when a long stopover site becomes a stationary period. Commonly, long stationary periods are defined as locations where individuals spend more time than is needed for refuelling. The use of multiple non-breeding sites could be part of a strategy in which birds temporarily suspend migration in order to optimise resource use during the non-breeding season, based on the availability of predictable food sources in the region (Arlt et al., 2015), and is strongly related to environmental conditions (Jones, 1995; Heckscher et al., 2011; Stach et al., 2016).

All five individuals tracked throughout their complete annual cycle utilised a first non-breeding site prior to arriving at APLORI, where they remained for approximately two months (between September and November). One individual even spent more time at the first non-breeding site than at the main breeding site in Europe. These sites were ~900 km from APLORI. Due to the presence of Whitethroats throughout the complete non-breeding season at APLORI (between September and April; Chapter 4), we were not expecting birds to have such an important first non-breeding site. This suggests that APLORI may be an important non-breeding ground for Whitethroats, acting as a second site for some birds, and a first site for others (Chapter 4).

The use of several non-breeding sites seems to be common for long-distance migrants. Many other species have been found to have up to two (Red-backed Shrike, Tøttrup et al., 2012; Common Rosefinch *Carpodacus erythrinus*, Stach et al., 2016; Whinchat, Burgess et al., 2020), three (Thrush Nightingale, Stach et al., 2012; Great Reed Warbler, Lemke et al., 2013; Reed Warbler, Koleček et al., 2016), and even four non-breeding sites (Purple Martin, Fraser et al., 2012). Whitethroats arrive at the Sahel savannah in central-eastern Africa at the end of the summer rains. During this period, habitats are green and productive and insect abundance is high, representing favourable foraging conditions (Stach et al., 2012; Tøttrup et al., 2012). As time passes, habitats dry and conditions become harsh (Moreau, 1972; Ottosson et al., 2005) causing birds to move to their main non-breeding grounds between November and December — in this case, central Nigeria — where rainfall ends later and conditions are sufficient to allow individuals to survive the season.

Seasonal rainfall patterns are the main driving force for the distribution and movement of migratory birds (Pearson & Lack, 1992). In South America, Veeries *Catharus fuscescens* are thought to relocate from one non-breeding site to another due to predictable seasonal flooding, so they select lowland forests as an initial non-breeding site and relocate to higher elevations or unflooded regions as the rainy season progresses (Heckscher et al., 2011). APLORI may provide a more secure environment for Whitethroats to spend the harshest non-breeding periods, as they remain there for over four months. Whinchats — another common Afro-Palearctic migrant in APLORI — tagged in the UK also had second non-breeding sites located 400 km to the west of the first (Burgess et al., 2020). Interestingly, the mean October and November precipitation at first non-breeding sites did not have a strong effect on individuals' departure date or the duration spent at them. We expected birds that departed the non-breeding sites earlier and that remained for a shorter period to have experienced lower precipitation values. However, an increase in sample size, and data from longer temporal scales, could help us better understand environmental predictors and how they shape the intra-African movement of long-distance migrants.

3.6.7 Migration differences according to sex and age

Different age- and sex-specific migratory strategies are linked to differential migration risks and energetic costs (Newton, 2008; McKinnon et al., 2013). First-years migrate later (Blackburn et al., 2019) and slower (McKinnon et al., 2014), due to their inexperience. In some species, there is sexual segregation at the non-breeding grounds and in migration timing (Röseler et al., 2017) as a result of the different roles and selection pressures experienced during the breeding season (McNamara et al., 1998; Newton, 2008).

For Whitethroats, Ottosson et al. (2002) observed that second-year individuals recorded in north-eastern Nigeria in spring passed 14 days later than adults, and of these two-year birds, males passed 23 days earlier than females. Adults arrived significantly earlier than first-years, despite leaving the breeding areas approximately three weeks after the latter (Ottosson et al., 2002). It is suggested that males cross the West Mediterranean Sea earlier than females, and adults slightly earlier than second-year birds (Escandell & García, 2011). Unfortunately, we cannot test these hypotheses because no geolocators were recovered from second-year birds. With such a small sample size, sexual differences also cannot be investigated. Anecdotally, however, one of the males undertook an anticlockwise loop migration and both males spent less time at the breeding grounds. Both males also showed a longer migration in autumn than in spring, which is not surprising as males tend to arrive earlier at the breeding grounds to establish and secure territories within higher quality habitats.

3.6.8 Conservation implications

The future of a species depends not only on its ability to adapt but on efficient conservation strategies at both the breeding and non-breeding grounds that will buffer the impact of future climatic and anthropogenic changes (Doswald et al., 2009; Lerche-Jørgensen et al., 2019). We identified the Sahel region as an important refuelling site during spring migration and as a first non-breeding site. Its conservation is crucial for the species (Vickery et al., 1999) and is regulated by rainfall patterns (Ockendon et al., 2014). A population crash observed in the 1960s showed how susceptible the species can be to major climate changes in the region (Winstanley et al., 1974), but also demonstrated the species' ability to recuperate and adapt (Ottosson et al., 2002). Their potential generalist traits, their use of a wide variety of resources throughout the year and their flexibility to use different migratory strategies might make this species resilient to certain changes. However, the effect these changes will have on the species will greatly depend on the degree of change and at what spatial scale changes occur.

Based on migration tracks, the mean annual Whitethroat time allocations for non-breeding sites, spring migration, breeding, and autumn migration are 55%, 9%, 22% and 14%, respectively. Africa, where individuals spend <65% of the year, is a region of rapid social and economic change that will have a strong impact on their resources and natural habitats. Strong land-use changes at these sites will have a diffuse impact on many Whitethroat breeding populations, so for alarming impacts to occur at a species level, these changes would need to occur at a very large scale. If this ensues, protection efforts will need to include larger geographic areas and consequently, greater logistic challenges would arise (Webster & Marra, 2005). Further full annual cycle studies of Afro-Palearctic migrants will help identify where species are more susceptible, so that conservation efforts can be directed accordingly (Ådahl et al., 2006; Holmes, 2007; Martin et al., 2007; Klaassen et al., 2014; Marra et al., 2015; Sergio et al., 2019), either by protecting one large area or focusing on several small ones.

3.7 Appendices

Appendix 3.1. Migration details.

Table A.3.1.1. Start date, end date, duration of stopovers, number of days flying, duration of migration, number of stopovers, distance travelled, and flight speed during spring and autumn migration.

Individual	**Start date**		**End date**		**Stopover (days)**		**Flying (days)**		**Duration (days)**		**Stopovers (number)**		**Distance (km)**		**Speed (km/day)**	
	Spring	*Autumn*	*Spring*	*Autumn*	*Spring*	*Autumn*	*Spring*	*Autumn*	*Spring*	*Autumn*	*Spring*	*Autumn*	*Spring*	*Autumn*	*Spring*	*Autumn*
75	30-Mar-19	3-Sep-19	10-May-19	29-Sep-19	36	21	5	5	41	26	3	1	4464	4039	893	808
81	25-Apr-19	25-Jul-19	7-May-19	25-Sep-19	5	45	7	19	6	64	1	3	5119	4023	731	212
83	6-Apr-19	16-Aug-19	24-May-19	20-Sep-19	37	18	14	19	51	37	4	2	5772	4427	412	233
89	12-Apr-19	18-Jul-19	7-May-19	19-Sep-19	20	59	5	5	25	64	3	3	5739	4365	1148	873
94	15-Apr-19	NA	25-May-19	NA	31	NA	9	NA	40	NA	3	NA	6132	NA	681	NA
108	17-Apr-19	5-Jul-19	13-May-19	18-Sep-19	19	68	7	7	26	75	3	4	5915	5221	845	746
Average	**12-Apr-19**	**1-Aug-19**	**14-May-19**	**22-Sep-19**	**25**	**42**	**8**	**11**	**32**	**53**	**2.8**	**2.6**	**5524**	**4415**	**785**	**574**

Table A.3.1.2. Start date, end date, and duration of breeding season.

Individual	**Start date**	**End date**	**Duration (days)**
75	10-May-19	03-Sep-19	116
81	07-May-19	25-Jul-19	79
83	24-May-19	16-Aug-19	85
89	07-May-19	18-Jul-19	72
94	25-May-19	NA	NA
108	13-May-19	05-Jul-19	53
Mean	**14-May-19**	**01-Aug-19**	**81**

Table A.3.1.3. Start date, end date, duration of the stationary period, flight duration, total duration, distance travelled, and flight speed during the first wintering site, and date of arrival at APLORI.

Individual	**Start date**	**End date**	**Stationary (days)**	**Flying (days)**	**Duration (days)**	**Distance (km)**	**Speed (km/day)**	**Arrival at APLORI**[1]
75	29-Sep-19	07-Dec-19	69	1	70	450	450	07-Dec-19
81	25-Sep-19	22-Nov-19	58	1	59	1035	1035	22-Nov-19
83	20-Sep-19	29-Nov-19	69	1	70	1217	1217	29-Nov-19
89	19-Sep-19	07-Nov-19	50	1	51	530	530	07-Nov-19
94	NA	NA	NA	NA	NA	NA	NA	15-Dec-19
108	18-Sep-19	06-Dec-19	78	1	79	515	515	12-Dec-19
Mean	**22-Sep-19**	**26-Nov-19**	**64.8**	**1**	**65.8**	**749.4**	**749.4**	**30-Nov-19**

[1] Date when the individual was first seen at APLORI

Appendix 3.2: Latitudes and longitudes obtained through geolocator data.

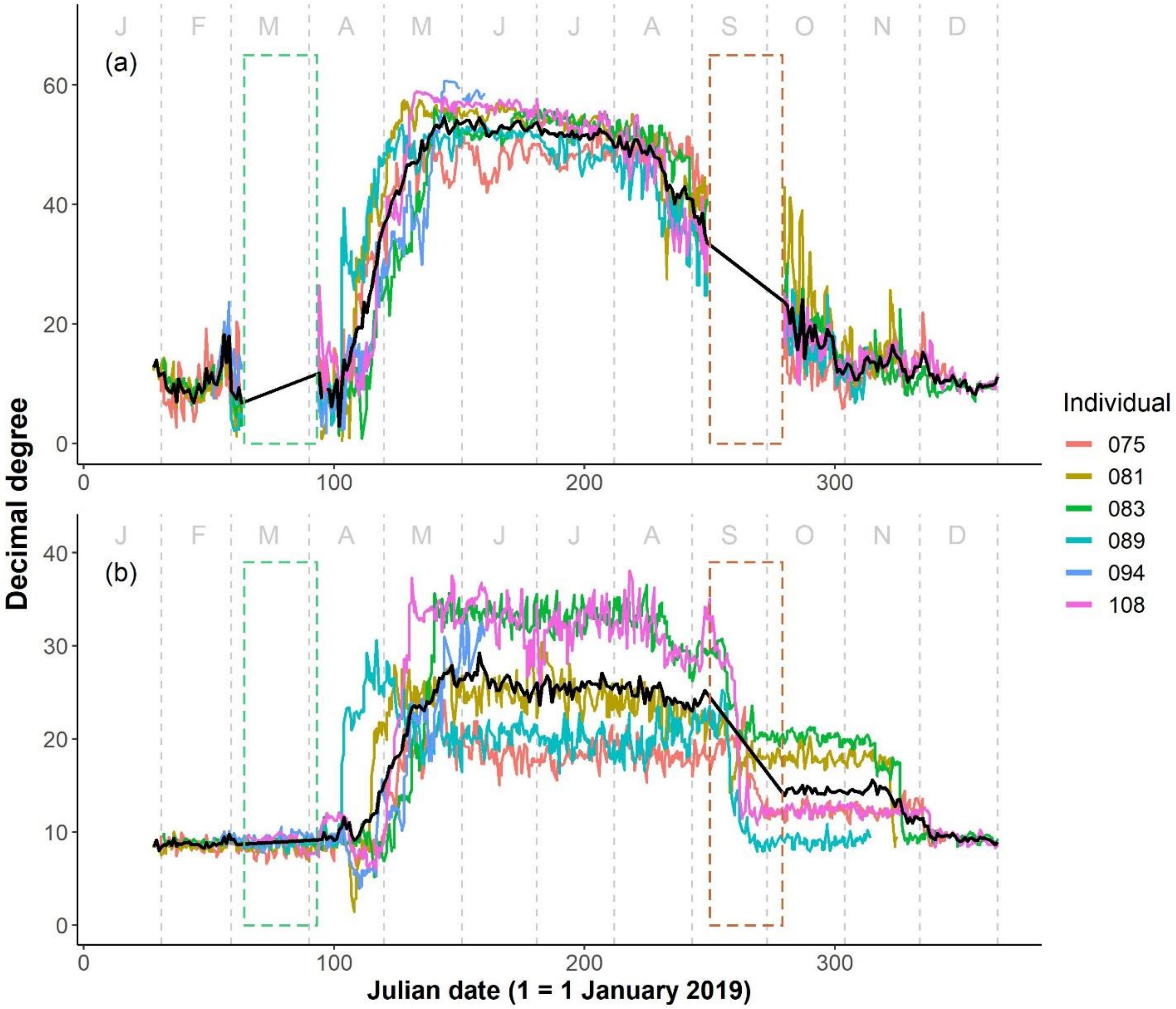


Figure A.3.2. Latitudes (a) and longitudes (b) obtained through geolocator data. Each colour represents a different individual. Black line is the overall mean; the mean was not calculated during equinoxes. Rectangles delineated by dashed lines represent equinoxes ± 14 days (green = spring, orange = autumn).

Chapter 4. Common Whitethroats show a continuum of residency patterns and a high degree of between-year site fidelity at non-breeding grounds

4.1 Abstract

The non-breeding period represents a significant part of an Afro-Palearctic migratory bird's annual cycle, thus whether individuals remain at a single site or are itinerant throughout this period, and whether they return to them year after year, will have important effects on their survival, future breeding success, migratory connectivity, and conservation. In this chapter, we aim to understand the temporal use and degree of between-year site fidelity of Common Whitethroats *Curruca communis* that are found in a six km^2 area during the non-breeding season in Nigeria. We estimated that the probability of detecting an individual at our study site when it was present was 33%. Residency periods varied widely across individuals, ranging from one to 165 days, and did not differ significantly with sex, year, or habitat, though first-year birds remained for significantly shorter periods than adults. Shorter residencies seem to suggest the use of more than one stationary non-breeding site rather than low winter survival. We found that our study site is important not only as a main non-breeding site but as a stopover and temporary site. A mean of, a minimum of 19% of individuals returned to the study site the following year. Passage birds seem to have lower return rates than individuals that remained for longer periods, but this could be a result of detection probabilities. Returning birds shifted, on average, less than 300 metres from one year to another, indicating that Whitethroats have a relatively high degree of between-year site fidelity at a very fine scale. First-year birds moved longer distances than adults. An individual's previous residency duration did not seem to strongly determine its residency duration the following year. Overall, the departure timing of individuals that were detected during late winter was similar across years, but long-term birds departed at more similar dates across years compared to passage birds. Spatial fidelity seems to be high and constant through years, but temporal fidelity and residency patterns vary, probably according to yearly and seasonal conditions. Whitethroats may be resilient to interannual habitat, climate, and anthropogenic changes at a site level, as long as individuals are able to find suitable habitats elsewhere, especially towards the end of the non-breeding season. Our results highlight the potential spatial and temporal complexity of the non-breeding period of a single migrant species and the importance of carrying out *in situ*, small-scale research throughout a migrant's annual cycle over several years.

4.2 Introduction

For Afro-Palearctic migratory birds, what occurs throughout the annual cycle is of great importance not only for survival at an individual and population level but for the overall future success of the species. Over 65% of a migrant's annual cycle occurs during the non-breeding period, where they experience unstable and challenging environmental conditions. What happens during this period will have significant carryover effects for many aspects of their survival and reproduction (Sherry & Holmes, 1996; Marra et al., 1998; Both et al., 2006; Pulido, 2007). Nevertheless, this period has been insufficiently studied and details regarding spatio-temporal movements are still not well known (Marra et al., 2015). Understanding winter residency, return rates and the degree of between-year site fidelity will contribute to a better understanding of migratory connectivity and how birds may respond to longer-term habitat and climate changes. This, in turn, will inform appropriate conservation efforts.

Frequently, small long-distance passerine migrants are treated as a relatively homogeneous group in terms of migratory strategies and winter habitat use. While this makes sense in broad terms – all individuals carry out extensive and harsh trans-Saharan flights, cross major ecological barriers, cope with changing habitats, and compete with resident species, other migrants and amongst themselves – concrete, small-scale information regarding site persistence and intra-African movements at non-breeding grounds is still lacking.

For many years there was a largely evidence-free assumption that small migrants tended to move across Africa, tracking changing seasonal conditions in a generally itinerant way (Moreau, 1972; Jones, 1995). More recently, increasing evidence has shown that this is strongly species- and population-specific (Bulluck et al., 2019), with some species visiting several different sites, *e.g*. Great Reed Warblers *Acrocephalus arundinaceus* (Hedenström et al., 1993), Willow Warblers *Phylloscopus trochilus* (Salewski et al., 2002; Thorup et al., 2019), Melodious Warblers *Hippolais polyglotta* (Thorup et al., 2019), and Chiffchaffs *Phylloscopus collybita* (Catry et al., 2003). Others, by comparison, spend longer periods at fewer sites, establishing and defending a single territory throughout the winter, *e.g*. Pied Flycatchers *Ficedula hypoleuca* (Ouwehand et al., 2016; Thorup et al., 2019), Common Redstarts *Phoenicurus phoenicurus* (Kristensen et al., 2013; Thorup et al., 2019), and Whinchats *Saxicola rubetra* (Blackburn & Cresswell, 2016b). In some cases, individuals from the same species, such as Black Redstarts *Phoenicurus ochruros* (Cuadrado, 1995) and Blackcaps *Sylvia atricapilla* (Belda et al., 2007), have been documented to show both strategies and to even change strategies in different years (Senar & Borras, 2004). In any case, it is important to characterise each species properly, even if there were to be a general residency pattern.

To remain at one specific site and maintain a territory during the non-breeding period could confer advantages in terms of local knowledge such as foraging locations, competitor densities, resource fluctuations and predators (Latta & Faaborg, 2001; Catry et al., 2004; Brown & Long, 2006; Lind & Cresswell, 2006). It could also increase the value of a site (Piper, 2011) and avoid high costs and unpredictability associated with moving long distances, likely leading to higher survival rates (Warkentin & Hernández, 1996; Cresswell, 2014). On the other hand, itinerant individuals might track ephemeral resources over a large area and are likely to move as environmental conditions change with the progression of the winter season, so as to optimise food availability (Newton, 2004; Ruiz-Gutierrez et al., 2016). In sub-Saharan Africa, the non-breeding season coincides with the dry season, so as time passes, habitats deteriorate, and movement to more southerly and mesic sites could be a good way to secure enough resources to survive the period.

Individuals of the same species have been shown to remain for longer at higher quality habitats (Sherry & Holmes, 1996; Latta & Faaborg, 2001; Bulluck et al., 2019). The duration an individual remains in a single area may therefore be an indication of the adequacy and quality of resources within a habitat, and/or an indication of the feeding strategy between generalist and specialist species (Cresswell, 2014). Longer periods of residency are expected for species with more generalist wintering strategies: it not only reduces competition with African resident species (Salewski et al., 2007) and other migratory species, but allows individuals to remain at unstable and poorer quality territories (Blackburn & Cresswell, 2016b). If there exist varying abilities by which individuals compete for resources and this were to depend on either age or sex, then we would expect different residency durations amongst residency categories and different proportions of individuals in each residency category across each year.

Compounding evidence shows that many Afro-Palearctic migrants not only remain for prolonged periods at non-breeding sites but that they also return to them year after year, regardless of the duration they spent at them previously. This is especially true of territorial individuals (Cuadrado, 1992; Salewski et al., 2000; Koronkiewicz et al., 2006; Cresswell et al., 2009; Blackburn & Cresswell, 2016b; Thorup et al., 2019). The degree of return rate, however, also depends greatly on the individual and species: whilst some species show high return rates year after year, others seem to have a more nomadic strategy, changing non-breeding locations from one year to another (Herrera & Rodriguez, 1979; Kelsey, 1989; Catry et al., 2003; Somershoe et al., 2009; Blackburn & Cresswell, 2016b; Thorup et al., 2019). Familiarity with these sites confers the same advantages as longer residency patterns, especially regarding knowledge of local and fluctuating food sources, competitor densities, and location of refuges.

Fidelity has also been detected at a temporal scale: individuals not only return to the same sites every year but return during similar times of the year. Proper timing is of critical importance in migratory species and is key for securing fitness because individuals need to time their arrival when resources are plentiful, not before they are available, and not when they are soon to disappear. Recording arrival and departure dates at a single location yields considerable information about the dynamics of settlement of the entire winter range, including information about the possible use of several non-breeding sites (Nolan & Ketterson, 1990).

According to the serial residency hypothesis (Cresswell, 2014), many Afro-Palearctic migrants are likely to be faithful to any site(s) that promote(s) their survival, thus we expect strong residency differences and return rates amongst individuals of different ages. This hypothesis predicts that first-years, which lack knowledge of small- and medium-scale locations of where to arrive, will reach the non-breeding ground stochastically and look for a suitable wintering area. Some will find a site and remain at it until migration, while others will continue their search elsewhere, many of them arriving at less suitable sites or even discovering new unknown suitable habitats. Whichever the case, if successful, individuals will reuse those sites in similar ways during subsequent years as adults. So, it is presumed that when an individual gets older, it might become more site-faithful and the older birds in a population might consist of a greater proportion of site-faithful individuals because of natural selection removing those that did not locate suitable sites.

Studying residency patterns and between-year site fidelity, however, is problematic because of detectability and the way that residency patterns themselves may determine the probability of detection. First, very few species are likely to be so noticeable that they will always be detected at a site when present, leading to false negatives, particularly with low sampling effort. Thus, low return rates could simply be the result of low resighting (recapture) probabilities. The Common Whitethroat *Curruca communis*, for example, the focal species of this study, is a secretive bird and requires some time to be able to detect it (Zwarts & Bijlsma, 2015), thus it is crucial to determine its probability of detection to fully understand its residency patterns.

Second, determining arrival and departure dates as well as site persistence and return rates greatly depends on when individuals are first marked, as well as where in the overall species distribution the study site is located. In general, higher return rates occur near either end of the migratory route (Catry et al., 2004), and long-term winter residents are more likely to be seen at the southern edge of their range. Overall, passage birds have lower chances of being detected than longer-term birds merely because they have a lower probability of being encountered.

Third, the methods utilised in undertaking the study affect the data. Efforts to describe temporal and spatial use have mainly been carried out through ringing schemes and tracking birds using geolocators. Results from ringing studies depend strongly on when and how often these efforts are undertaken. For complete and precise small-scale non-breeding site persistence and return rates data, daily efforts should be undertaken throughout the period, and the assumption that all individuals and species have the same capture probability is erroneous and will have important effects on study conclusions. Ideally, ringing is carried out across several sites with equal effort, but this is rarely done and has never so far been done within sub-Saharan West Africa. Results from tracking studies are potentially unbiased, except that small passerines can only be tracked with archival tags, leading to only the tracks of survivors or individuals with some degree of annual site fidelity (to allow recapture) being recorded. Furthermore, with geolocators, position estimates have a high degree of uncertainty and fail to provide residency patterns at a very precise spatial scale.

Following small passerine long-distance migrants over large spatial and temporal scales during the non-breeding period is impossible until better, more appropriate technology is developed (Catry et al., 2003). It is still possible, however, to study small-scale temporal and spatial use and compare repeatability through individuals that show some degree of fidelity in a small area, as long as the previously mentioned limitations are fully considered. In this study, we use intense resighting efforts throughout the non-breeding period at a single site, over several years so we can fully understand, at an individual level, how Whitethroats use the non-breeding grounds at a fine spatial and temporal scale.

4.3 Aims

Many studies based on ringing recoveries and sporadic encounters have speculated that Whitethroats are site-faithful to their wintering grounds and remain there for a considerable period. To our knowledge, this is the first study to research wintering residency at a very fine spatial scale and during the totality of the non-breeding season. The general aim of this chapter is to understand residency patterns and the degree of between-year site fidelity of Whitethroats that are found in a six km^2 area during the non-breeding season in Nigeria and to explore how these patterns fit into the serial residency hypothesis. The specific aims and corresponding predictions are as follows:

1) To calculate the probability of detecting an individual during a visit when it is present in the area (detection rate). Whitethroats inhabit dense thickets, show inconspicuous behaviour, and are relatively quiet during the non-breeding period, thus we need to establish how many visits are necessary to get a reasonable chance of detecting a bird, and our ability to determine false from correct negatives.
2) To identify within-season residency patterns. Having established detectability rates we can then determine whether we have sufficient effort to say with any reasonable certainty that an absence is a true absence. Because APLORI is close to, but not at the most southern part of the species' distribution in West Africa, we expect it to be both an important stopover and a stationary non-breeding site for the species. We therefore expect to find two kinds of residency pattern: individuals passing through during both spring and autumn, and some individuals that will remain throughout the entirety of the non-breeding period.
3) To understand differences in the frequency of occurrence of residency patterns with age and sex of individuals. The serial residency hypothesis predicts that first-years arrive at the non-breeding ground stochastically and look for a suitable wintering area. Some may find a local site, but some continue migrating further south, so we predict that there will be important differences between adults and first-years and that a greater proportion of long-term residents will be adults. There is no evidence of migratory segregation across sexes in Whitethroats, thus we expect to see a similar proportion of females and males in each residency category.
4) To determine yearly changes in the proportion of individuals in each residency pattern (residents vs transients). There is likely to be a year-to-year variation in the proportion of individuals in each residency category, mainly due to a variable number of first-years arriving at the study site each year. The number of adults each year should, however, reflect the number of first-years and adults that were residents in the previous year. We also expect resident individuals to remain for a similar duration the following year, whilst passage birds of the previous year should increase their duration of stay.
5) To calculate the degree of between-year site fidelity and whether there are differences across age and sex. It is expected that a significant proportion of individuals return to the study area, or even the same bush, each year. Individuals that remained for longer periods the previous year are expected to return at higher rates compared to passage individuals.

6) To determine whether individuals leave the study site at similar times every year. We anticipate that some individuals, especially adults and winter residents, will depart the study area at similar times every year, while first-year and passage birds will be less repeatable.

4.4 Methods

4.4.1 Study site, mist-netting, resighting efforts, and radio tags

See Chapter 2.

4.4.2 Detectability rates

Because the duration of the sampling effort determines how species "presence" is interpreted, we calculated detection probability with data obtained from individuals that were considered obvious long-term winter residents, defined as individuals that were ringed before 15 January of its respective year or the year before, remained at the study area for over 60 days, and were seen during at least three visits. In other words, we used data from individuals that we knew were present at the study site during each visit to ensure that their non-detection was due to detectability factors and not due to absence or death. This assumed that birds did not leave their home range at any time and that their behaviour reflected similar behaviours to those individuals that remained for shorter periods. We used information collected from 20, 16, and 15 individuals during years 1, 2, and 3, respectively. All data were analysed separately by year and returning individuals were included in every year they were detected: excluding them would underestimate the proportion of adults.

Detection rates were calculated as the number of times a bird was detected (number of encounters) divided by the total visits to its territory between its first detection (excluding date it was ringed) until its last detection for each year (Formula 1). From now on, these results are referred to as data obtained "manually".

Formula 1: $$Detection\ rates = \frac{Number\ of\ encounters}{Total\ number\ of\ visits}$$

We then proceeded to obtain an encounter probability, analysing the same data using Cormack–Jolly–Seber (CJS) models in MARK software (White & Burnham, 2009) to confirm our initial estimates. CJS models estimate both apparent survival (φ) and the encounter probability (p), where the former is the probability that an individual survives from one sampling occasion to the next, and the latter is the probability that, given that the individual is alive and in the sample, it is in fact encountered (Hammond, 2018; see Chapter 6 for more details). Given that we used capture histories from individuals which we knew were present and alive ($\varphi = 1$), we were only interested in obtaining the encounter probability for each year. We set detection to be constant throughout all encounters ($\varphi(.)p(.)$).

Additionally, we calculated detection rates of three radio-tagged individuals that were detected at least during three visits in year2. Every time the antenna detected a radio-tagged individual, we proceeded to find it in the same manner that we would normally carry out during resightings (Chapter 2). We then estimated detectability rates by dividing the number of visits during which an individual was detected in normal conditions (either when heard or seen) by the total number of visits by that same individual, detected via the radio tag antenna.

The final overall detection rate was then obtained by averaging all seven estimated detection rates: detections obtained manually and in MARK for all three years (six detection rates), and detection obtained through radio-tagged individuals (one detection rate). To compare detectability rates between years, General Linear Models (GLMs) were performed. To estimate whether they were constant throughout the year, we calculated detectability rates during the first and second half of each individual's visit periods and determined whether there were differences using a paired *t*-test. All data were analysed separately by year using R version 3.6.3 (R Core Team, 2020) and RStudio version 1.1.456.

4.4.3 Within-winter residency patterns

Proving different residency categories

To evidence that individuals remained for different periods throughout the non-breeding season at our study site – that individuals have different within-winter residency strategies – we compared the observed frequencies of the number of visits individuals were detected each year, with that expected by chance, assuming that all individuals were long-term winter residents. To do this, we first calculated the number of individuals seen *per* year and the respective mean number of visits. We ran 50 iterations to obtain a representative mean of birds detected each visit, assuming that (1) birds were present in the area throughout the study, *i.e*. long-term winter residents, and (2) that the detection rate *per* visit was 0.33 (as calculated below). We then compared these estimates with our observed data using a two-sample *t*-test. We expect that if our observed frequencies match those expected by chance, then all individuals are long-term winter residents. If frequencies do not match, however, we believe that individuals have different duration of residency periods. All years were analysed separately. Individuals seen in multiple years were not excluded from any analyses.

We repeated this same analysis using data from individuals that were observed at least twice throughout the year to eliminate individuals that were likely to be simply passage birds. By doing this, we eliminate individuals that may have been passing by and detected by chance, and not necessarily utilising resources from the area. If afterwards, we still observe differences in expected and observed frequencies, then we are highly confident that not all individuals detected at our study site are long-term winter residents.

Residency categories

Once we provided evidence that individuals undertook different residency strategies, we estimated the number of days individuals spent in the study area (obtained by counting the days between when individuals were first and last seen) and categorised individuals as described in Table 4.1. Individuals detected across more than one year were categorised independently each year.

Table 4.1. Description of each residency category.

Category	Description
Long-term winter residents	Remained >= 60 days at the study site, was detected two or more times after ringing, and seen at least once after January
Short-term winter residents	Remained between 8 and 59 days at the study site *
Passage birds	Ringed between October and December. Only detected when ringed or Remained <= 7 days at the study site
Unknown	Ringed between January and April. Only detected when it was ringed or Unclear pattern

* If individuals were ringed during January or February, these individuals could potentially be long-term winter residents.

These categories could include an unknown number of individuals that may not have migrated beyond APLORI but could have settled close by, just outside of our study sites. We do not believe predation would account for differences in residency duration.

Chi-squared tests (χ^2) were carried out to determine whether the proportion of individuals in each residency category was similar in each year. This analysis was repeated excluding passage birds. Individuals in the “unknown” category are excluded from this and all further analyses.

Residency periods across years, age, sex, and location

We carried out GLMs to understand whether residency periods, defined as the number of days an individual was present and detected in the area, varied by year, age, sex, and location. Two distinct datasets were used, one including all individuals (except individuals for whom we could not define a residency category, “unknowns”), and one including individuals that were detected for at least two days in its respective year. All birds that could not be aged or sexed were excluded from models that included these variables as predictors. First-year Whitethroats are difficult to sex accurately (Waldenström & Ottosson, 2000), so models using sex as an independent variable only include adults. Because of this, modelling for the effects of age and sex in residency periods were undertaken separately. Because there was a low netting effort during year3, first winter birds are lacking and all data from year3 were excluded from these analyses.

We used a model averaging approach for models that had the same sample size using the "*dredge*" and "*model.avg*" function from the "*MuMin*" package in R (Barton, 2020). This procedure entails carrying out all possible models from a base model (in this case, either days ~ age + year + location or days ~ sex + year + location), and calculating a weighted average of parameter estimates, such that parameter estimates from models that contribute little information about the variance in the response variable are given little weight (Grueber et al., 2011). We then averaged all models that were within three AIC units of each other (ΔAICc<3) and proceeded to run a simple model using age or sex as the only predictors. All analyses were undertaken in R and a statistical significance level of $p<0.05$ was chosen to reject the null hypotheses.

4.4.4 Between-winter site fidelity

Return rates

We estimated the number and proportion of individuals that returned from one year to the next. We used GLMs of the family binomial to investigate the effects of year, previous age, sex, previous residency, and interactions among these variables on return rates.

Degree of site fidelity

To determine the degree of between-year site fidelity of individuals that returned for at least two non-breeding seasons – how far an individual moved from year *i* to year *i*+1 – we calculated the centroid coordinate for each individual in each year and estimated the distance between the centroids using the "*distHaversine*" function from the "*geosphere*" package version 1.5.10 in R (Hijmans, 2019; Fig. 4.1). All individuals' sightings were paired, reflecting the distance between the centroid at year *i* and the centroid of the following year it was detected (year *i*+1). Individuals were grouped into group A, "individuals detected in years 1 and 2"; group B, "individuals detected in year 2 and 3"; and group C, "individuals detected in years 1 and 3 not seen in year2". Individuals that were seen during all three seasons were not excluded from the analysis and were added to both groups A and B but not C.

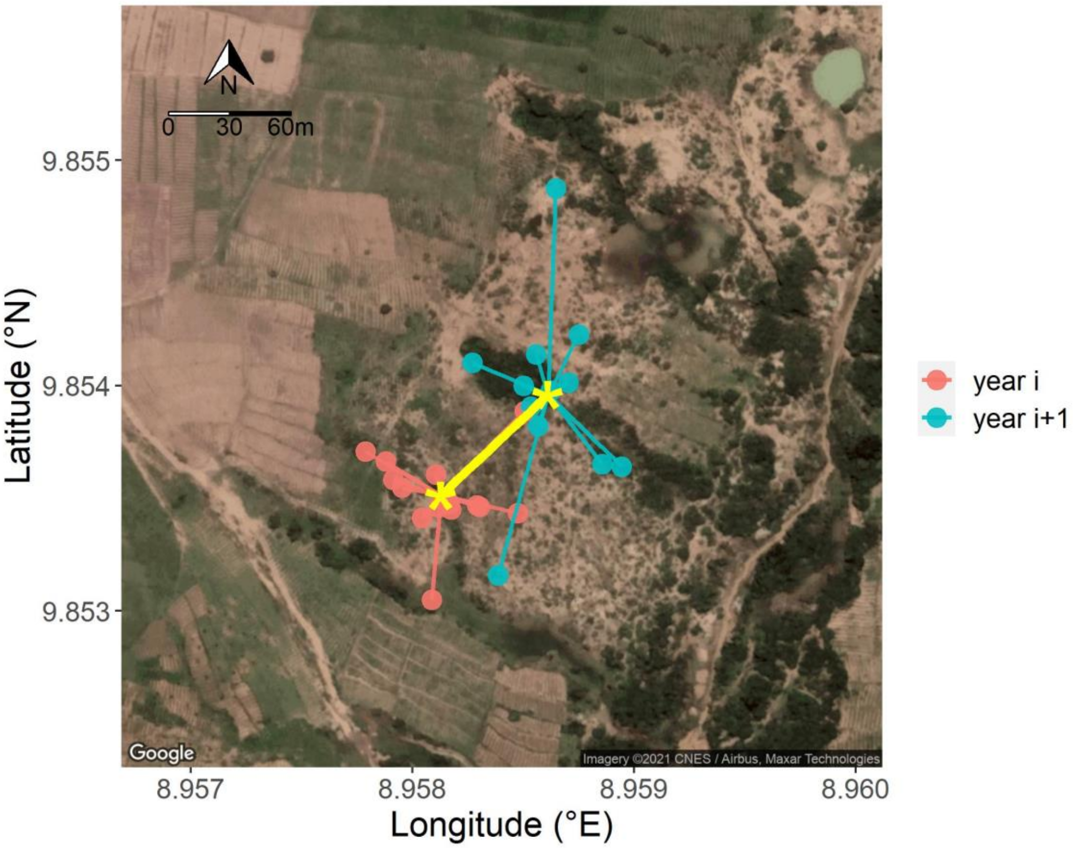


Figure 4.1. Between-years site fidelity. Here we show an example of the distance move between years from one individual. Each point represents the coordinate at which it was detected and each colour represents the different years. The centroid was obtained for each year (yellow star) and the distance between them was calculated (yellow line).

GLMs were carried out to explore whether the distance moved from one year to another was dependent on age at year *i* (previous age), sex, location at year *i* (previous location), and residency at year *i* (previous residency). We also carried out a stepwise AIC model selection using the function "*stepAIC*" from the R package "*MASS*" (Venables & Ripley, 2002) for the following model: dist ~ preage + group + preres + loc2 + preage*preres + preage*group + preage*loc2 to obtain the best model. All birds that could not be aged or sexed were excluded from models that included these variables as predictors and all individuals whose previous residency was "unknown" were also excluded.

Residency period repeatability

To explore whether individuals remained for similar periods across different years, or whether they repeated residency categories the following years, we estimated the percentage of individuals that remained (or changed) in each residency category. We carried out a linear model and estimated the correlation between the number of days spent in year *i* with the number of days spent in year *i*+1. We also determined whether there were individual differences in the time spent at the study site from one year to the next using paired *t*-tests.

4.4.5 Departure dates

Exact arrival dates were difficult to obtain because the starting date of observations varied across years. Departure dates, however, can be analysed and compared through years. We tested departure date repeatability of individuals seen during at least two years. Year3 birds were excluded from this analysis because resightings that year ended earlier, and final resightings are not likely to reflect true departure dates. We excluded records of all birds that were seen after 25 February (three weeks before the end of observations), to exclude birds that are highly likely to have not left before our last resighting efforts in that year. We estimated repeatability using the *"rpt"* function in the "*rptR*" package (Stoffel et al., 2017). This uses a linear mixed model framework where the groups compared for repeatability are specified by a random effect (*i.e*. individuals). Confidence intervals were estimated by running 1000 bootstraps. We calculated repeatability for adults and first-year birds, as well as for each residency category (*i.e*. long-term, short-term, and passage birds).

To describe population variation, we pooled all observed departure dates across the first two years (some individuals had two or more observations), from individuals that left after January of their respective years and calculated the difference between each date and the date of earliest sighting, before calculating the mean, standard error (SE), and range. To describe intra-individual variation, we used data from individuals that were detected during at least two years. We calculated the difference between the two values for each individual observed in two years and calculated the mean, SE, minimum and maximum values across all individuals. GLMs were performed to test for differences between individuals categorised by previous residency and previous age.

4.5 Results

4.5.1 Detectability rates

The mean of all seven detection rates (manual detections from years 1, 2 and 3, MARK detections from years 1, 2 and 3, and detection from radio-tagged birds in year2) is 0.33. This means that the probability of detecting a Whitethroat at our study site when it is present is, on average, 33% SE = 0.02), or once every three visits (Fig. 4.2). Detection rates were similar between years when undertaken manually (mean = 0.36, SE = 0.02, $F(_{2,48})$ = 0.13, p = 0.88) and in MARK (mean = 0.29, SE = 0.03, $F(_{2,48})$ = 1.48, p = 0.24) and were similar across methods during all three years (year1: $t(_{38})$= 0.88, p = 0.38; year2: $F(_{2,32})$ = 2.44, p = 0.10; year3: $t(_{28})$= 1.18, p = 0.25).

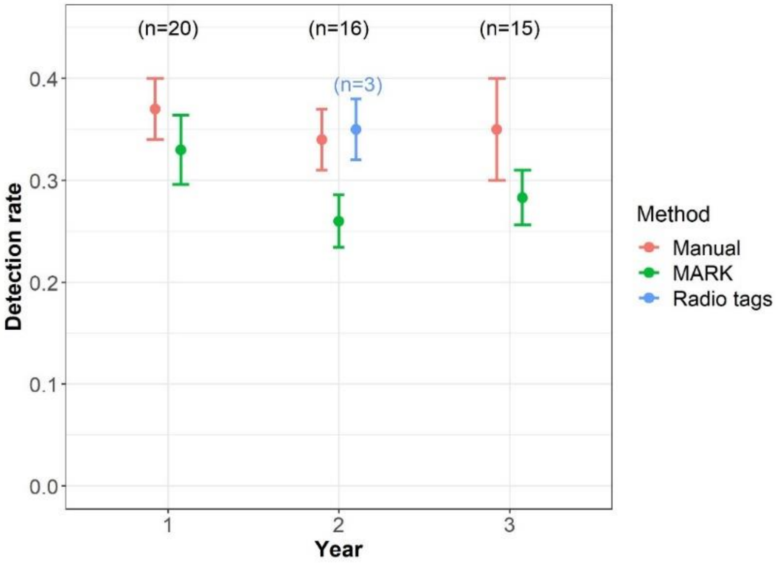


Figure 4.2. Detection rates. Mean detection rates and respective standard errors of known long-term resident birds in each year using distinct methods (red = manually, green = MARK, blue = manually from radio-tagged birds). Sample sizes during each year are shown on top. In year2 "(*n* =3)" represents the sample size of radio-tagged birds. No clear differences in the detection rates were seen across years and methods.

When separating each individual's visits into two groups, the first half and second half, we found that detectability rates in year1 seem to be higher during the second half of the visits (paired *t*-test: $t_{(19)}$=-6.2, $p < 0.001$). However, in years 2 and 3 detectability rates were similar between the first half of the visits and the second half (paired *t*-test year2: $t_{(15)}$=0.51, $p = 0.62$; paired *t*-test year3: $t_{(14)}$=-0.87, $p = 0.40$; Fig. 4.3).

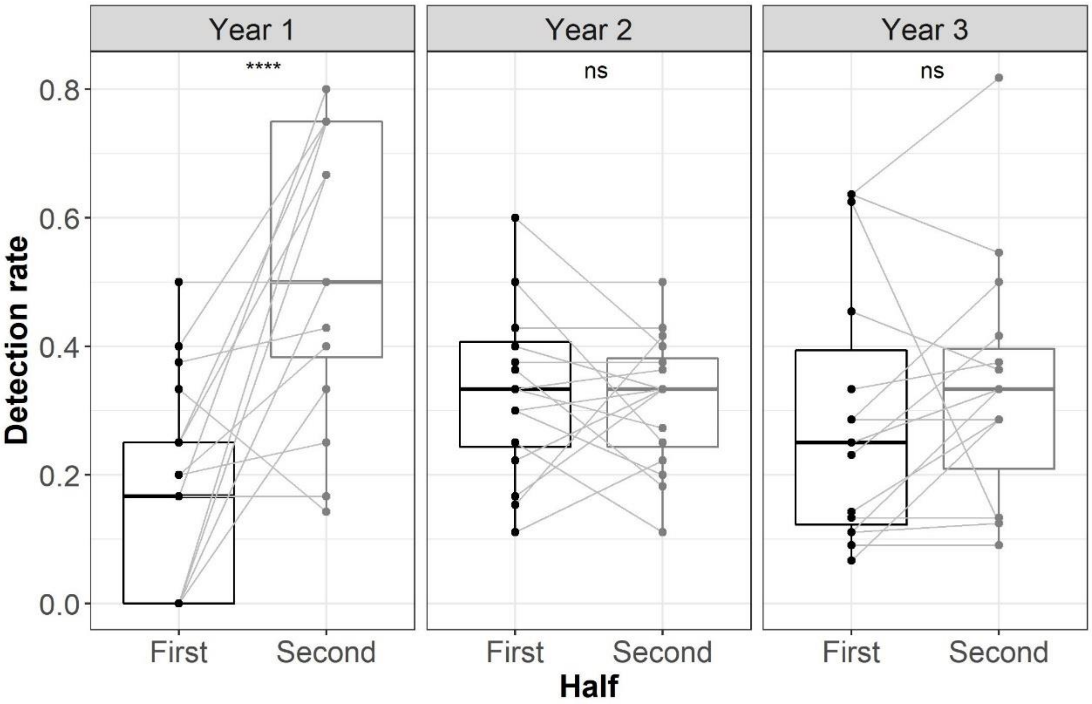


Figure 4.3. Changes in detection rates. Changes in mean detection rates between the first and second half of the visits of known long-term resident birds in each year. Black boxplots represent the first half of the visits and dark grey boxplots the second half of the visits. Light grey lines connect the same individuals. Detectability rates during year1 seem to be higher during the second half of the visits but there were no differences in years 2 and 3.

4.5.2 Within-winter residency patterns

Proving different residency categories

We found that the expected frequencies of the number of visits during which individuals were predicted to be detected was statistically different from what was observed when analysing both the dataset with information from all individuals and the dataset with individuals that were detected at least twice during the year (Fig. 4.4; Table 4.2). These results are similar across years. With this, we confirm that not all birds seen at our study sites are long-term winter residents.

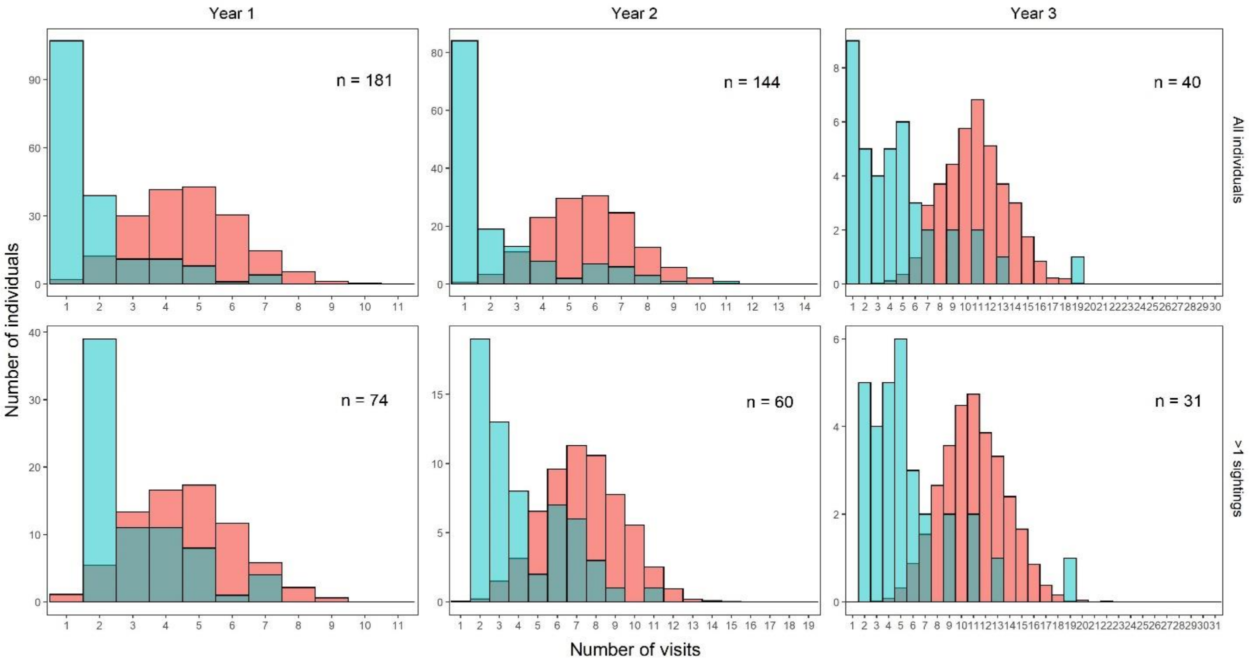


Figure 4.4. Expected (red) and observed (blue) frequencies of the number of individuals that were detected at different number of visits. Graphs in the first row were obtained from data gathered from all individuals and graphs from the second row were obtained from data of individuals that were seen at least twice during the year. In all graphs, blue bars (observed data) and red bars (expected data) rarely overlap. We observed many more individuals than expected only once or twice if all were long-term residents when detectability rate was estimated to be 0.33.

Table 4.2. Statistical summary of number of detections during expected and observed visits. Statistical summary of the expected and observed number of visits at which individuals were detected during all three years and using two datasets: (1) "all data", information from all detected individuals, and (2) "> 1 sightings", information from individuals detected at least twice during the year. All the expected mean visits were statistically different from the observed mean visits. A statistical significance level of p <0.05 was chosen to reject the null hypotheses.

Year	**Dataset**	***n***	**Expected mean visits**	**SE**	**Observed mean visits**	**SE**	**Results from *t*-tests**
1	all data	181	4.64	0.12	1.86	0.10	$t_{(360)} = 18$, $p < 0.001$***
1	> 1 sightings	74	4.62	0.19	3.09	0.17	$t_{(146)} = 6.1$, $p < 0.001$***
2	all data	144	5.67	0.14	2.30	0.18	$t_{(286)} = 14.9$, $p < 0.001$***
2	> 1 sightings	60	7.30	0.27	4.12	0.29	$t_{(118)} = 8.1$, $p < 0.001$***
3	all data	40	10.8	0.39	4.62	0.61	$t_{(78)} = 8.6$, $p < 0.001$***
3	> 1 sightings	31	10.8	0.46	5.68	0.68	$t_{(60)} = 6.3$, $p < 0.001$***

Residency categories

Individuals were categorised as seen in Table 4.3 (for more details see Appendix 4.1).

Table 4.3. Number of individuals in each residency category per year. Percentages of individuals in each category, excluding unknown birds, are shown in parenthesis. The total number in parenthesis includes unknown individuals.

Residency category	Year1	Year2	Year3
Long-term winter residents	41 (30%)	31 (35%)	21 (52%)
Short-term winter residents	7 (5%)	15 (17%)	7 (18%)
Passage birds	90 (65%)	43 (48%)	12 (30%)
Unknown	*44*	*55*	*0*
Total	**138 (182)**	**89 (144)**	**40 (40)**

There was a significant difference in the number of individuals in each residency category during all years (year1: $\chi^2 = 75.70$, df = 2, $p < 0.001$; year2: $\chi^2 = 13.30$, df = 2, $p = 0.001$; year3: $\chi^2 = 7.55$, df = 2, $p = 0.03$; Fig. 4.5). However, these results need to be interpreted with care as they are highly contingent upon sampling efforts – *e.g.* larger proportion of passage birds in year1 reflect a higher netting effort earlier in that year. For this reason, we cannot make any comparisons across years (see Appendix 4.2 for more details).

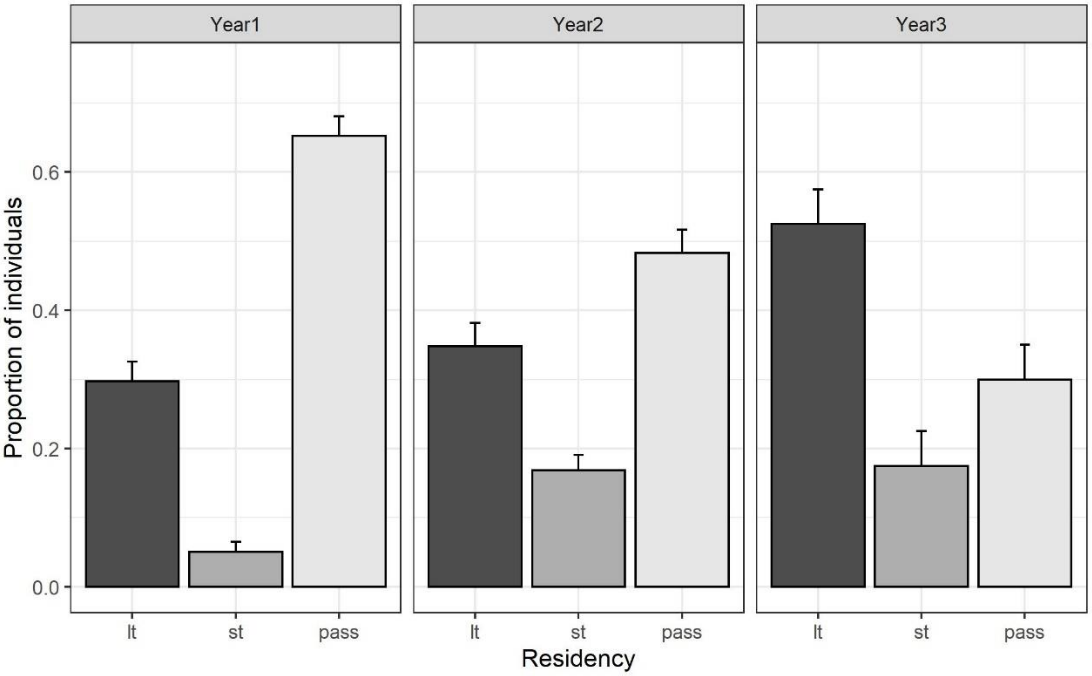


Figure 4.5. Proportion of individuals in each residency category during each year. The 25% and 75% quartiles are shown as confidence intervals obtained through bootstrapping each category 1000 times. The proportion of individuals was different in all residency categories each year. lt = long-term winter residents, st = short-term winter residents, and pass = passage birds.

When excluding all passage birds from the previous analysis, we found that the number of long-term winter residents was higher than short-term winter residents in all years (year1: $\chi^2 = 24.08$, df = 1, $p < 0.001$; year2: $\chi^2 = 5.57$, df = 1, $p = 0.02$; year3: $\chi^2 = 7$, df = 1, $p = 0.008$).

Residency periods across years, age, sex, and location

Residency periods, defined as the number of days an individual was present and detected in the area, varied widely across individuals, ranging from one day to 165 days (mean = 31 days ± 3 days, $n = 341$), and from two days to 165 days (mean = 76 days ± 4 days, $n = 135$) when excluding individuals only seen once. Residency periods of individuals that were seen at least twice did not seem to differ significantly with age, sex, year, or location (Table 4.4). Similar results were obtained when pooling all individuals, except that first-year birds remained for significantly shorter periods when compared to adults (Table 4.4; Appendix 4.3).

Table 4.4. General Linear Model results of residency period predictors. In all models age = adult, sex = female, year = 1, and loc = Crops were the base categories. A statistical significance level of *p* <0.05 was chosen to reject the null hypotheses. Significant *p*-values are highlighted in bold and italics. Residency period does not seem to vary according to sex, location, year, and age. All interactions were non-significant.

Birds that remained at least 2 days at the study site

AGE *n* = 98

	Full model average (days ~ age + year + loc)				Average of all models ΔAIC < 3				Simple model (days ~ age)			
Variable	Estimate	Adjusted SE	*z*	*p*	Estimate	Adjusted SE	*z*	*p*	Estimate	SE	*t*	*p*
(Intercept)	78.148	6.27	12.46	< 0.001	78.22	5.97	13.1	< 0.001	78.36	5.81	13.48	< 0.001
ageJ	-6.34	9.57	0.66	0.51	-5.39	9.33	0.58	0.56	-5.39	9.22	-0.58	0.56
year2	-6.01	16.93	0.36	0.72	-5.5	16.74	0.33	0.74				
locForest	-19.56	13.21	1.48	0.14	-18.93	13.1	1.45	0.15				
locReserve	-2.22	9.43	0.24	0.81	-1.34	9.15	0.15	0.88				

SEX *n* = 50

	Full model average (days ~ sex + year + loc)				Average of all models ΔAIC < 3				Simple model (days ~ sex)			
Variable	Estimate	Adjusted SE	*z*	*p*	Estimate	Adjusted SE	*z*	*p*	Estimate	SE	*t*	*p*
(Intercept)	86.78	9.02	9.62	< 0.001	88.25	9.27	9.53	< 0.001	85.57	9.35	9.15	< 0.001
locForest	-44.14	25.71	1.71	0.09	-44.1	25.66	1.72	0.09	-3.68	12.28	-0.3	0.77
locReserve	-21.43	16.01	1.34	0.18	-21.4	15.97	1.34	0.18				
sexM	-0.94	13.12	0.07	0.94	-0.9	13.1	0.07	0.95				
year2	-0.52	13.02	0.04	0.97	-0.53	13	0.04	0.97				

All birds

AGE *n* = 204

	Full model average (days ~ age + year + loc)				Average of all models ΔAIC < 3				Simple model (days ~ age)			
Variable	Estimate	Adjusted SE	*z*	*p*	Estimate	Adjusted SE	*z*	*p*	Estimate	SE	*t*	*p*
(Intercept)	40.04	7.17	5.59	< 0.001	40.56	7.23	5.61	< 0.001	44.89	4.72	9.52	< 0.001
ageJ	-14.5	7.12	2.04	***0.04***	-14.56	7.1	2.05	***0.04***	-15.82	6.74	-2.35	***0.02***
year2	10.59	7.47	1.42	0.16	10.44	7.44	1.4	0.16				
locForest	10.98	14.17	0.77	0.44								
locReserve	2.61	11.74	0.22	0.82								

SEX *n* = 81												
	Full model average (days ~ sex + year + loc)				Average of all models ΔAIC < 3				Simple model (days ~ sex)			
Variable	Estimate	Adjusted SE	*z*	*p*	Estimate	Adjusted SE	*z*	*p*	Estimate	SE	*t*	*p*
(Intercept)	48.43	8.88	5.46	< 0.001	46.6	9.04	5.16	< 0.001	47.44	8.5	5.61	< 0.001
year2	10.72	12.07	0.89	0.37	10.55	12.01	0.88	0.38	7.82	11.67	0.67	0.5
sexM	8.09	11.93	0.68	0.5	7.82	11.85	0.66	0.51				
locForest	-5.02	31.85	0.16	0.88								
locReserve	3.67	17.74	0.21	0.84								

4.5.3 Between-year site fidelity

Return rates

36 out of 181 (20%) individuals returned from year1 to year2 (group A), 24 out of 144 (17%) individuals returned from year2 to year3 (group B), and seven individuals from year1 failed to return in year2 but then returned in year3 (group C). 12 individuals were seen during all three years. In group A, a similar proportion of adults and first-year birds returned the following year: 13 out of 62 (21%) adults and 22 out of 96 (23%) first-years. In group B however there were clear differences between individuals of different ages: 20 out of 90 (22%) adults and 3 out of 50 (6%) first-years returned. Most individuals from group C were first-year birds in year1. Residency-wise, in group A, 14 out of 43 (33%) long-term winter residents returned, 2 out of 7 (29%) short-term residents returned and 10 out of 90 (11%) passage birds returned. In group B, 12 out of 31 (39%) long-term winter residents returned, 3 out of 16 (19%) short-term residents returned and 5 out of 40 (13%) passage birds returned. The GLM showed statistical differences in passage birds, which showed lower return rates than the other residency categories in both years ($p = 0.001$), and a weak trend between first-years and adults in year2, where first-years had lower return rates ($p = 0.09$). All other variables and interactions were non-significant.

Degree of site fidelity

The distance moved from one year to another varied greatly among individuals (Fig. 4.6). On average, however, individuals moved less than 300 metres (Table 4.5) and this figure was similar amongst all groups ($F_{(2,51)} = 0.006$, $p = 0.99$), showing that Whitethroats have a relatively high degree of between-year site fidelity and that they tend to return to similar areas across years.

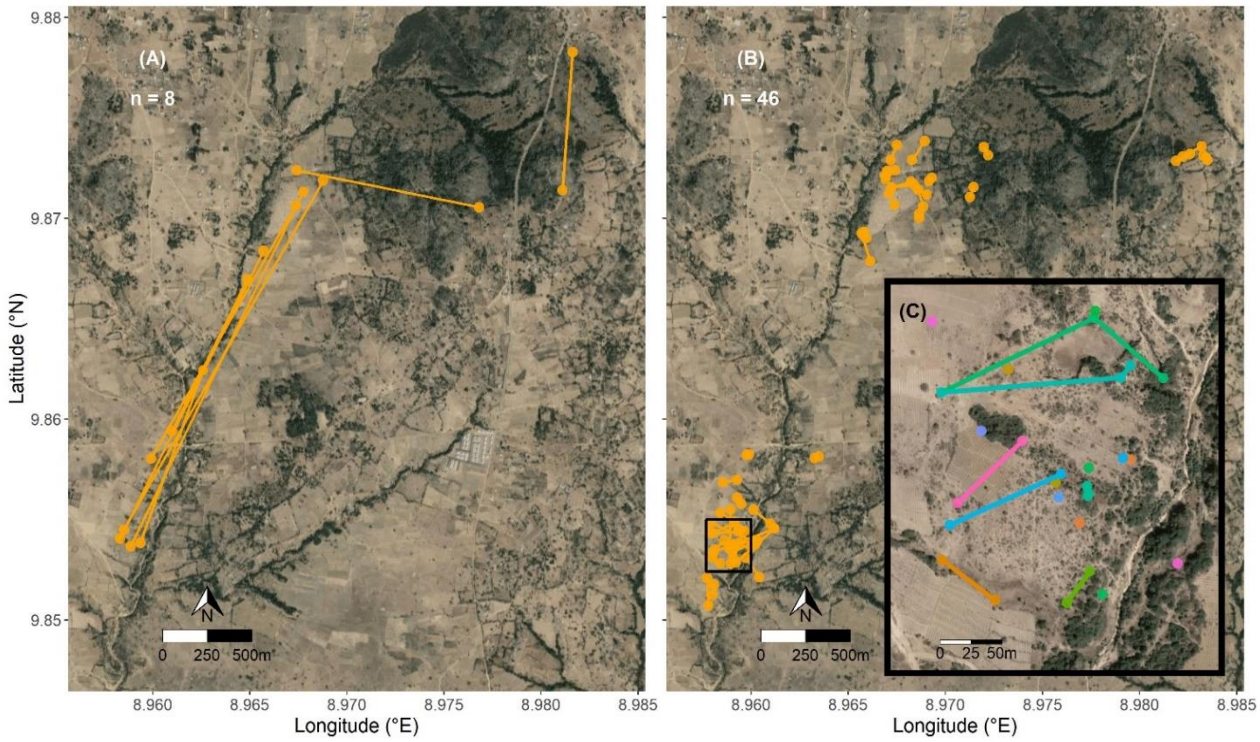


Figure 4.6. Distances shifted between years. Distances moved between year *i* and year *i*+1 by individuals that moved an above mean distance (>300m; A) and a below mean distance (<300m; B). Sample sizes are shown in each map. A subset of individuals is shown with a higher definition in map C. Here, each colour represents a different individual. Individuals that do not have a line moved out with the confines of the box. Overall, individuals did not move long distances from one year to another.

Table 4.5, Distance moved between years. Descriptive statistics of the distance (in metres) moved between years according to groups, previous age, sex, previous residency, and previous location. Group A = individuals detected in years 1 and 2, B = individuals detected in years 2 and 3, and C = individuals detected in years 1 and 3 but were not seen in year2.

Variable		***n***	**Min distance (m)**	**Max distance (m)**	**Mean distance (m)**	**SE**	**Median distance (m)**
Group	A	28	6.3	2106.9	298	101	99.2
	B	21	7.8	2239.6	285	129	71.7
	C	5	80.1	942.7	273.1	167	120.1
Previous age	Adult	28	7.8	1790.8	203.8	73	81.3
	First-year	19	6.3	2239.6	441.7	169	99.7
Sex	Female	20	6.3	1018.1	148.1	50	99.7
	Male	15	13	1790.8	241.7	125	71.7
Previous residency	Long-term	28	6.3	2239.6	207	179	55.9
	Short-term	6	71.7	288.1	130.3	32	106.8
	passage	16	17.5	2106.9	481.4	178	132.5
Previous location	Crops	43	6.3	2239.6	306	88	95.3
	Forest	3	51.5	767.5	292.8	237	59.2
	Reserve	4	13	120.1	60.5	26	54.5

The distance shifted between years did not vary significantly according to previous age ($F_{(1,45)}$ = 2.1, *p* = 0.16), sex ($F(_{1,33})$ = 0.58, *p* = 0.45), previous location ($F_{(2,47)}$ = 0.36, *p* = 0.70) or previous residency ($F_{(2,47)}$ = 1.61, *p* = 0.21; Table 4.5; Fig. 4.7). However, the stepwise AIC model selection when running dist ~ preage + group + preres + loc2 + preage*preres + preage*group + preage*loc2 indicated that the model with the lowest AIC was dist ~ preage + group + preage*group. Results from the latter model show that first-years shift longer distances than adults though this is not highly significant ($F_{(1,41)}$ = 3.3, *p* = 0.08), and a highly significant interaction between both variables ($F_{(2,41)}$ = 14.2, *p* < 0.001). *Post-hoc* Tukey tests showed that in group B (from year2 to year3), first-years shifted longer distances than adults.

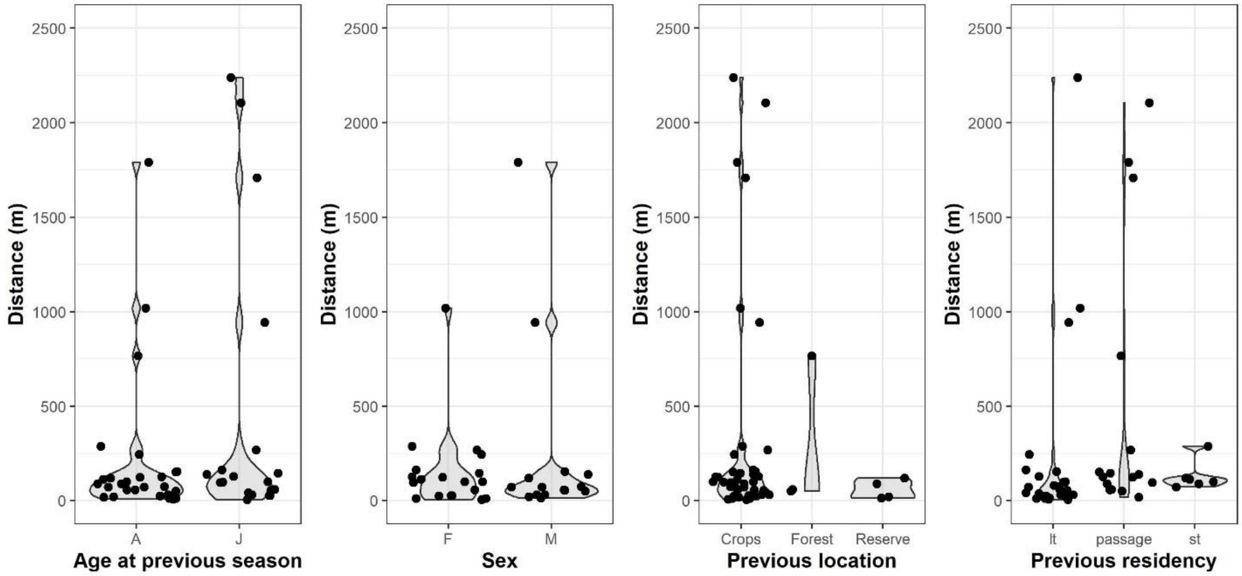


Figure 4.7. Distance moved according to previous age, sex, and previous location and residency.

Residency repeatability

The degree of residency category repeatability, *i.e*. whether individuals remained in the same residency category through different years, varied across individuals (Fig, 4.8). 72% of long-term winter residents remained as such the following year, but 28% switched to short-term winter residents or became passage birds. Many short-term winter residents, when they returned, returned as passage birds, and half the passage birds remained as such the following year, while the other half remained for longer periods the following year (Fig. 4.8).

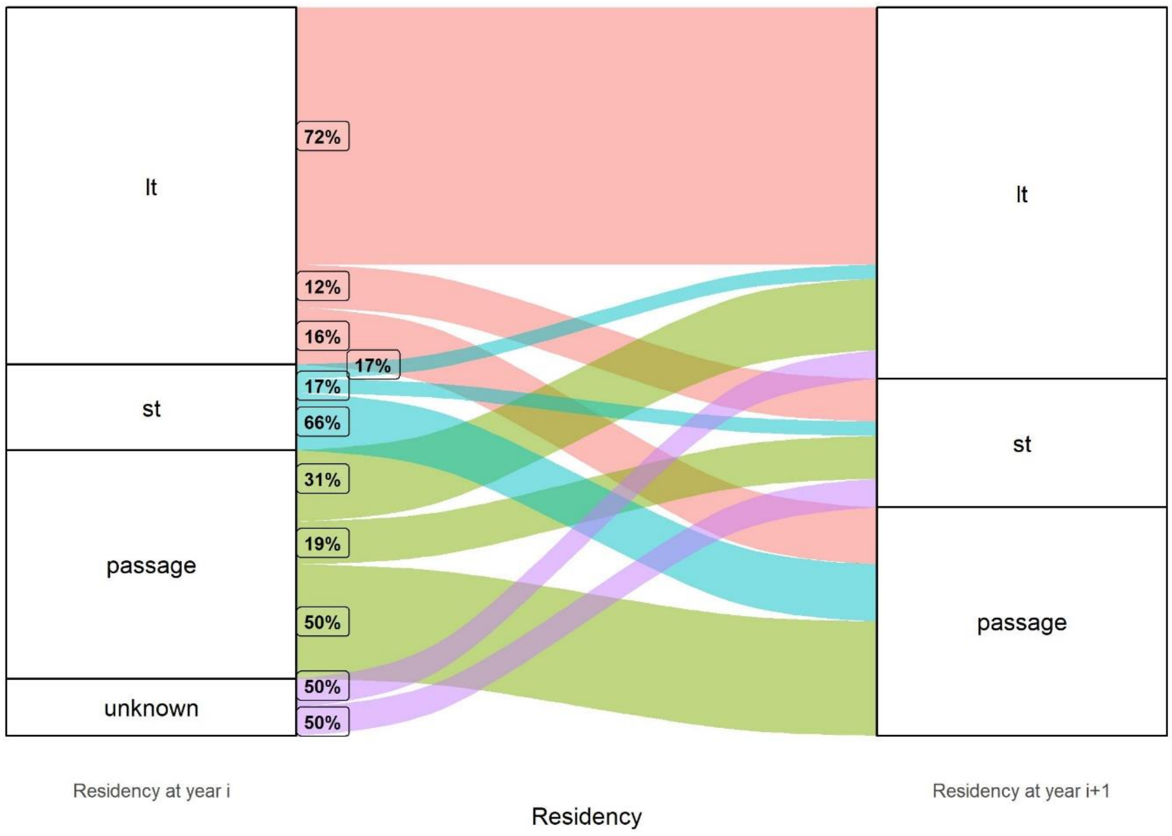


Figure 4.8. Residency repeatability. Change of individuals' residency category from one year to the following year it was detected. Percentage in the square represents the proportion of individuals of the residency at year *i* that are in the residency at year *i*+1, as is observed by the width of the bands. Colours represent the previous residency category. Lt = long-term winter resident and st = short-term resident.

When comparing the duration (in days) of individuals from one year to another, we found that there was a significant somewhat positive correlation between the duration in year *i* and duration in year *i*+1 (correlation R = 0.32, *p* = 0.026), individuals that remained for longer periods in year *i* remained longer periods in year *i*+1 but, in general, individuals remained a shorter period in comparison to their previous year (Fig. 4.9).

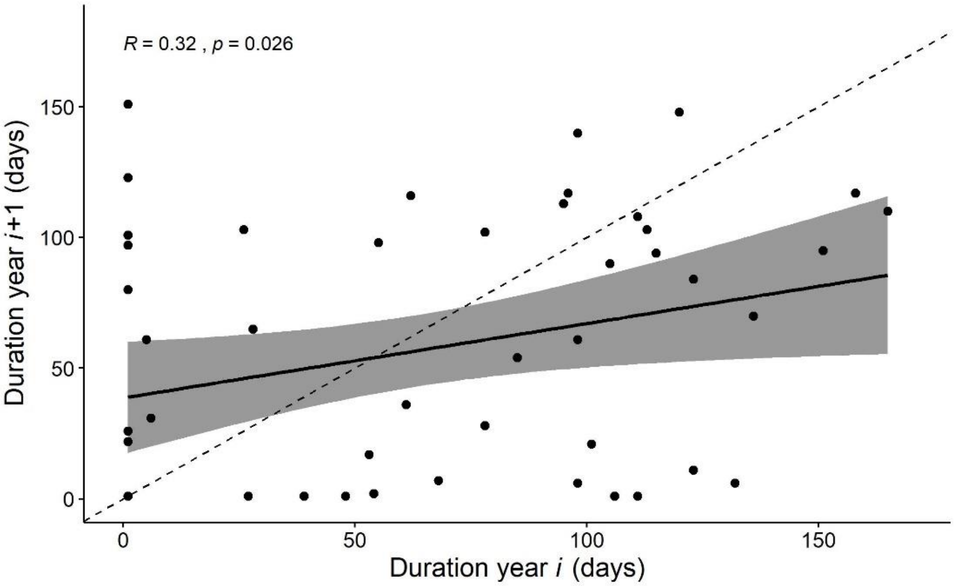


Figure 4.9. Changes in duration between years. Linear correlation between the number of days an individual spent at the study site in year *i* and the number of days an individual spent at a location in year *i*+1. The dotted line represents a constant residency period during both years. Dots above the dotted line represent individuals that remained longer in year *i*+1 than the previous year and dots below the line represent individuals that remained a longer period in their first year. R = correlation between variables and *p*-value represent a significant positive trend.

When categorising individuals into previous residency groups, we found that long-term winter residents spent less time at the study site in year *i*+1 than in year *i* (paired *t*-test: $t_{(27)}$=-3.15, *p* = 0.004), while passage birds spent more time at the site the latter year (paired *t*-test: $t_{(15)}$= 3.3, *p* = 0.005). Short-term winter residents did not vary statistically (paired *t*-test: $t_{(5)}$=-1.03, *p* = 0.35; Fig. 4.10), though most of them reduced their duration.

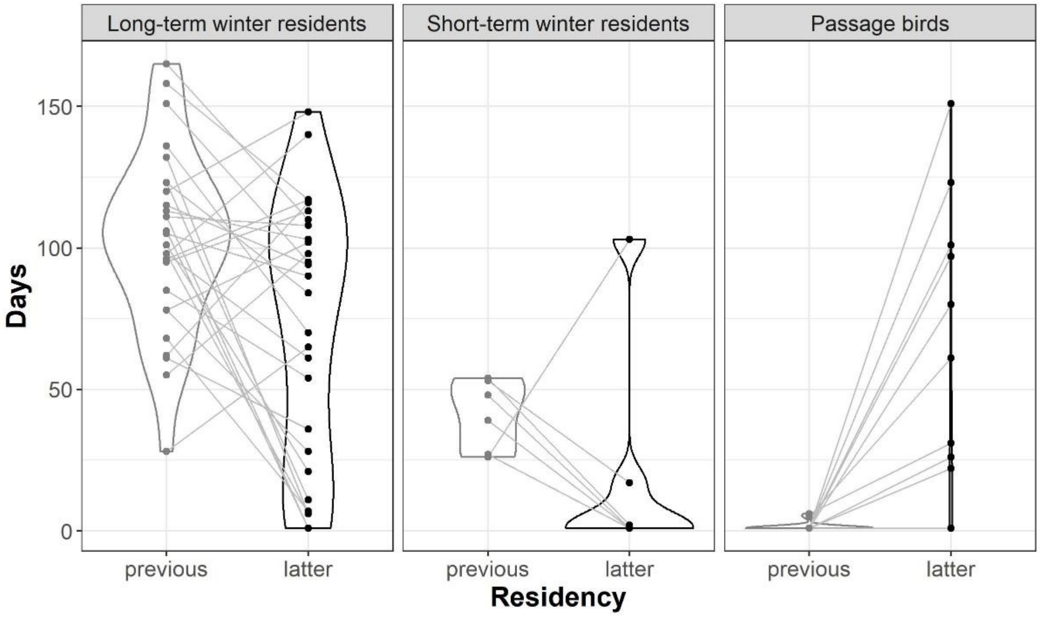


Figure 4.10. Changes in residency period (days) between years, grouped according to previous residency. Dark grey boxplots represent the duration spent in year *i*, whilst black plots represent the duration in year *i*+1. Light grey lines connect the same individuals. Long-term winter residents spent less time the latter year, passage birds spent more time and short-term winter residents did not seem to change significantly.

4.5.4 Arrival and departure date

Because of the residency continuum, exact arrival and departure dates were difficult to estimate, and a mean would reflect departure dates from all individuals, no matter what residency pattern they show. The earliest bird APLORI's 10-year ringing database has registered was caught on 22 September. During our study, we recorded an individual as early as 20 of September, though observations had only started a week prior (Appendix 4.4). The latest departure that APLORI has records for is 10 May. The latest individual that we observed was 23 April. Departure dates for individuals seen between January and April during years 1 and 2 did not vary between years ($F_{(1,179)}$ = 0.02, *p* = 0.90), between adults and first-years ($F_{(1,179)}$ = 0.002, *p* = 0.89), or between males and females ($F_{(1,137)}$ = 0.03, *p* = 0.31).

Individual departure date repeatability

Individuals that were seen during at least two years showed relatively low repeatability values (*r* = 0.15, Table 4.6).

Table 4.6. Differences in departure dates between two years.

		Intra-individual variability (Individuals seen during at least 2 years)								Population variability (Individuals from years 1 and 2)			
		n	Mean ± SE	Median	Min	Max	*r*	CI	*p*	*n*	Mean ± SE	Median	Max diff
Age	Adult	21	46 ± 8.8	39	1	126	0.10	0, 0.492	0.37	104	62 ± 2.5	68	109
	first-years	18	52 ± 8.6	55	4	120	0.146	0, 0.56	0.31	80	62 ± 3	68.5	98
Res	Long-term	20	36 ± 8.4	20	4	126	0.147	0, 0.401	0.16	72	57 ± 2.4	60	92
	Short-term	6	33 ± 10	36	3	69	0.10	0, 0.494	0.37	14	42 ± 8.6	39	89
	Passage	14	71 ± 10.3	77	1	124	0.146	0, 0.568	0.31	11	48 ± 9.7	35	88

The difference (in days) between the departure date in year *i* and that of year *i*+1 was statistically significant when categorising individuals by their residency at year *i* ($F_{(2,37)} = 4.3$, $p = 0.02$). This means that long-term birds departed at more similar dates across years compared to passage birds (Table 4.6). When categorising individuals by their previous age, we found that there was no significant difference between adults and first-year birds ($F_{(1,37)} = 0.27$, $p = 0.61$): individuals from both categories had similar differences in departure dates.

4.6 Discussion

In this chapter, we studied the residency patterns and degree of between-year site fidelity during three consecutive years of Whitethroats in a small area in central Nigeria, throughout their non-breeding period. Our results show that the probability of detecting an individual at our study site when it is present is 33% and that this rate is similar throughout the entire non-breeding period. We found a continuum of residency patterns, ranging from individuals simply passing through, to individuals that remained for most of the season. The number of days an individual spent at the study site did not vary significantly by sex, year or location, but first-year birds remained for significantly shorter periods than adults. Many individuals returned to the study site from one year to the next: 20% of individuals returned from year1 to year2, and 17% from year2 to year3. A few year1 birds returned in year3 but were not detected in year2. Passage birds had lower return rates compared to individuals that remained for longer periods, and returning birds moved a mean of less than 300 metres between years. An individual's previous residency duration did not seem to strongly determine its residency duration the following year. Overall, the departure timing of individuals that were detected during late winter was similar across years, but long-term birds departed at more similar dates across years compared to passage birds. Here we will discuss (1) detection probabilities of Whitethroats, and how this compares to other Afro-Palearctic migrants; (2) within-year residency patterns; (3) return rates and degree of between-year site fidelity; (4) degree of residency category repeatability across years; and (5) differences in departure date repeatability. We will then attempt to explain all the results in a single modification to the serial residency hypothesis – strong location fidelity across years, but the timing of movement to additional sites determined by conditions in each year.

Before discussing the results, it is important to restate the potential limitations and biases of studies looking into residency and fidelity of long-distance migrants at a small scale, such as ours. For a complete picture of residency patterns, the full non-breeding period must be studied in its entirety. At which part of the species' non-breeding range the study is undertaken is important, as is which part of the season, because birds on passage can easily be confused with itinerant birds (individuals that move over a large area with no fixed territory) and sampling effort can greatly impact the number and proportion of individuals in each residency pattern (*e.g*. a larger proportion of passage birds could be due to higher netting effort). Seasonality may act as a confounding variable, because return rates at a single site can vary greatly depending on the stage of the non-breeding season: whether it is early in the season, or later. If a study was undertaken during the migration periods, when more passage birds are observed, then lower return rates would be expected than if the study was carried out during the middle of the non-breeding season, when detected birds are more likely to be residents, and thus have higher probabilities of being detected throughout the study. And lastly, itineracy and residency are subjective terms and depend greatly on the methods, duration of the study as well as their definition (is residency over 15 days or over 2 months?).

4.6.1 Detection probabilities

Few species are likely to be so noticeable that they will always be detected when present at a site, no matter how experienced and talented an observer is. Estimating detection probabilities is essential for estimating accurate abundance, density, and survival rates, and – in the case of this study – for calculating precise residency periods and return rates. Failing to acknowledge and account for detection probabilities will generate unrealistic data.

Our results support the idea that birds belonging to the *Sylviidae* family have relatively lower detection rates than other passerine birds (Johnston et al., 2014; Zwarts & Bijlsma, 2015). The probability of detecting a colour-ringed Whitethroat at our study site, when it is present, is 33%, or once every three visits. This value is very similar to that obtained for Whitethroats at their breeding sites in the UK (30%; Johnston et al., 2014) but seems to be relatively low when compared to detectability at the non-breeding grounds of other Afro-Palearctic migrants such as Whinchats (63% detection probability; Blackburn & Cresswell, 2016b) and Chiffchaffs (recapture probability 66%; Catry et al., 2003), though there are only very few studies that have addressed and calculated detection probabilities during this period. This finding coincides with Zwarts and Biljsma (2015) who compared detectability rates of several tree-dwelling migrants in various countries in West Africa. They found that 69% of Whitethroats were detected during the first half of their observation time, similar to Subalpine Warblers *Curruca cantillans* but significantly less than most of the resident birds and other Afro-Palearctic migrants (*e.g*. species of the *Phylloscopus* genus had >80% detection during the first half of their observation time). Species with lower detection probabilities require more visits to ensure presence and/or true absence (Sliwinski et al., 2016), so despite individuals having relatively low detectability rates, we consider that our high sampling effort (sites were visited at least once a week, for over 20 weeks each year) was sufficient to compensate for this.

Detectability, in addition to being highly species-specific, varies according to other variables like time of day and season, habitat type, behaviour, physical attributes (*e.g*. vegetation density), and observer experience (Farnsworth et al., 2002; Zwarts & Bijlsma, 2015). Here we did not find any significant differences between years and conducted most of the observations in the morning when birds were more active (pers. obs.). We were not able to compare detection rates between habitats due to a small sample size in the Forest habitat, and this could be an indication of potentially lower detection rates or lower densities, simply because individuals prefer more open habitats, though this should be further explored. We did not find strong differences throughout the season, though detection rates were lower during the first half of the visits in year1. This could, however, be due to the lack of experience of the observers at the time and may not reflect true detectability differences. Extreme temperatures did seem to result in fewer detected individuals, but temperatures were rarely low, and we constantly alternated starting places in the early morning when temperatures were usually lower and ended them before mid-day to avoid the heat.

Whitethroats are inconspicuous and quick, and inhabit dense bushes in open areas, so the intermediate degree of detectability is not surprising. Because we aimed to estimate detection probabilities of colour-ringed individuals, many of our resighting detections were eliminated when individuals could not be identified correctly (when not all three colour rings were observed). Thus, detection probabilities of Whitethroats as a species could be higher in studies where there is no need to identify individuals (*e.g*. point counts) and in studies that are carried out in pristine sites where no anthropogenic activities occur that could modify the birds' behaviour.

4.6.2 Residency patterns

One of our most surprising results was the continuum in residency periods. We had expected to find two clear patterns: individuals that were passing through, especially during the migration periods, and individuals that would remain throughout the entirety of the non-breeding period. Instead, we found that site persistence varied significantly amongst individuals, ranging greatly between one and 165 days: some individuals merely passed through, others stayed for days or weeks, and others remained for months. Overall, the mean persistence duration was similar throughout years, so residency dynamics at a species level may not be changing strongly across years. In the Gambia, Whitethroats were also observed to have different degrees of site persistence: 45% of trapped individuals were retrapped during the same winter and remained at the area from two to 84 days, though most individuals were caught less than a month after ringing (King & Hutchinson, 2001). In Senegal, individuals were mainly passing through and very few birds remained for prolonged periods (King & Hutchinson, 2001). Because of our high sampling effort as well as similar return rates between individuals of different residency patterns, the evidence is fairly compelling that shorter stays truly reflect shorter residencies and not detectability issues or mortality.

Different wintering strategies of individuals at the same site have also been recorded for other long-distance migrants: 27% of Blackcaps in Spain (Belda et al., 2007) and 8% of Chiffchaffs in Portugal were residents (Catry et al., 2003), whilst the rest were categorised as transients. This could have several explanations. First, individuals could have genetic differences due to parallel evolution of morphological and behavioural adaptations, making some individuals more inclined to lead either a nomadic or a resident lifestyle (Senar & Borras, 2004). However, we cannot be sure whether individuals that were categorised as “passage” or “unknown” at our study site remained itinerant throughout the season, or if they were in fact *en route* to a stationary non-breeding site elsewhere. These genetic differences could also reflect individuals from different breeding populations though this is highly unlikely as individuals switched strategies across years, and results from the geolocator and ringing studies indicate a somewhat low connectivity (Chapter 3).

The second explanation could be due to habitat quality changes throughout the season. The broad residency spectrum, from continual and variable movement to winter residency, appears to reflect a gradient in predictability in food supplies (Newton, 2008). As time passes, habitats dry and resources change, so competition could increase and some individuals may decide to leave the area to find other more suitable habitats elsewhere, while others may risk staying (for example those that are better competitors or are already in the best territories). Our study site could be at carrying capacity and only allow a certain number of individuals to remain throughout the season (Brown, 1969). If that were the case, we would also expect some individuals to broaden their home ranges as resources decrease. Either way, these changes could not be possible if Whitethroats were not generalists and could not change their behaviour in sync with habitat changes. At our study site, individuals were seen to switch diets according to available resources: they were seen eating insects and fruits and foraging in bushes, whilst flying, and on the ground. Whitethroats seem to be able to exploit a wide range of habitats and conditions both at the wintering grounds and during migration (Stoate & Moreby, 1995).

Short-term residencies, during both autumn and spring, may indicate the use of multiple important non-breeding sites. In Chapter 3, we identified that all our geolocated individuals had a first important non-breeding site before arriving at our study site in November. Because there are very few Whitethroat records in APLORI's ringing database between September and October, we believe that most of the individuals seen at the study site, including most of our colour-ringed birds, are arriving from their first non-breeding site south of the Sahara Desert. If some of these birds were then to be short-term residents, this would mean that individuals could potentially have more than two important stationary non-breeding sites. Multiple site use by individuals has been well described for several migrants in the Palearctic systems (McKinnon et al., 2013) and might well be the rule rather than the exception. Purple Martins *Progne subis* have been recorded to have up to 4 wintering sites (Fraser et al., 2012; McKinnon et al., 2013). Why some individuals of the same species have a different number of wintering sites, however, is yet to be understood.

We predicted that adult birds would remain at non-breeding sites longer than first-year birds due to their previous experience and potential dominance. This prediction was met when taking all colour-ringed individuals into account but was not met when we excluded birds that were only seen once. This shows that individuals seen once were mainly first-year birds, and when taking them into account it demonstrates that adults' previously gained knowledge works as an advantage over first-year birds, resulting in overall longer durations, or more direct migratory routes with less exploring. These results are in line with the serial residency hypothesis. Many first-year birds probably arrive stochastically at our study site looking for suitable wintering sites. Many will need to explore the terrain and scout for resources, and whilst some will remain at it until migration to a second site later in the non-breeding season, or back to Europe in the spring, others may continue their search elsewhere, making a relatively immediate migratory scale movement.

Sex, on the other hand, did not play an important role in residency duration. Some migratory species have been found to have sexual habitat segregation at the non-breeding grounds, especially New World warblers (López-Ornat & Greenberg, 1990; Latta & Faaborg, 2001). Males have been found to be dominant over females and are expected to occupy the more optimal habitats (Latta & Faaborg, 2001), resulting in longer residencies. In this study, we did not find either sexual habitat segregation or differences in residencies between females and males. Whitethroats do not seem to have strong (or any) reproductive/breeding pressures acting during this period, and there seems to be no difference by sex in dominance-based territory occupancy or foraging patterns on the study site (pers. obs.*).*

Individuals remained for similar periods at all three distinct habitats (*i.e*. Forest, Reserve, and Crops). As the Forest has denser vegetation, a higher number of resident species and competition, and overall abundance and densities seems to be low, we predicted that individuals would show shorter residencies in this habitat compared to individuals at the Reserve and Crops, where habitats seem to be more suitable. Even though individuals did remain for a shorter time in the Forest habitat, this was not statistically significant. This would then mean that dynamics and resource availability throughout the season in the Forest are like those in the Reserve and Crops, resulting in some individuals passing through whilst a small number of individuals have sufficient resources to remain throughout the season. This could potentially mean that individuals maintain larger home ranges in the Forest.

4.6.3 Return rates

Many long-distance migrants have been recorded to return year after year to the same non-breeding sites both in the Nearctic-Neotropical and Afro-Palearctic systems (Moreau, 1969; Salewski et al., 2000; Blackburn & Cresswell, 2016b). The biggest problem is that most detailed studies of winter site fidelity have been conducted at small areas year after year, so while such records are useful in confirming site fidelity, it does not reflect the proportion of surviving birds that settle elsewhere (Newton, 2008). Here we found that a mean of 18.5% of individuals returned from one year to the next, an intermediate return rate in comparison to other Palearctic migrants (Table 4.7) and to Whitethroats at their breeding grounds (0–64%, da Prato & da Prato, 1983; 14.5%, Boddy, 1992). Similar patterns are seen in the Neotropical system, where some species do not return to the same sites, *e.g*. House Wrens *Troglodytes aedon* (0% return rates; Somershoe et al., 2009) and Ovenbirds *Seiurus aurocapilla* (2%; Somershoe et al., 2009) while others show high yearly return rates, *e.g*. Prairie Warblers *Setophaga discolor* (50% return rates; Latta & Faaborg, 2001), and Black and White Warblers *Mniotilta varia* (40%; Wunderle & Latta, 2000).

Table 4.7. Return rates of Afro-Palearctic long-distance migrants. Rows are arranged from lower to higher return rates.

Species	Country	Return rates (%)	Author(s)
Melodious Warbler *Hippolais polyglotta*	Ghana	0	Thorup et al., 2019
Willow Warbler *Phylloscopus trochilus*	Ghana	0.03	Thorup et al., 2019
Pied Flycatcher *Ficedula hypoleuca*	Ghana	0.05	Thorup et al., 2019
Chiffchaff *Phylloscopus collybita*	Portugal	5.1	Herrera & Rodriguez, 1979
Blackcap *Sylvia atricapilla*	Spain	5.3	Herrera & Rodriguez, 1979
Melodious Warbler *Hippolais polyglotta*	Ivory Coast	5.8	Salewski et al., 2000
Chiffchaff *Phylloscopus collybita*	Portugal	8*	Catry et al., 2003
European Robin *Erithacus rubecula*	Spain	10.8	Herrera & Rodriguez, 1979
Common Whitethroat *Curruca communis*	Nigeria	18.5	This study
Blackcap *Sylvia atricapilla*	Spain	18.8	Cuadrado, 1992
Pied Flycatcher *Ficedula hypoleuca*	Ivory Coast	23.4	Salewski et al., 2000
Blackcap *Sylvia atricapilla*	Spain	28	Belda et al., 2007
Whinchat *Saxicola rubetra*	Nigeria	30	Barshep et al., 2012
European Robin *Erithacus rubecula*	Spain	32	Cuadrado, 1992
Common Redstart *Phoenicurus phoenicurus*	Ghana	33	Thorup et al., 2019
Marsh Warbler *Acrocephalus palustris*	Zambia	47	Kelsey, 1989
Whinchat *Saxicola rubetra*	Nigeria	54	Blackburn & Cresswell, 2016b
Spotted Flycatcher *Muscicapa striata*	Ivory Coast	100 **	Salewski et al., 2000

*Return rates of only long-term resident birds
**Sample size was 1

Not only did many individuals return the following year, but they moved on average less than 300 m from one year to the next, proving a high degree of between-year site fidelity at a very small spatial scale, though less than Whinchats at the same study site, which moved <30 m (Blackburn & Cresswell, 2016b). Bearing this in mind, we would expect some individuals to have been missed the following years not because they did not return, but because they shifted hundreds of metres, just outside of our study plots.

If the annual mortality rate of migrants is around 50%, then a minimum of 20% reflects a substantial level and degree of between-year site fidelity for our species, suggesting that the benefits of site fidelity outweigh the benefits of visiting unknown locations every year. Fidelity across years confers the same advantages as longer residency patterns, especially regarding knowledge of local and fluctuating food sources, competitor densities, and location of refuges, and this seems to secure and increase an individual's survival. Lower return rates, on the other hand, may be due to changes in habitat quality between years, shift of territories between years, and/or birds not encountered upon returning to the study areas (Remsen & Good, 1996; Brown et al., 2000).

Return rates were different amongst individuals from different age categories: first-year birds showed lower return rates than adults, at least from year2 to year3. These results are not surprising. First-year birds lack knowledge of small and medium scale locations regarding where to arrive, thus their first non-breeding period is full of uncertainty and stochasticity. Some individuals will find a suitable site immediately and remain at it until spring migration, while others will continue their search elsewhere, many of them arriving at less suitable sites or even discovering new unknown suitable habitats. This also explains why there was a higher number of passage birds that were first-year individuals. Second-year and older birds will tend to reuse non-breeding sites, becoming more site-faithful over time. Some studies have argued that higher return rates in adults could be due to greater survival from the previous year. Though this may be true for a few individuals, we think that because individuals had already carried out a first migration, when the highest mortality rates occur, then overall age-related survival differences are unlikely at this stage. Additionally, we detected individuals that skipped a year (individuals from group C), and most of them were first-year birds. Something similar was observed in the Gambia, where a few individuals were seen two or three years after ringing (King & Hutchinson, 2001). We suspect that these individuals either shifted some metres just outside of our study plots and were not detected, or they found enough resources at their previous non-breeding site that they did not need to return to our site in year2 (see below).

Both short-term and long-term winter residents had statistically higher return rates than passage birds. Winter residency increases knowledge of an area and ensures that there are sufficient resources available to overcome the season. For this reason, experienced individuals will most likely return to the same site that had previously guaranteed its survival, whilst individuals that merely passed through may have opted to stopover elsewhere, though stopover site fidelity has been recorded in many species (Catry et al., 2004). These results, however, may not be due to biological reasons but methodological ones: the probability of detecting an individual increases with its length of stay, so passage birds are less likely to be detected than winter residents. As a result, we highly suspect that passage bird return rates, as well as overall return rates could be underestimated, but to what degree we do not know.

4.6.4 Residency repeatability

Even though most of the long-term winter residents remained as such the following year, many of them remained a shorter duration the following year. This result is surprising because we would expect individuals with a successful previous experience to repeat the same behaviour the following years as to guarantee their winter survival. When we further investigated the previously long-term individuals that drastically changed their residency, we found that most of them were seen at the end of the following season, during spring. The reason for this might be comparable to what happened to individuals from group C: either they remained close by but went undetected, or they remained longer at their previous wintering site due to better yearly habitat conditions that year and delayed the return to our site once they could stay no longer. If this were correct, we would expect that many individuals do not return to our study site when conditions are better further north, and only decide to come back when conditions are not proving to be optimal. On the other hand, we were not surprised to find that individuals that were passage birds increased their duration of stay overall the following year. Given many of them were first-year birds, they lacked the experience and dominance to gain an empty territory, and arrived on the non-breeding grounds later than adults, by which time fewer sites would have been available. By the following year, returning earlier in the season and as adults, they could occupy empty territories that allowed them to remain for longer periods.

4.6.5 Departure date

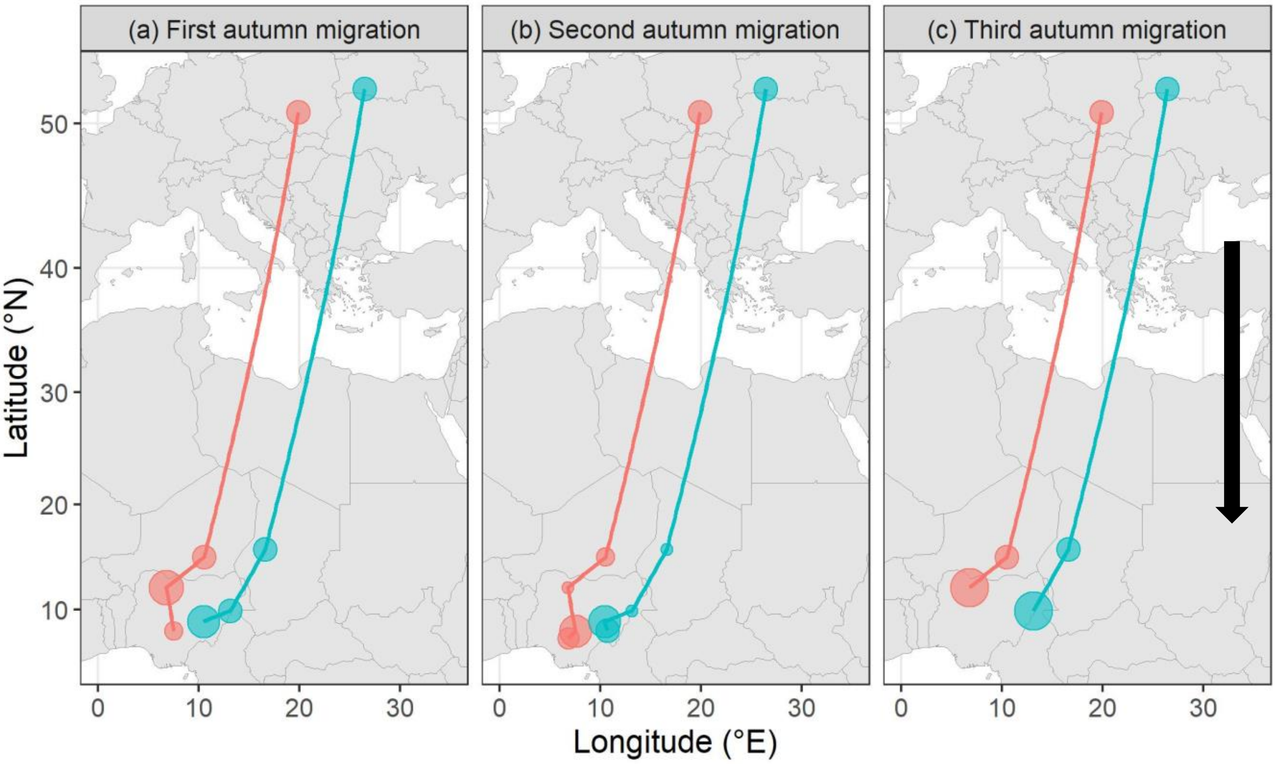
Whitethroats arrive at APLORI from late September onward, peaking in November and December, and leave by May, peaking between March and April. Because we do not have enough information regarding arrival dates, from now on we will focus on discussing departure dates exclusively.

Proper timing of migration is of critical importance in migratory species and is key for securing fitness. In spring, birds need to optimise their time of arrival at the breeding grounds to increase reproductive success by obtaining higher quality territories and mates, without arriving too early, when weather is unfavourable and resources are still lacking (Kokko, 1999; Drent et al., 2003). Post-breeding is less constrained, and individuals are expected to be more variable (McNamara et al., 1998). The longer the migratory journey, the harder it is to predict circumstances at the breeding site (Hötker, 2002). During recent years, many birds have advanced their timing of reproduction in response to climatic and food availability changes (Visser & Both, 2005) but have not always been synchronised. Failure to synchronise and coincide with these changes (termed “phenological mismatch”) is having severe negative impacts on migratory populations (Cotton, 2003; Both et al., 2006; Visser et al., 2006; Saino et al., 2010). Here we found that, on average, individuals did not change their departure timing from year1 to year2, but a couple of years cannot give us a true idea of whether departure timing varies in the species. Departure from the non-breeding grounds has been seen to correlate with arrival at breeding sites (Kristensen et al., 2013; Ouwehand & Both, 2017), though later departing individuals have been seen to migrate faster to compensate for lost time (Yohannes et al., 2009). As our study site is located at the southern part of the distribution, and individuals have different breeding sites, the first individuals to leave the site are not necessarily the first ones to arrive at their respective breeding grounds (Chapter 3). To see whether Whitethroats will have problems due to phenological mismatches, they should be studied in more northern sites than ours, in the Sahel area, before they cross the Sahara Desert.

Individuals at our study site showed lower intra-class correlation departure coefficients ($r = 0.15$) than other Afro-Palearctic migrants (range 0.06 – 0.82, Both et al., 2016) but there are a few things to consider with these results. Firstly, repeatability indicates how consistently individuals differ from each other and is not necessarily a measure of individual repeatability across years (Conklin et al., 2013). Secondly, departure from our study site does not necessarily imply that individuals have started spring departure, they could have just moved to another non-breeding site, so comparisons should be taken with caution. Finally, low repeatability fits well with the idea that individuals do not always remain for similar periods across years, and therefore it is perhaps not surprising that some individuals left the area on different dates.

4.6.6 Conclusion

Our results are consistent with, but also suggest some small modifications to the serial residency hypothesis (Cresswell, 2014). Instead of individuals repeatedly settling at the same wintering sites during the same periods year after year, we think that individuals vary their timing at the sites depending on yearly conditions. We predict that spatial site fidelity and repeatability are high with little variation across individuals, but temporal fidelity varies individually and according to yearly conditions (Fig. 4.11).



(a) First autumn migration:
Scenario 1 – "intermediate year" (red): Individual arrives at first non-breeding site. Remains until habitat deteriorates. Moves to second non-breeding site, where resources are sufficient to remain until spring migration.
Scenario 2 – "intermediate year" (blue): Individual arrives at first non-breeding site. Remains until habitat deteriorates. Moves to second non-breeding site. Remains until habitat deteriorates. Moves to third non-breeding site, where resources are sufficient to remain until spring migration.

(b) Second autumn migration:
Scenario 1 – "bad year" (red): Individual arrives at first non-breeding site. Remains until habitat deteriorates. Moves to same second non-breeding site as previous year. Remains until habitat deteriorates, spending less time than previous year. Moves to third non-breeding site. Remains as long as possible until habitat deteriorates. Moves to fourth non-breeding site, where resources are sufficient to remain until spring migration.
Scenario 2 – "bad year" (blue): Individual arrives at first non-breeding site. Remains until habitat deteriorates. Moves to same second non-breeding site as previous year. Remains until habitat deteriorates, spending less time than previous year. Moves to same third non-breeding site as previous year. Remains as long as possible until habitat deteriorates. Moves to fourth non-breeding site, where resources are sufficient to remain until spring migration.

(c) Third autumn migration:
Scenario 1 – "good year" (red): Individual arrives at first non-breeding site. Remains until habitat deteriorates. Moves to second non-breeding site, where resources are sufficient to remain until spring migration. No need to continue migration.
Scenario 2 – "good year" (blue): Individual arrives at first non-breeding site. Remains until habitat deteriorates. Moves to second non-breeding site, where resources are sufficient to remain until spring migration. No need to continue migration.

Figure 4.11. Theoretical synthesis. Example of two hypothetical individuals distinguished by colour for three consecutive years. Diagram represents southward movement from breeding sites (autumn migration and wintering sites; spring migration is excluded). Stopover sites between breeding sites and the first non-breeding site are overlooked. The size of the dots represents the duration of stay. The black arrow shows the direction of migration. Spatial yearly site fidelity is high, but timing varies according to yearly and seasonal conditions.

Individuals stay stationary at a suitable site and remain there for as long as possible. Some proportion of the population will stay there all the northern winter, most likely those that are better competitors and are at overall higher quality sites and better environmental conditions, whilst others will move to a second site. This might never happen to an individual, and for some individuals this might only happen in their second or third autumn non-breeding season, depending on the specific year's conditions. The following year the same first site will be revisited; if conditions are stable and the site adequate to secure its survival throughout the period then there would be no need to migrate elsewhere. If not, then it would migrate to the same second site, and so on. When individuals reach the limits of their potential distribution, such as our study site, then they will return only in occasional years of widespread food shortage or suboptimal conditions in the previous sites (Newton, 2008). We would therefore predict that apparent survival at a sub-Saharan non-breeding site will correlate positively with latitude. Some individuals may get unlucky and will need to change sites several times, which makes them appear itinerant, whilst others will remain as long-term winter residents at few sites. Regardless of any particular year's conditions, the number of migration steps and distance of migration is minimised and matched to environmental conditions.

In summary, results suggest that spatial fidelity is high and constant through years, but temporal use or temporal fidelity and site persistence may vary and a possible explanation for this might be variation in yearly and seasonal conditions. In other words, timing is important: individuals revisit locations at very precise scales but do not necessarily repeat them at the same time. There is temporal flexibility but not spatial flexibility, except in the sense there is always an option to make a potentially dangerous further migration to an unknown area if conditions became untenable. But these hypotheses can only be tested fully when small birds such as Whitethroats can be tracked with non-archival tags so that wintering locations regardless of site fidelity and long-term survival can be seen.

4.7 Appendices

Appendix 4.1. Number and percentage of individuals in each residency category.

Table A.4.1. Number and percentage of individuals in each residency category per year.

Residency category	Year1	Year2	Year3
Ringed	107	73	5
Long-term winter resident	41 (55%)	26 (37%)	20 (57%)
Autumn short-term resident	NA	9 (13%)	2 (6%)
Winter short-term resident	4 (5%)	4 (6%)	4 (11%)
Spring short-term resident	8 (11%)	3 (4%)	0 (0%)
Autumn transient	6 (8%)	8 (11%)	1 (3%)
Winter transient	3 (4%)	4 (6%)	5 (14%)
Spring transient	0 (0%)	5 (7%)	1 (3%)
Unknown	12 (16%)	12 (17%)	2 (6%)
Total	**181**	**144**	**40**

Appendix 4.2. Proportion and number of individuals in each residency category across years.

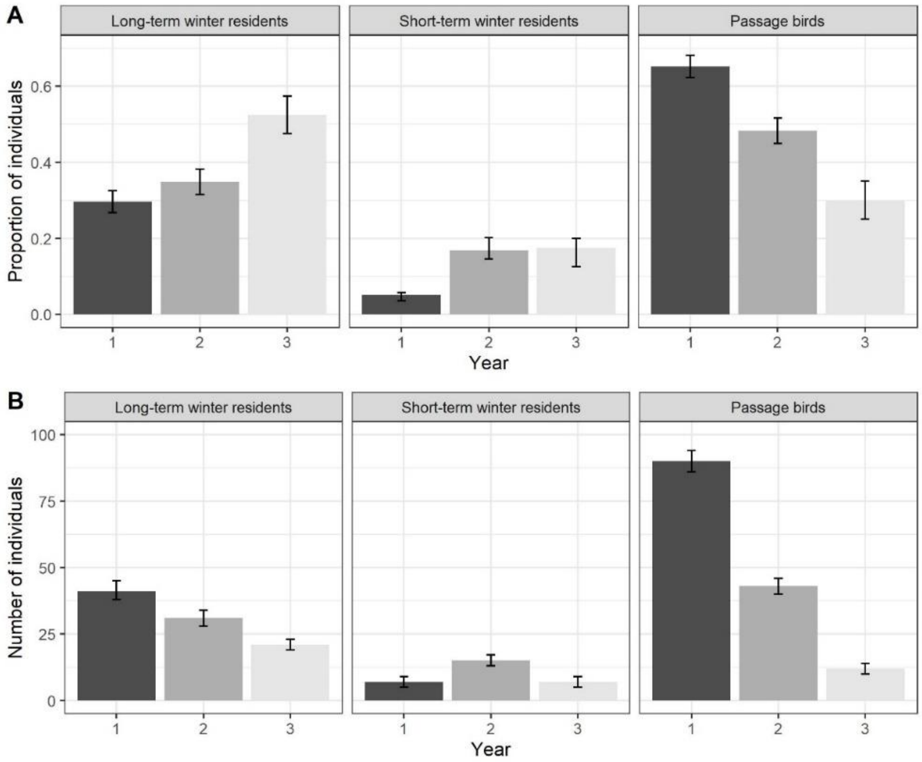


Figure A.4.2. Proportion (A) and number (B) of individuals in each residency category across years. 25% and 75% quartiles are shown as confidence intervals obtained through bootstrapping each category 1000 times. Number and proportion of individuals changes through years.

Appendix 4.3. Residency periods across years, age, sex, and location.

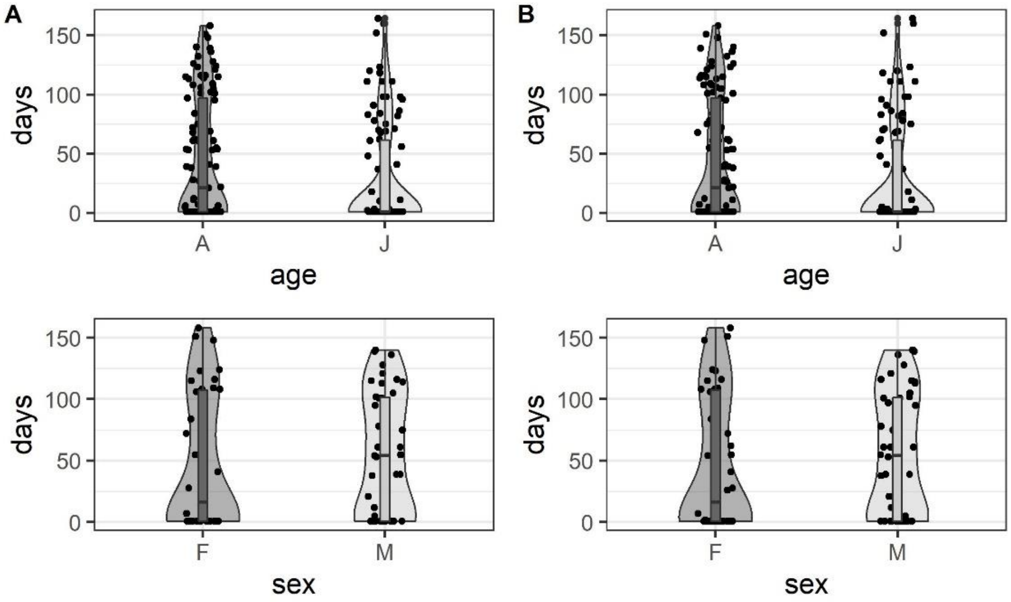


Figure A.4.3. Residency periods (in days) across years, age, sex, and location. (A) individuals that were detected >= 2 days all individuals and (B) all individuals.

Appendix 4.4 Arrival and departure dates.

ARRIVAL DATES

Earliest in record	
APLORI’s ringing dataset	24 September 2005
Resightings	10 September 2018
Year2. Birds that arrived before 31 Dec	
Earliest bird	10 September 2018
Mean	17 November 2018
Latest bird	7 December 2018
Median	21 November 2018
Geolocated birds	
Earliest bird	7 November 2019
Mean	26 November 2019
Latest bird	7 December 2019

DEPARTURE DATES

Latest in record	
APLORI’s ringing dataset	10 May 2006
Resightings	23 April 2019
Year1. Seen after 1 January	
Earliest bird	4 January 2018
Mean	8 March 2018
Latest bird	12 April 2018
Median	13 March 2018
Year2. Seen after 1 January	
Earliest bird	17 January 2019
Mean	7 March 2019
Latest bird	23 April 2019
Median	8 March 2019
Year1. Long-term winter residents	
Earliest bird	24 January 2018
Mean	18 March 2018
Latest bird	11 April 2018
Median	21 March 2018
Year2. Long-term winter residents	
Earliest bird	21 January 2019
Mean	19 March 2019
Latest bird	23 April 2019
Median	25 March 2019
Years 1 and 2	
Earliest bird	4 January
Mean	7 March
Latest bird	23 April
Median	10 March
Years 1 and 2. Long-term winter residents	
Earliest bird	22 January
Mean	18 March
Latest bird	19 April
Median	23 March
Geolocated birds	
Earliest bird	30 March 2019
Mean	12 April 2019
Latest bird	25 April 2019

Chapter 5. Fine-scale spatial use and habitat preference show evidence that Common Whitethroats are generalists at their non-breeding grounds

5.1 Abstract

Finding suitable habitats in which to spend the non-breeding season is crucial for Afro-Palearctic migratory birds because the quality of these habitats will likely have strong carryover effects on many aspects of their breeding success and overall survival. Understanding individual habitat preferences, a bird's ability to make small-scale movements to utilise the best habitats, and how individuals cope with seasonal changes to these habitats will give insight into an individual's flexibility to use multiple locations, overall habitat availability for a species, and so the degree of resilience populations may have to future habitat changes. In this chapter, we aim to measure wintering Common Whitethroats' *Curruca communis* fine-scale spatial movements, habitat preferences, and predictors of home range size. We then quantify how these change throughout the season to determine how flexible individuals are in their habitat use and to understand whether habitat becomes limited at our study site, causing individuals to have larger home ranges and/or to move to new sites as the season progresses. We calculate home ranges using Minimum Convex Polygons, and the mean distance between detections during three consecutive seasons (2017 – 2020). We explore how ranges and distances change between years and vary by age and sex. We then describe habitat preference at different spatial scales (site- and home range-scale), and habitat and spatial use changes throughout a single non-breeding period (2018 – 2019). We further explore how habitat preference is influenced by age and sex, and its effect on residency patterns and home range sizes. Finally, we quantify the time allocated to daily activities. Overall, a range of results showed that Whitethroats utilised habitats that were in abundance and had small home ranges with little significant variation through years, age, sex, and duration of residency, despite habitat changing through winter. The mean distance between an individuals detections (*i.e*. fine-scale movements; mean distance = 47 m ± 3.4 m) did not vary across years or by sex, but by age: first-years moved longer distances than adults. Winter residents established small home ranges (mean size = 3405 ± 435 m^2) with little variation by year, age or sex. Within home ranges, shrub cover decreased at the end of winter whilst bare ground cover and anthropogenic activities increased. Long-term winter residents had larger home ranges during the first half of the non-breeding season though short-term residents had similar range sizes whether resident in autumn or spring. At a site-scale, individuals were more likely to occupy relatively treeless, open sites with shrubs and some presence of anthropogenic activities. At a home range-scale, individuals generally used shrubby areas and avoided very open areas, and this preference was stronger in November than in February. First-years and adults showed similar habitat preference. Females also showed similar habitat preference to males, though females used areas with higher shrub and herb cover. Mean fine-scale movements were similar amongst individuals from different residency patterns. The degree of habitat change within home ranges of short-term winter residents was similar to long-term winter residents. Larger home ranges were correlated with potentially lower habitat quality. The proportion of time spent carrying out certain behaviours changed throughout the non-breeding season, reflecting priorities of initial territory establishment and pre- and post-migration periods. Because unoccupied sites had similar habitat characteristics as occupied sites, there was weak evidence for dominance-based habitat occupancy and as residency duration seemed little affected by habitat quality, we suggest that core wintering habitats do not limit Whitethroats so long as large shrubs are present. Individuals at core wintering sites can overcome strong seasonal changes by remaining at deteriorating sites, but why some individuals choose alternative wintering sites as a strategy is not clear.

5.2 Introduction

At least two billion Palearctic passerine and near-passerine birds migrate annually from Europe to spend the non-breeding season in sub-Saharan Africa (Hahn et al., 2009), where they remain for the largest portion of the annual cycle and where they experience challenging environmental pressures. Many of these species have suffered constant and often severe population declines over the last 50 years (Sanderson et al., 2006) and, due to their complex annual cycle, the exact causes of these declines are difficult to pinpoint and remain unclear. Nevertheless, because several breeding population trends have been highly correlated with conditions at the non-breeding grounds (Winstanley et al., 1974; Zwarts et al., 2009; Ockendon et al., 2014), loss and deterioration of wintering habitats and stopover sites are suspected to be playing an important role in these declines (Vickery et al., 2014).

Key to the Afro-Palearctic bird's survival, therefore, are the activities it undertakes during the non-breeding period: an inability to find suitable habitats will likely have strong negative carry-over effects on many aspects of its subsequent migrations and overall fitness (Newton, 2010). For example, if an individual remains at a low-quality habitat, we expect it to have a poorer body condition compared to individuals occupying higher quality habitats, which will decrease its winter survival probability, influence its departure date and migration, and could potentially lead to its arriving at lower quality breeding territories, negatively affecting its future breeding success. Thus, detailed information on habitat preference and its relation with an individual's home range size, age, and sex across all stages of the annual cycle, including non-breeding periods, give insights into habitat availability, flexibility to changing seasonal conditions, and susceptibility to habitat loss and degradation. Such data is essential for designing effective management plans to stop and revert these declines (Vickery et al., 1999; Blackburn & Cresswell, 2015).

How birds overcome these challenges and the strategy they use to select and utilise non-breeding habitats is highly related to the degree of specialism of a species' habitat requirements. In other words, whether they are generalists (*i.e*. feed on a variety of resources and thrive in a range of habitats) or specialists (*i.e*. feed on limited resources and have stricter habitat requirements). Each strategy reflects a trade-off between the capacity to exploit a variety of resources and the ability to use each one (Julliard et al., 2006). More specialised species can use resources more efficiently but have lower dispersal abilities, are more strongly regulated by intraspecific competition, and are constrained to certain habitats, whilst generalists are less restrictive of their habitat requirements, can exploit a variety of resources, can survive in suboptimal habitats and are more likely to cope with habitat changes both within and between non-breeding seasons (Salewski et al., 2002; Julliard et al., 2006). Therefore, specialism is a good strategy for unchanging and predictable conditions while generalism is a good strategy for changing and unpredictable conditions. In particular, Afro-Palearctic migrants arrive south of the Sahara Desert just after the peak of the rainy season when plenty of food is still available and remain even whilst resources decrease and overall conditions become harsh (Zwarts et al., 2009). Additionally, they meet resident bird species and other long-distance migrants with which they might have to compete with for space and food.

Overall, Afro-Palearctic migrants seem to be generalists during the non-breeding season, even to a similar degree as their Afrotropical resident counterparts (Ivande & Cresswell, 2016), and thus occupy a wide variety of habitats, both natural and human-modified. Once at the non-breeding grounds, however, and even when individuals are generalists, there is a trade-off between finding optimal high-quality habitats and reducing the costs of moving. As the dry season progresses habitats deteriorate, so individuals can either opt to remain at a low-quality habitat that could potentially lead to death or a decrease in fitness, or risk moving to another unfamiliar site, which increases risks through further migration. Under this scenario, generalists could probably decide to remain at suboptimal habitats, facing higher competition as the season progresses but avoiding the risk of moving and discovering new terrain, whilst specialists would have to find other sites with their specific requirements, assuming an increased risk of predation due to movement and initial unfamiliarity with a new site.

How individuals utilise non-breeding habitats is also important. To survive the non-breeding season and cope with deteriorating conditions, many Afro-Palearctic migrants restrict their activities to small areas that secure and contain all the necessary resources (*i.e*. home ranges). Differences in the degree of generalism within and between species, and the ability of individuals to deal with changing conditions will be reflected in their space use (*i.e*. the size of their home range) and the number of different home ranges used during the non-breeding period (*i.e*. the period of residency within a particular home range; Chapter 4). Home ranges also depend on the individual and species (Greenberg, 1986; Salewski & Jones, 2006) and their size can indirectly reflect habitat quality, as larger territories are required to meet energy requirements when food resources are low and unpredictable (Harestad & Bunnell, 1979; Zabel et al., 1995; Williams et al., 2016). In addition, activity budgets, or how individuals distribute their energy to daily activities, may compensate for low territory quality. Activity budgets may then provide an index of how well migrants meet energetic demands in relation to food resources, habitat quality (*i.e*. longer foraging time may reflect lower food resources), and local environmental changes (by changes in time used to carry out a certain behaviour; Aborn & Moore 2004).

Undoubtedly, not all habitats can be optimal and variable intraspecific densities of migrants across sites show that habitat selection and even competition occurs at some scale, even within generalist species. Given selection of appropriate winter home ranges affects overall survival, some species exhibit dominance-based habitat occupancy, where habitats with optimal resources are occupied by behaviourally dominant birds (mainly larger and more experienced individuals, *i.e*. adults and/or males) and subdominant individuals (smaller and inexperienced individuals, *i.e*. first-years and/or females) are forced to occupy lower-quality habitats or adopt a non-territorial strategy (Hutto, 1980; Mazerolle & Hobson, 2004; Brown & Long, 2006). Therefore, home range size is influenced by several internal (*e.g*. sex, age) and external (*e.g*. resource availability) factors, so home range can also indirectly reflect habitat quality (Blackburn & Cresswell, 2016b; Willemoes et al., 2017). Individuals found in suboptimal home ranges, particularly as the dry season progresses, will then need to decide whether the risk of moving to another home range in an unfamiliar area outweighs the risk of running out of resources.

The decision as to whether to remain or move is extremely important in a region as seasonally changeable as Africa. Rains occur in the Sahel region from July to September and, as one progresses further south, rainfall occurs for longer periods until reaching the equator, where rain is constant throughout the year (Jones, 1995). Thus, the quality of habitats above the equator varies strongly throughout the season and may only be suitable for a species for a limited period (Morel, 1973; Jones, 1995). Additionally, West Africa is currently undergoing high anthropogenic habitat changes, especially due to deforestation and conversion to agriculture, decreasing the quality of many sites. To overcome this, individuals need to decide whether to move south following the rains to secure resources or adapt to the changes by increasing home range size and/or increasing foraging effort at the same site. An individual's decision, however, may not be constant through the years as habitats depend on the extent of summer rainfall across West Africa, which vary annually. There may be "good" years where there is abundant habitat available and little change throughout the dry season, and "bad" years where there is limited habitat available that is rapidly degrading throughout the period and individuals may vary strategies accordingly. Rainfall has been gradually declining through much of the 20th Century (Zwarts et al., 2009).

The Common Whitethroat *Curruca communis* is a widely distributed Afro-Palearctic migrant that breeds across Europe and into Siberia. During the non-breeding period, they inhabit scattered scrub and thickets, bushes at oases, open woodland with good shrub cover, and gardens (Urban et al., 1997). In Nigeria, specifically, they have been seen to inhabit open wooded savannahs with high shrub cover and also have been seen to avoid dense tree growth and areas with trees and shrubs > 2.5 m (Moreau, 1972; Wilson & Cresswell, 2006). Mixed Sahelian woodlands have been found to act as important habitats for Whitethroats during spring migration compared to woodlands of lower diversity and tree density, rangelands, and farmlands (Vickery et al., 1999).

Whitethroats underwent a large population decline in the mid-1960s. In Europe, they were abundant and widely distributed until 1968, and from then until 1973 many populations declined by over 60% (Winstanley et al., 1974). These declines were associated with a shortage of food, water, and shelter availability in their African grounds caused by extreme drought conditions in the Sahel (Winstanley et al., 1974; Hjort & Lindholm, 1978; Baillie & Peach, 1992; Newton, 2004). Even though its population trends are currently increasing (BirdLife International, 2019), populations have yet to fully recover (Zwarts et al., 2009), suggesting that the number of birds that the wintering areas can support has reduced (Baillie & Peach, 1992). This highlights how dependent Whitethroats are upon conditions at the non-breeding grounds and emphasises the importance of studying habitat preferences and habitat use during this period. Despite this, little research has been carried out and much data is still lacking for many migratory species.

In this chapter, we utilise a natural experiment where we expect habitat to deteriorate throughout the non-breeding season to draw conclusions regarding the Whitethroats' degree of specialism and overall habitat availability by determining whether individuals compensate for this by expanding their home range or moving to another site.

5.3 Aims

The general aim of this chapter is to measure how individual fine-scale spatial movements, habitat preference, and predictors of home range sizes of Whitethroats found in a guinea savannah change throughout the non-breeding period, to determine the species' flexibility in habitat use and whether habitat becomes limited at our study site, causing individuals to establish larger home ranges and/or move to new areas as the season progresses. The specific aims and corresponding predictions are the following:

1) To determine Whitethroats' fine-scale movements and home range sizes and how they vary between years and individuals from different age and sex groups. We predict that individuals will move short distances and use relatively small home ranges within our study site. We also predict that individuals will, in general, have a similar degree of movement and home range size across years, so long as environmental conditions are similar. If not, we expect longer distances to be travelled and larger areas to be used during years with harsher conditions (*e.g*. dry years). We expect first-year birds to, on average, arrive at lower-quality areas, which will require them to move longer distances and use larger home ranges. No breeding occurs during this period, thus we do not expect strong differences between sexes.
2) To confirm and understand how habitats used by Whitethroats at the beginning of the non-breeding season change throughout the period (between November and April). As the non-breeding season progresses, conditions become drier, crop cover decreases and human activities such as wood extraction and bushfire incidences increase, thus we expect habitats to have less available/optimal resources towards the end of the season. We therefore expect there to be an overall reduction of vegetation biomass, especially bushes and herbs, towards the end of the seasons. Because of this, we expect individuals to move longer distances as the dry season progresses when resources are scarce and limited, increasing distance travelled and home range size.
3) To describe habitat preferences at a site- and home range-scale and how these change throughout the season and between individuals from different age and sex groups.

Whitethroats have been reported to winter in open wooded savannahs with good shrub cover and to avoid areas with tall trees (Cramp, 1992; Wilson & Cresswell, 2006), thus we expect individuals to mainly occupy areas with similar characteristics and to avoid densely wooded areas. Within home ranges, we expect individuals to use patches of dense bushes where birds can forage, detect predators, and seek protection. By the end of the winter, we expect an important change in an individual's home range composition: shrub, herb, and crop cover should decrease, and home ranges should then encompass more open areas with sparse vegetation, thus we do not expect birds to show clear habitat preferences at this time. Because first-year birds arrive stochastically and later than adults, we would expect them to arrive at unoccupied lower-quality areas with higher tree and herb densities compared to adults. Winter habitat segregation between sexes does not seem to occur frequently in small Afro-Palearctic migrants, so we do not expect strong habitat preference differences between males and females.

4) To test how spatial use changes with residency patterns and to test whether habitat characteristics influence home range size. We expect movements and home range sizes to strongly correlate with residency pattern: passage birds, for example, will be scouting the area, moving longer distances, and may not be as spatially restricted as winter residents. On the other hand, we expect winter residents to occupy small home ranges. As winter progresses we expect to find a greater, more detrimental degree of habitat change in home ranges occupied by short-term winter residents compared to those occupied by long-term winter residents: the former potentially leave the area due to lack of resources, while the latter remain at a single site and expand their home range to meet their requirements. We also expect that home range size will depend on certain habitat characteristics and quality: that smaller home ranges will reflect higher quality and that this relationship will be stronger for long-term winter residents.
5) To quantify time allocation to daily activities and how it changes throughout the non-breeding season. We expect individuals to spend more time carrying out aggressive behaviours such as perching, scanning, and vocalising at the beginning of the season whilst scouting the area and establishing a home range, and an increase in foraging effort during migration periods. We also expect activities that require less movement during the peak winter period when temperatures are low and there is low intraspecific competition.

5.4 Methods

5.4.1 Study site, mist-netting, resighting efforts, and residency categorisation

See Chapter 2 for general methods and Chapter 4 for residency categorisation parameters.

5.4.2 Fine-scale movements and home ranges

To understand and determine the degree of fine-scale movements amongst individuals, we obtained the centroid of each individual's detections and calculated the mean distance between all detections and their respective centroid (Fig. 5.1a; Appendix 5.1) using the "*distHaversine*" function from the "*geosphere*" package version 1.5.10 (Hijmans, 2019) in R. We excluded all individuals that were detected only once during a non-breeding season.

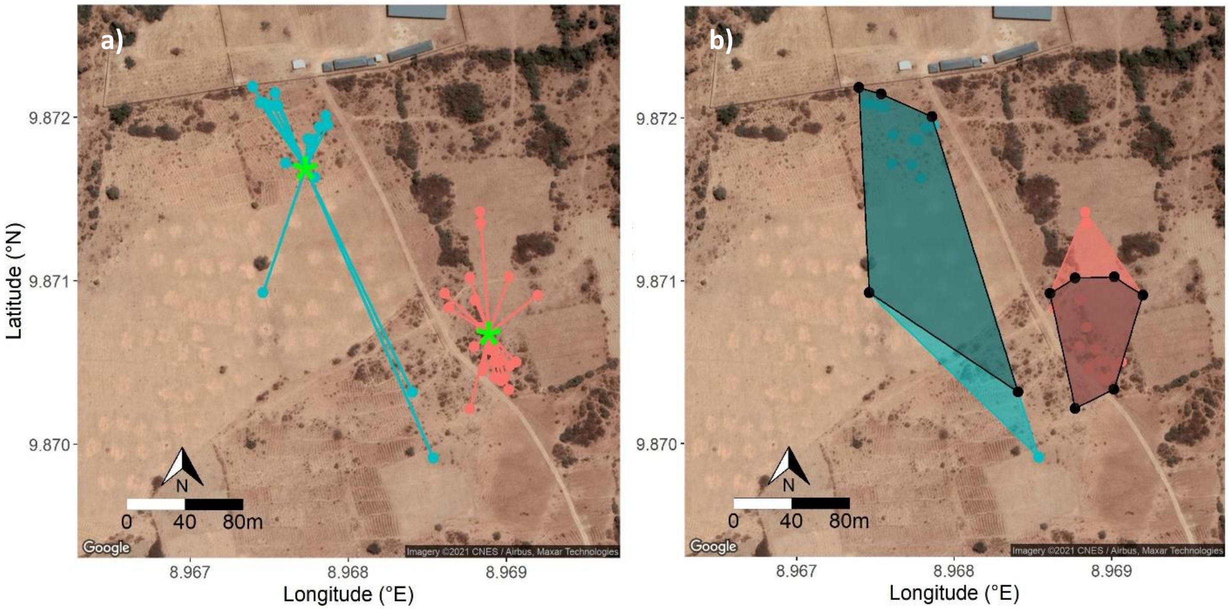


Figure 5.1. Fine-scale movements and home ranges. a) Fine-scale movements obtained by calculating the centroid (shown with a green star) and averaging the distance between all the detections and their respective centroids (mean of all lines) of two individuals in year1. Each colour represents an individual and each point represents the coordinate it was detected at. b) Minimum Convex Polygons (coloured polygons) and 95% Minimum Convex Polygons (black polygons) of the same two individuals.

We then calculated the home range (defined as the area traversed by the individual in its normal activities or the area that contains all necessary resources that may or may not be defended or habitat used by individuals; Burt, 1943), of individuals that had at least five detections throughout a non-breeding season using the "*mcp*" function from the "*adehabitatHR*" package version 1.5.10 in R (Calenge, 2006). To determine home ranges, we calculated the Minimum Convex Polygon (MCP) by identifying and connecting the outermost points of each individual's locations and calculating the area in m^2 (White & Garrott, 1990; Fig. 5.1b). Even though this method has a series of disadvantages (*e.g*. it highly correlates with sample size and could include areas that individuals did not necessarily visit; Barg et al., 2005) it is a simple method to estimate broad spatial coverage and can be compared with results from other studies. In many studies, the 95% MCP (Fig. 5.1b; Appendix 5.1), the smallest spatial area in which an animal carries out 95% of its activities, is also calculated to eliminate potential outliers and long dispersal trips. However, we believe that in the case of this study, where we have few detections per individual and work at a very fine spatial scale, MCPs could give us a better understanding of the spatial behaviour of the birds we are studying. Nevertheless, we will present results obtained from both methods. All individuals analysed were either short-term winter residents or long-term winter residents (individuals that remained from eight days to six months at the study site; see Chapter 4 for more details). We pooled data obtained from mist-netting captures, weekly resightings, and radio tags. Both fine-scale movements and home ranges were calculated for three consecutive non-breeding seasons (2017 – 2020).

5.4.3 Habitat sampling

Habitat sampling was carried out during year2 in (1) late November, once individuals were detected at least three times and had potentially settled at their territories, and (2) February, at the start of spring migration. Twenty-one territories were sampled: 14 of them were identified as areas utilised by long-term winter residents (Fig. 5.2a) and seven of them by short-term autumn residents (Fig. 5.2b). To understand habitat preference at a site-scale, *i.e*. whether individuals select territories based on the presence or absence of certain characteristics, a 50-m diameter plot (~1950 m^2) was surveyed at the centre of each territory, which was located by averaging the longitude and latitude coordinates of all an individual's detections. If the territory was big and the plot did not cover areas where individuals were usually seen, then it was moved where it would encompass most of the detections and would be more representative of the actual territory and habitat preference (purple plots in Figs. 5.2a and b). Some plots from long-term winter residents were shifted in February as detections increased, whilst the same plots were sampled in February for short-term winter residents. Additionally, a 50-metre diameter plot was surveyed at 13 random sites that had no or very sporadic bird detections (Fig. 5.2c). The same plots were repeated in November and February.

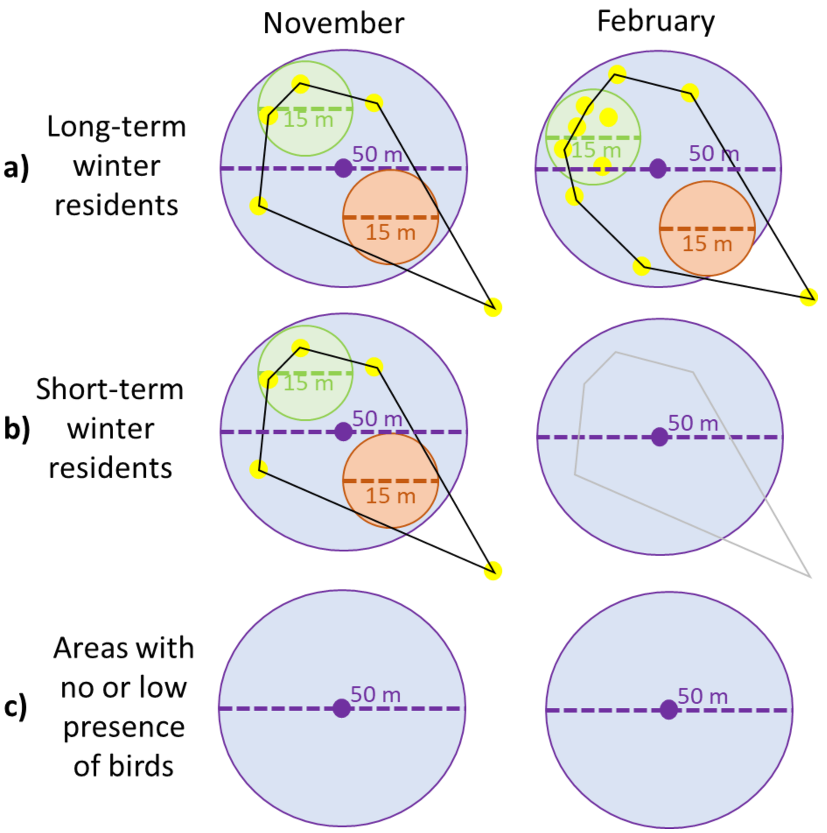


Figure 5.2. Vegetation sampling. Yellow dots represent detections and black polygon represents the territory (Minimum Convex Polygon). Purple circles represent 50-m diameter plots. Green 15-m diameter circles represent areas where birds were mostly seen ("present" area), and red 15-m diameter circles represent areas where birds were never, or rarely, seen ("absent" area).

To understand habitat preference at a home range-scale, *i.e*. whether individuals utilise small areas with certain characteristics within a territory, two 15-m diameter plots (~180 m^2) were surveyed, one where birds were mostly seen ("present" plot; green plots in Figs. 5.2a and b) and one where birds were never, or rarely, seen ("absent" plot; red plots in Figs. 5.2a and b). Plots could shift according to new detections. This was carried out during both months (November and February) for long-term winter residents and only sampled in November for short-term winter residents. Three of the 14 long-term residents were in fact regarded as short-term individuals until subsequent vegetation sampling was completed, thus their 15-m plots within territories were not sampled in February. Sampled variables are described in Table 5.1.

Table 5.1. Description of sampled habitat variables.

Variable codes	Description
Trees	Percentage of tree coverage
Shrubs	Percentage of shrub coverage
Herbs	Percentage of herb coverage
Bare_rock	Sum of the percentage of bare ground and rock coverage
Crops	Percentage of active crop coverage
Grazing	Presence (1) or absence (0) of cow and goat grazing
Human_act	Presence of human activities scaled from “0-3”. 0=no activity, 1= low intensity, 2=medium intensity, 3=high intensity. Examples of activities are wood extraction, presence of human faeces, road building, clearing, tin mining, and presence of bushfire.

5.4.4 Daily activity budgets

From October to April of years 2 and 3 we analysed the behaviour of Whitethroats by carrying out time-activity budget observations on encountered individuals, regardless of whether they were ringed. Observations were undertaken between 0630 and 0930 hrs, and again between 1500 and 1800 hrs. A total of 142 observations were undertaken, 96 in year2 and 46 in year3. Once birds were detected, they were observed continuously for up to 280 seconds. The durations of all activities were recorded on a sheet of paper whilst observing the birds. The following activities were noted: (1) perching and resting: regarded as the time an individual was seen still without engaging in any obvious active behaviour, (2) flying: time spent flying between bushes, (3) foraging: time spent chasing after prey or actively eating insects, fruits or flowers, (4) scanning: time spent vigilant, (5) preening: time an individual spent preening its feathers, (6) moving in the bush: time spent moving within a bush (most of these observations are likely to be individuals foraging), and (7) vocalising: time spent calling or singing. We also added an “unknown” category for instances where it was unclear what the individuals were doing, mainly because the bird was not visible. All birds were observed with binoculars and a two-minute settling period was left whenever any kind of disturbance occurred that could have affected an individual’s normal behaviour.

We proceeded to calculate the proportion of time spent on each activity (excluding the time spent “unknown”) for each individual. We then grouped and calculated the mean proportion of time spent undertaking each activity throughout the non-breeding period. For this, we divided the period into three stages: (1) “early-stage”, which comprised data collected in October and November and represented autumn migration and territory scouting and settlement, (2) “mid-stage”, which comprised data collected between December and February, representing the “stationary” winter period, and (3) “late-stage", which comprised data collected in March and April and represented the preparation for spring migration.

Inter- and intra-specific interactions were also recorded and are described in Appendix 5.2.

5.4.5 Statistical analyses

All statistical analyses were carried out in R version 4.0.5 (R Core Team, 2020) and RStudio version 1.4.1106. A statistical significance level of $p < 0.05$ was chosen to reject the null hypotheses. Birds that could not be confidently aged or sexed were excluded from models including age and sex as predictors. The sequential Bonferroni procedure was used to correct for Type I errors that might arise from multiple tests of the same hypothesis.

Fine-scale movements and home range size

General Linear Models (GLMs) were used to compare both fine-scale movements and home range sizes across years and between individuals from different age and sex groups (*i.e*. first-year and adult birds, and female and male adult birds). Because the total number of detections could have an important effect on home range size and could then act as a confounding variable for the total duration at the site (*i.e*. individuals that remained longer were more likely to be detected), we decided to explore this further, *a priori*, by performing the following ANOVA: MCP ~ duration (days) + total detections. We then found that the more detections an individual had, the larger its home range ($F(_{1,72}) = 8.1$, $p = 0.006$), but home range did not vary statistically according to residency duration ($F(_{1,72}) = 2.3$, $p = 0.13$; Fig. 5.3) when controlling for number of detections. To account for this and, to obtain reliable results, we randomly selected five detections from each individual, calculated their MCPs and 95 MCPs and repeated the analyses. Five detections were chosen to maximise both the number of detections and sample size. Because similar results were found when using all detections, we present these results in the Results sections and show the results from the five random detections in Appendix 5.3.

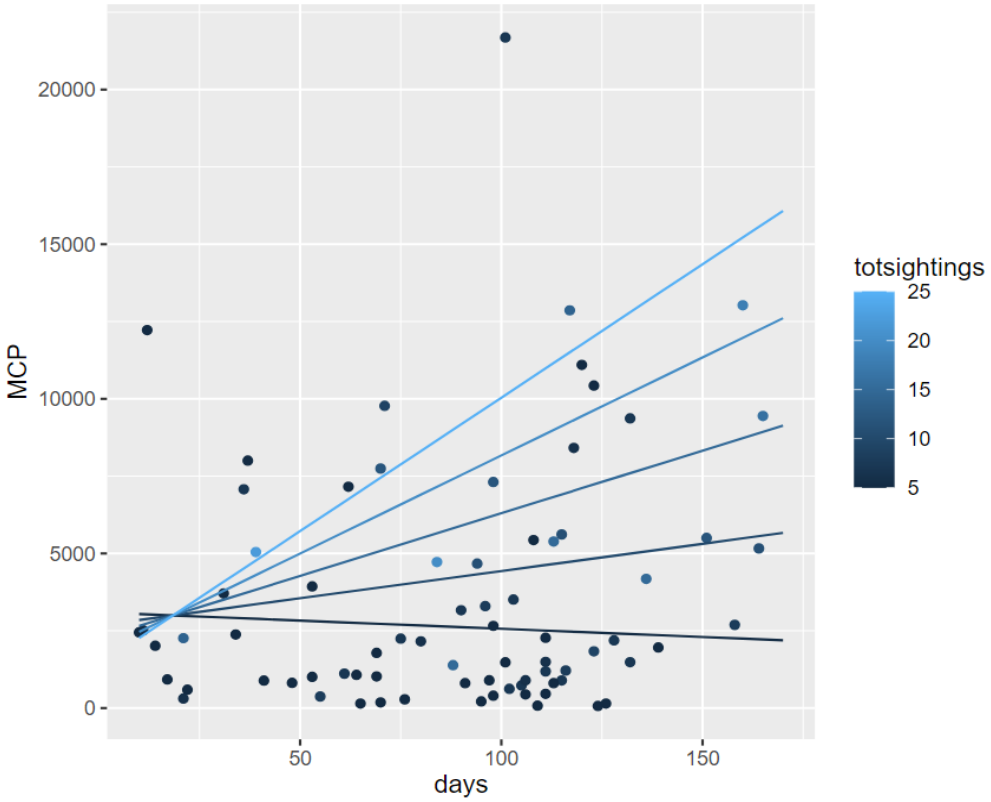


Figure 5.3. Relation between the duration spent at the study site and home range size, accounting for the total number of detections. The more detections, the more pronounced the positive effect.

Habitat change

Paired *t*-tests and Chi-squared tests (χ^2) were used to measure changes in habitat variables between November and February within home ranges. Data were obtained from the 50-m plots within the home ranges of short- and long-term winter resident birds (*n* = 21). Because only two individuals had crops within their territories, this habitat variable could not meaningfully be statistically compared.

To test whether individuals change spatial behaviour across the non-breeding season, we performed a GLM to compare the mean distance travelled by individuals early in the season (data collected between October and December) with later in the season (between January and April) in years 2 and 3. Data from year1 was excluded because no resightings were carried out during the first half of the fieldwork period. Additionally, we compared home range size changes in two ways: (1) we performed a *t*-test to compare home range sizes between autumn and spring short-term residents, and (2) we examined data from long-term residents that had over 10 detections (at least five between October and December ("early") and five between January and April ("late")), estimated their respective home ranges during both periods and performed paired *t*-tests to determine whether there were differences (early *vs*. late).

Habitat preference

We conducted several Principal Component Analyses (PCAs) to understand habitat preference at the site- and home range-scales. PCAs are a multivariate statistical technique that reduces the number of variables while retaining most of the data's variation (Ringnér, 2008). They construct new variables (or characteristics) based on the measured variables to obtain principal components: the first principal component will explain most of the data's variation, then the second, etc. This technique is effective for addressing the problems that arise from large number of variables, multicollinearity and small sample sizes (Graham, 2003). In most cases, we used the three highest scored principal components per dataset to account for > 70% of the total variation. Although taken into account, results from the third principal component did not have an important impact on our results and are not going to be explained further, other than stating their *p*-values. For every PCA, we carried out a Bartlett's Test of Sphericity to test for a significant correlation between variables: if variables are not correlated, a data reduction technique like a PCA cannot compress variables into linear combinations and is not suitable for this analysis.

To characterise home ranges and explore general habitat preference (or site-scale), two PCAs were carried out with data obtained from all the 50-m diameter plots (21 from home ranges and 13 from random plots), the first for data collected in November (from now on PCA50n; Bartlett's test: $\chi^2(_{21}) = 1119$, $p < 0.001$), and the second for data collected in February (from now on PCA50f; Bartlett's test: $\chi^2(_{21}) = 1108$, $p < 0.001$). The top two principal components of each PCA were further explored to understand how the variables were grouped and correlated and what type of habitat they broadly represented (*e*.*g*. bushy, forest, anthropogenically modified). Binomial GLMs were then calculated to explore whether the occurrence (presence *vs*. absence) of an individual at the plots were associated with any of the three principal components (occurrence ~ PC1 + PC2 + PC3). Additionally, to test whether individuals showed a strong preference for a particular habitat variable, which we predicted were bushes, we performed *t*-tests comparing the coverage percentages of habitat variable between plots surveyed within occupied home ranges with those surveyed at random sites and unoccupied home ranges.

To understand individual preferences for certain habitat variables at a very fine scale, within a home range, PCAs were carried out from data obtained from the present and absent 15-m plots surveyed within home ranges – one for November (from now on PCA15n; Bartlett's test: $\chi^2(_{21}) = 1393$, $p < 0.001$) and another for February (from now on PCA15n; Bartlett's test: $\chi^2(_{21}) = 649$, $p < 0.001$). Similar to above, all three principal components for each PCA were further explored to try to understand how variables were grouped and correlated and what type of habitat they represented. Binomial GLMs were then calculated to explore whether occurrence (presence vs. absent) was statistically defined by any of the three principal components (occurrence ~ PC1 + PC2 + PC3) and *t*-tests were performed to compare variables between absent and present plots within home ranges.

Additionally, *t*-tests and Chi-squares were performed to assess habitat preference differences at both scales between adult and first-year birds and between adult females and males.

Home range and habitat structure

General Linear Models (GLMs) were used to compare fine-scale movements between individuals from different residency patterns (*e.g*. passage birds, short-term winter residents and long-term winter residents) and to explore whether home range size varied according to residency duration at the site.

To test whether habitat variables changed more in areas used by individuals that left the area (short-term autumn residents) than among individuals that remained throughout the non-breeding season (long-term winter residents), we carried out a PCA (PCAres) to compare the differences between November's and February's 50-m plots (*e*.g. tree cover November – tree cover February for each individual) for each habitat variable amongst both groups. Because the first two components explained 75% of the total variation, the GLM used to explore whether the decision to leave or remain was statistically defined by any of the first two principal components (residency_pattern ~ PC1r + PC2r, family = binomial). Crop cover was excluded from the analysis because it was the only variable that did not show any difference between months. We then examined what were the changes in PC1r and PC2r for the two residency classes (*e.g*. PC1r ~ res and PC2r ~ res).

A PCA (PCAhab) was carried out to explore whether home range size varied according to habitat structure. To do this, we used information collected from the 50-m plots surveyed within territories and averaged the November and February values of each habitat variable for each individual. We used information gathered from both short-term and long-term winter residents. Predictors of territory size were further explored with GLMs including the first three principal components, accounting for residency pattern (MCP ~ PC1 + PC2 + PC3 + residency). Because neither age nor sex was significantly important for explaining home range sizes (see Fig. 5.5) and the sample size was small, they were excluded from the model. We also investigated whether these principal components had any interaction within residency patterns, this is to say, whether the three PCs affected the home ranges of short-term and long-term winter residents similarly (MCP ~ PC1*residency + PC2*residency + PC3*residency). Because PC1 had the least effect, was not statistically significant either as a single variable (Bonferroni *p*-

value = 1) and did not have a significant interaction with residency (Bonferroni *p*-value = 1), it was excluded from the model. The final model was MCP ~ PC2*residency + PC3*residency.

Daily-activity budgets

Wilcoxon tests were performed to compare the proportion of time spent during each activity between the early (October – November), mid (December – February) and late (March – April) stages of the non-breeding season.

5.5 Results

5.5.1 Fine-scale movements and home range sizes

Seventy-four individuals were detected at least twice during year1, 60 during year2 and 31 during year3 (Appendix 5.1). One individual detected in year1 moved, on average, over 500 m, twice the distance that the second-longest individual moved, thus was considered an outlier and was removed from further analyses.

On average, the mean distance between all an individual's detections and its respective centroids, representing the general movement within an area of one individual, was 47 m (± 3.4 m; Fig. 5.4). There was no statistically significant difference of the mean distance across years ($F_{(2,161)} = 0.8$, $p = 0.45$) with a mean distance of 51 m (SE = 5.7 m) in year1, 44 m (SE = 5.3 m) in year2, and 41 m (SE = 5.8 m) in year3. Mean distance was significantly different between first-year birds and adults ($F_{(1,152)} = 6.7$, $p = 0.01$), first-year birds moved longer distances (mean = 58 m, SE = 7 m, adults mean = 40 m, SE = 3.8 m), although the biological significance of the difference (18 m) was not large. No differences were observed in the mean distance across sexes of adult birds ($F_{(1,80)} = 0.15$, $p = 0.7$; mean males = 39 m, SE = 5.6 m and mean females = 36 m, SE = 5.8 m; Fig. 5.4).

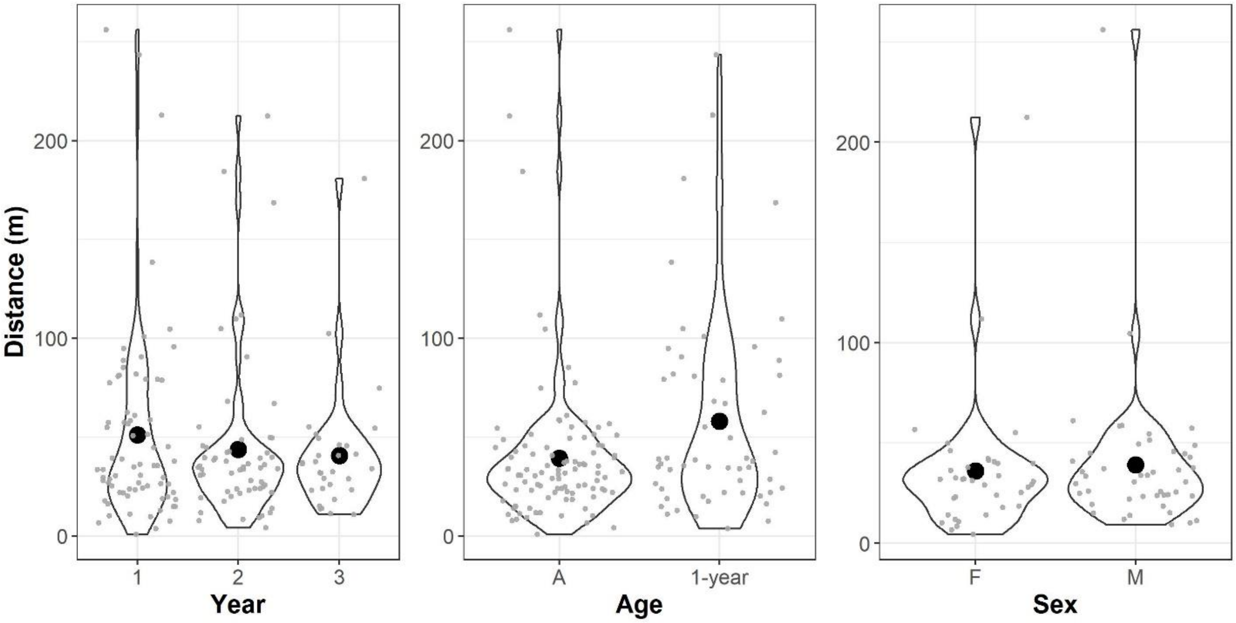


Figure 5.4. Mean distance between detections and centroids of all individuals seen at least twice within a non-breeding season. The black dot represents the mean for each category. There were no significant differences between categories.

Individuals established and maintained small home ranges at the study site. We calculated the MCPs and 95% MCPs of 82 individuals: 26, 34, and 22 individuals in years 1, 2, and 3, respectively (Table 5.2, Fig. 5.5a, Appendix 5.1).

Table 5.2. Home range sizes. Home ranges obtained from MCPs and 95% MCPs from individuals who had at least five detections throughout a non-breeding season. Values are presented in m^2 as means ± SE. *n* = sample sizes.

Year		**All**	**Age**		**Sex**	
			Adults	**First-years**	**Females**	**Males**
	n	82	55	23	21	25
all	MCP	3405 ± 435	3079 ± 519	3860 ± 852	2789 ± 705	2876 ± 575
	95% MCP	1524 ± 208	1364 ± 196	1767 ± 513	1286 ± 351	1539 ± 296
	n	26	10	13	4	3
1	MCP	2460 ± 652	1996 ± 768	2487 ± 1044	3275 ± 1780	1561 ± 657
	95% MCP	798 ± 197	683 ± 319	927 ± 302	1191 ± 764	348 ± 210
	n	34	23	10	8	13
2	MCP	3710 ± 604	2619 ± 581	5645 ± 1250	2245 ± 784	3093 ± 901
	95% MCP	1905 ± 398	1248 ± 245	2858 ± 1042	995 ± 434	1473 ± 335
	n	22	22	0	9	9
3	MCP	4052 ± 1079	4052 ± 1079	NA	3056 ± 1356	3001 ± 938
	95% MCP	1796 ± 376	1796 ± 376	NA	1586 ± 674	2031 ± 627

The 95% MCPs were close to being statistically significantly different between years ($F_{(2,73)} = 2.46$, $p = 0.09$); year2 individuals had slightly larger home ranges, but not strongly significant, than individuals in years 1 and 3 but full MCPs did not vary significantly ($F_{(2,73)} = .75$, $p = 0.48$). Even though first-year birds tended to have larger home ranges when compared to adults, this difference was not statistically significant in either of the MCP methods (95% MCP: $F_{(1,70)} = 1.5$, $p = 0.22$; MCP: $F_{(1,70)} = 1.43$, $p = 0.24$; Fig. 5.5b). There were also no differences amongst adult females and males (95% MCP: $F_{(1,42)} = 0.3$, $p = 0.59$; MCP: $F_{(1,42)} = 0.005$, $p = 0.95$; Fig. 5.5c). Results were similar when exploring the data of five randomly selected detections for each individual: home range did not vary statistically according to time spent at the study site (95% MCP: $F_{(1,74)} = 0.003$, $p = 0.95$; MCP: $F_{(1,74)} = 0.08$, $p = 0.79$) or to all other variables (Appendix 5.4).

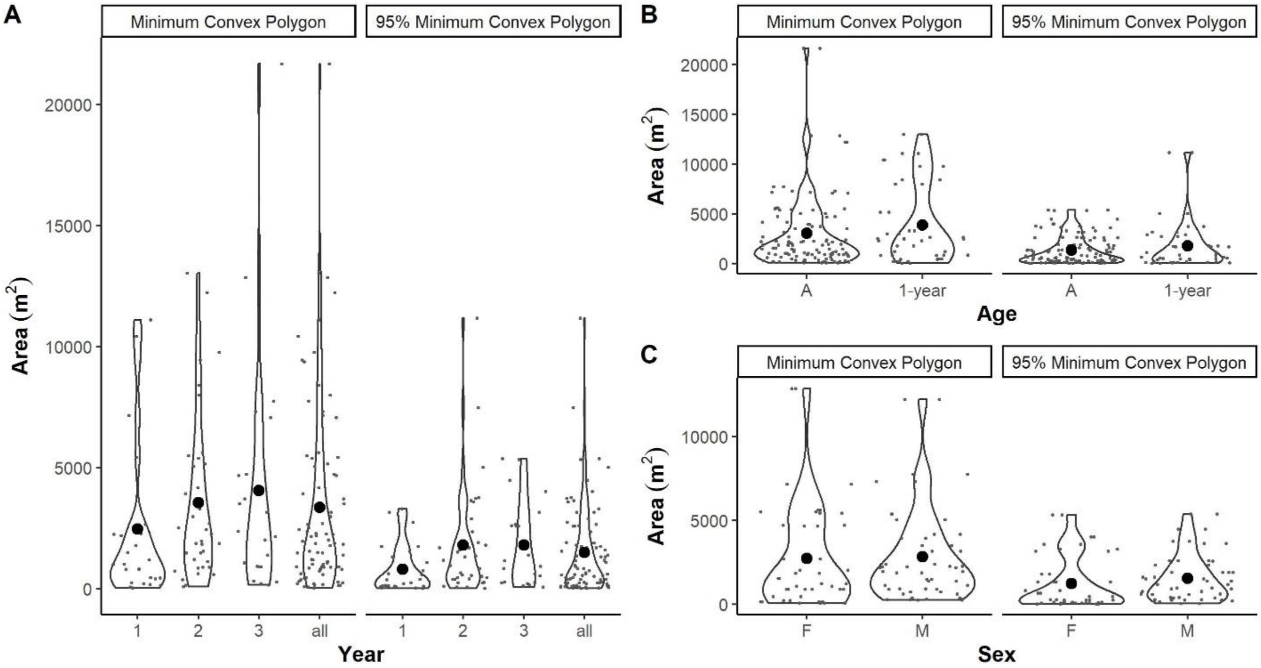


Figure 5.5. Home ranges. Home ranges (m^2) obtained from MCPs and 95% MCPs (a) across years, (b) from first-years and adults and (c) from adult females and males. All individuals had at least five detections throughout the non-breeding season. The "all" category contains pooled data. Big black dots show means. Scattered dots represent exact values of each individual.

5.5.2 Habitat changes throughout the non-breeding period

Vegetation changes

Some habitat characteristics of home ranges changed significantly between November and February (Table 5.3, Fig. 5.6): shrub cover decreased at the end of the season whilst bare ground and rock cover increased. The intensity of anthropogenic activities also increased significantly during the end of the season ($\chi^2(_3)$ = 12.1, p = 0.007). The other variables (*i.e*. tree, herb, and crop cover, and grazing ($\chi^2(_1)$ = 0.23, p = 0.63)) remained similar throughout. In November, home ranges have higher shrub cover whilst in February, at the end of the dry season, human activities become more intense and home ranges encompass more open ground.

Table 5.3. Habitat change between November and February. Results from paired *t*-tests. Crop cover and grazing variables are excluded from the table. Bold *p*-values indicate statistical significance with an alpha value of 0.05. *n* = 21 individuals.

Habitat variable	**Mean November**	**Mean February**	***t***	***p*-value**
Tree cover	5.2	4.3	1.4	0.18
Shrub cover	57.5	38.2	6.1	**< 0.001**
Herb cover	25.8	22.5	1.2	0.23
Bare ground and rock cover	9.5	32.9	-6	**< 0.001**

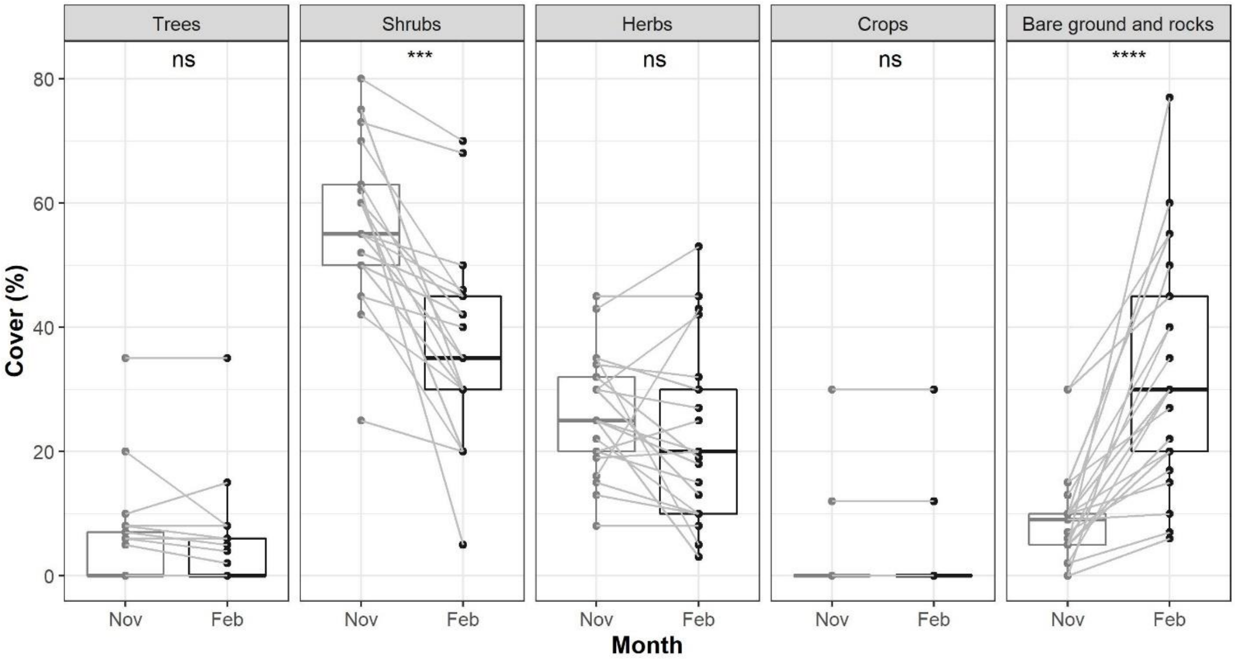


Figure 5.6. Changes in tree, shrub, herb, crop and bare ground and rock percentage cover. Grey lines join same individuals. Significance is specified as ns (non-significant) or with *** (highly significant).

Fine-scale movements and home range changes

The mean distance between all detections of an individual in years 2 and 3 during October and December was similar to the mean distance between January and April ($F_{(1,109)} = 0.005$, $p = .94$; mean early = 35.8 m, SE = 3.7 m and mean late = 35.3 m, SE = 4.9).

Seasonality (early = October – December and late = January – April), however, did not seem to statistically influence home range sizes as autumn short-term residents had similar home ranges to spring short-term residents (mean autumn = 3933 m^2, SE = 1100 and mean spring = 2402 m^2, SE = 1037; $t = 0.97$, df = 15, $p = 0.35$), though autumn birds tended to have larger home ranges. However, when comparing changes in home ranges of long-term winter residents that had at least five detections during each period, individuals had larger home ranges between October and December when compared to between January and April (paired *t*-test: $t = 2.34$, df = 10, $p = 0.04$; Fig. 5.7). Note this is the opposite direction to predicted.

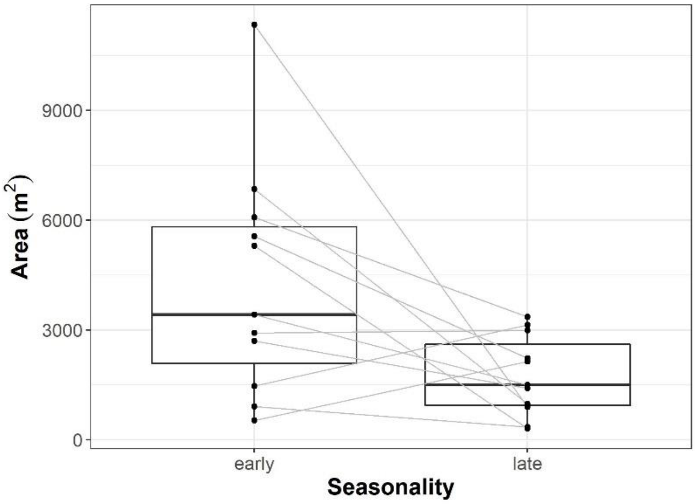


Figure 5.7. Changes in home ranges. The difference in home range size of long-term winter residents between the early part of the season (October – December) and the late part of the season (January – April). Individuals decreased the size of their home range.

5.5.3 Habitat preference

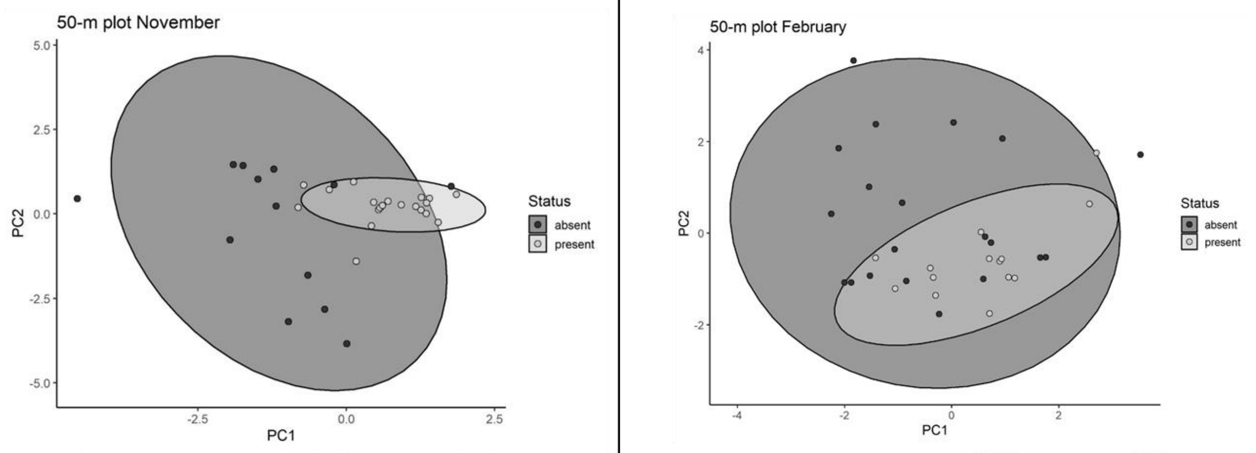
At a site-scale

PCA results from the 50-m plots surveyed at home ranges and randomly selected sites show that in November (PCA50n) the first principal component (PC1N, which accounted for 27% of the total variation) was correlated with a strong presence of shrubs, an important degree of human activities and grazing, a moderate presence of bare ground and rock cover, and a very low presence of trees (Fig. 5.8). The second component (PC2N, accounting for 22% variation) correlated with a moderate presence of trees, shrubs, herbs, bare ground and rock cover, human activities and a very low crop coverage and grazing presence. GLMs showed that a positive PC1N (Bonferroni *p*-value = 0.016) significantly explained the presence of birds in the plots meaning that, during this month, individuals would be more likely to occupy relatively open sites with shrubs, a presence of anthropogenic activities and no trees. PC2N was not significant (Bonferroni *p*-value = 1, Fig. 5.8).

In February, the first principal component (PC1F, which accounted for 27% of the total variation) was correlated with strong anthropogenic-related activity and open areas, and with a moderately low presence of herbs, trees, crops, and grazing (Fig. 5.8). On the other hand, PC2F (27% variation) presented a heavily forested habitat with very low cover of shrubs, crops, and grazing. None of these principal components were a statistical predictor for the absence or presence of birds during this month (Fig. 5.8).

a) PCA50n

b) PCA50f



a)

```
                  PC1        PC2
trees     -0.63572700  0.1645963
shrubs     0.46488754  0.2393847
herbs     -0.03407535  0.3299307
bare_rock  0.25800632  0.2198009
crops     -0.08679258 -0.7560622
grazing    0.43701391 -0.3984690
human_act  0.33688017  0.1674177
```

b)

```
                  PC1         PC2
trees     -0.24523614  0.56811210
shrubs     0.07615401 -0.52061017
herbs     -0.36598243  0.08368377
bare_rock  0.62077673  0.06912507
crops     -0.28554104 -0.18232291
grazing   -0.15352603 -0.59962184
human_act  0.55646113  0.04055179
```

Bonferroni corrected *p* values when *pres_abs~PC1+PC2+PC3*:
PC1N (shrubby with anthropogenic presence): *p* = **0.016**
PC2N (vegetative with low anthropogenic presence): *p* = 1
PC3N (highly shrubby): *p* = 0.07

PC1F (open area with strong anthropogenic presence): *p* = 0.13
PC2F (forest): *p* = 0.18
PC3F (low vegetation with strong anthropogenic presence): *p* = 1

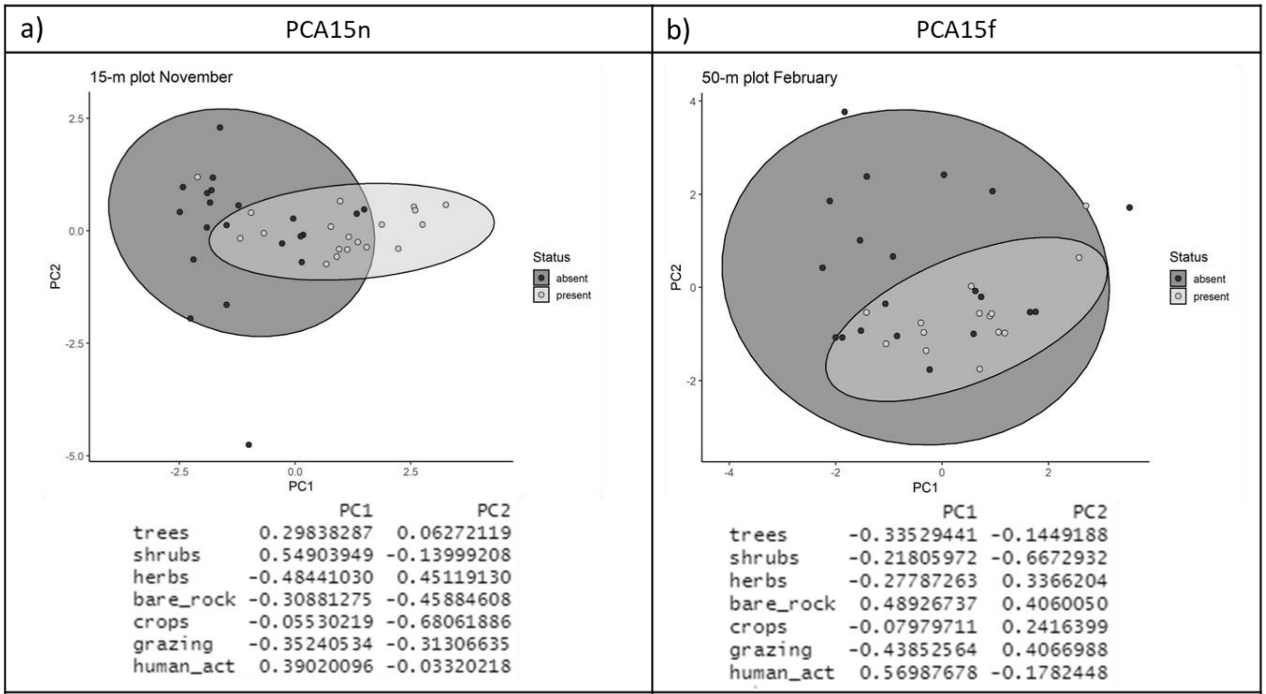
Figure 5.8. PCA results from 50-m plots. PCA results from the 50-m plots surveyed at occupied home ranges and randomly selected sites in November 2018 (a) and February 2019 (b). Significant Bonferroni *p*-values below 0.05 are highlighted in bold.

Additionally, and complementing the PCA results, *t*-tests showed that during both sampling periods shrub cover was statistically higher (Nov: t = -6.9, df = 32, p < 0.001 and Feb: t = -3.8, df = 32, p < 0.001) and tree cover was statistically lower (Nov: t = 3.1, df = 32, p = 0.004 and Feb: t = 3, df = 32, p = 0.005) in plots within occupied home ranges compared to unoccupied plots. Presence of crops was only higher in unoccupied plots during November (t = 2.6, df = 32, p = 0.01). All other coverage variables were non-significant.

In Fig. 5.8 we can also observe that the "absent" status cluster is larger than the "present" status cluster, showing that the unoccupied plots had more differences amongst themselves than when compared with occupied home ranges. Additionally, because in both November and February the "present" status clusters highly overlap with the "absent" status clusters, we can conclude that some unoccupied plots have similar habitat characteristics to occupied and preferred plots. This is more evident in February than in November, *i.e*. enough habitat was available and unoccupied.

At the home range-scale

PCA results from the 15-m "absent" and "present" plots located within territories showed that in November (PCA15n), the first principal component (PC1n, which accounted for 41% of the total variation) was correlated with an important degree of human activity and a strong presence of shrubs and to a lesser degree trees, along with a very low presence of bare ground and rock cover, herbs, and grazing (Fig. 5.9). The second component (PC2n, 16% of variation) was correlated with a strong presence of herbs and no anthropogenic impact, crops or shrubs or bare ground and rock cover. GLMs showed that a positive PC1n (Bonferroni *p*-value = 0.001) supported the presence of birds, thus individuals would be more likely to prefer parts of the territory that had shrubs and some anthropogenic presence and would greatly dislike areas with bare ground and rock cover, and herb presence (Fig. 5.9). In February, the first principal component (PC1f) was correlated to a strong anthropogenic and open habitat, with very low vegetation and the presence of grazing (Fig. 5.9). The second principal component (PC2f) was correlated to a moderate presence of herbs, bare ground and rock cover, crops, and presence of grazing, with low cover of trees and human activities and extremely low presence of shrubs (Fig. 5.9). During this month, no principal component was a statistical predictor for the absence or presence of birds. In November half of the "absent" status cluster overlapped with the "present" status cluster, suggesting that within home ranges, individuals highly prefer to remain at spaces that have shrubs and trees and some sort of anthropogenic activity, and plots with a high presence of grazing with herbs and bare ground and rock cover are avoided. In February, home ranges seem to be more homogenous so individuals are less strict as to what part of them they use and would reflect why "absent" and "present" areas were similar in February measurements.



```
                  PC1         PC2
trees       0.29838287  0.06272119
shrubs      0.54903949 -0.13999208
herbs      -0.48441030  0.45119130
bare_rock  -0.30881275 -0.45884608
crops      -0.05530219 -0.68061886
grazing    -0.35240534 -0.31306635
human_act   0.39020096 -0.03320218
```

```
                  PC1         PC2
trees      -0.33529441 -0.1449188
shrubs     -0.21805972 -0.6672932
herbs      -0.27787263  0.3366204
bare_rock   0.48926737  0.4060050
crops      -0.07979711  0.2416399
grazing    -0.43852564  0.4066988
human_act   0.56987678 -0.1782448
```

Bonferroni corrected *p* values when *pres_abs~PC1+PC2+PC3*:
PC1n (shrubs and trees with anthropogenic presence): *p* = **0.001**
PC2n (strong presence of herbs): *p* = 1
PC3n (strong anthropogenic presence with shrubs): *p* = 0.37

PC1f (open area with strong anthropogenic presence): *p* = 1
PC2f (open area with grazing and crop presence): *p* = 0.17
PC3f (open area with grazing and tree presence): *p* = 0.84

Figure 5.9. PCA results from the 15-m plots. PCA results from the 15-m plots surveyed within territories PCAs in November 2018 (a) and February 2019 (b). Significant Bonferroni *p*-values below 0.05 are highlighted in bold.

Additionally, *t*-tests showed that in both months shrub cover was statistically higher (Nov: *t* = - 5.5, df = 40, *p* < 0.001 and Feb: *t* = -2.6, df = 20, *p* = 0.018) and bare ground and rock cover was statistically lower (Nov: *t* = 3.1, df = 40, *p* = 0.003 and Feb: *t* = 2.3, df = 20, *p* = 0.03) in "present" plots compared to the "absent" plots. In all cases, significances were stronger in November. Herb cover was lower in "present" plots during November (*t* = 3.8, df = 40, *p* < 0.001) only. All other coverage variables were non-significant. Within home ranges, individuals seem to prefer and use shrubby areas and seem to avoid general open areas.

First-years and adults seem to show similar habitat preferences during November, at both a site- and home range-scale. In February, however, first-year birds tended to stay in areas with less grazing at a site-scale. Moreover, at a home range-scale adults used areas with a higher shrub cover, a lower bare ground and rock cover, and with less human activity impact (Table 5.4). Females and males also show similar habitat preferences throughout the season, with minor differences. Though not strongly significant, females occupied areas at a site-scale with a higher shrub cover in November. Similarly, females at a home range-scale in February used areas with more shrub and herb cover than males.

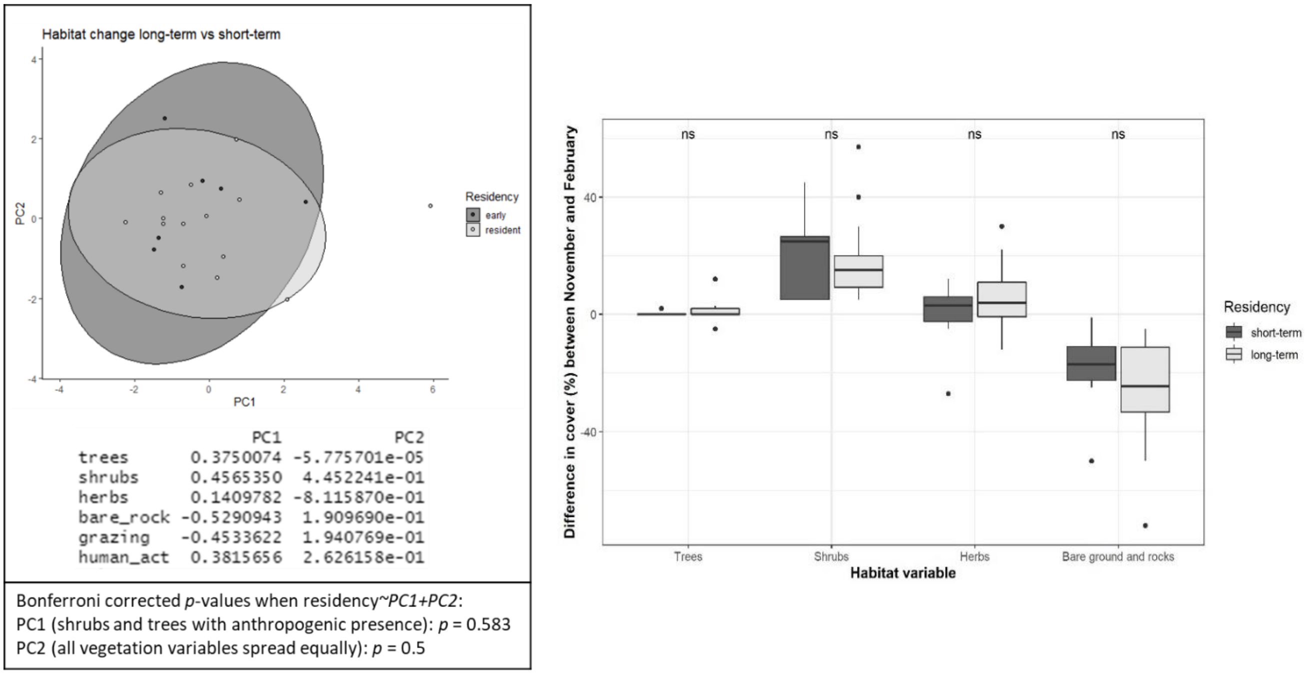
Table 5.4. Differences in habitat characteristics. The range of habitat characteristics at a site- and home range-scale within plots during November and February according to age and sex. Results from *t*-tests and Chi-squares are shown to assess differences between adults and first-years and adult females and males. Significant differences are in bold.

		Age							**Sex**						
		Adults (*n* = 15)		**First-years (*n* = 5)**		**Results**			**Females (*n* = 6)**		**Males (*n* = 8)**		**Results**		
		mean	**SE**	**mean**	**SE**	**t/ χ^2**	**df**	***p***	**mean**	**SE**	**mean**	**SE**	**t/ χ^2**	**df**	***p***
November site-scale	tree	4.7	2.4	7	3.7	-0.51	18	0.62	3	1.9	6.5	4.2	-0.68	12	0.51
	shrub	56.3	3.7	64	3.3	-1.12	18	0.28	62.2	3.8	49	4.8	2	12	0.06
	herb	25.5	2.5	23.4	3.5	0.44	18	0.67	24.8	4.5	27.2	3.1	-0.46	12	0.66
	crop	2.8	2.1	0	0	0.76	18	0.46	2	2	3.8	3.8	-0.37	12	0.72
	bare and rock	10.7	2.4	5.6	1.3	1.21	18	0.24	8	1.8	13.5	4.1	-1.1	12	0.3
	grazing					5.42	2	0.7					3.8	2	0.15
	human activities					6.21	4	0.18					5.3	4	0.25
February site-scale	tree	4.5	2.4	4.2	1.8	0.08	18	0.94	3.5	2.5	5.9	4.2	-0.44	12	0.67
	shrub	39.3	3.9	36.8	11	0.27	18	0.79	43.7	6	32.1	3.4	1.79	12	0.1
	herb	20.9	3.3	21.2	5.9	-0.04	18	0.97	19.3	6.7	23.5	3.7	-0.58	12	0.57
	crop	2.8	2.1	0	0	0.76	18	0.46	2	2	3.8	3.8	-0.37	12	0.72
	bare and rock	32.5	4.8	37.8	9.9	-0.53	18	0.6	31.5	9.5	34.8	5.8	-0.31	12	0.76
	grazing					7.11	2	**0.03**					3.17	2	0.21
	human activities					6.15	4	0.41					3.49	4	0.75
November home range-scale	tree	3.1	1.7	2	1.2	0.36	18	0.72	4.5	2.9	2.5	2.5	0.53	12	0.61
	shrub	70.3	4.2	73.6	7.4	-0.39	18	0.71	77	7.6	65.4	5.3	1.3	12	0.22
	herb	22.9	3.8	19	5.8	0.52	18	0.61	17.2	7.5	26.5	4.3	-1.15	12	0.27
	crop	0	0	0	0	na	na	na	0	0	0	0	na	na	na
	bare and rock	3.7	1.3	5.4	3	-0.61	18	0.55	1.3	0.9	5.6	2.2	-1.61	12	0.14
	grazing					2.4	2	0.3					2.4	2	0.3
	human activities					2.34	2	0.31					2.77	2	0.25
February home range-scale		(*n* = 9)		(*n* = 1)					(*n* = 4)		(*n* = 4)				
	tree	2.2	2.2	0	na	0.32	8	0.76	5	5	0	0	1	6	0.36
	shrub	64.4	6.4	15	na	2.45	8	**0.04**	76.2	3.8	48.8	9	2.8	6	**0.03**
	herb	13.9	3.2	10	na	0.38	8	0.71	7.5	1.4	20.8	5.5	-2.3	6	0.06
	crop	0	0	0	na	na	na	na	0	0	0	0	na	na	na
	bare and rock	19.4	5.7	75	na	-3.1	8	**0.01**	11.2	4.7	30.5	9.8	-1.8	6	0.13
	grazing					3.16	2	0.21					1.9	2	0.38
	human activities					12.2	6	0.06					10.34	6	0.11

5.5.4 Variation in space use by residency pattern and home range size predictors

All individuals, no matter how long they stayed at the site, moved similar distances. No differences were observed in the mean ranging distance across individuals of different residency patterns ($F_{(2,137)}$ = 0.83, *p* = .44; mean long-term winter residents = 45 m, SE = 4.2 m, mean short-term winter residents = 54 m, SE = 9.2 m, and mean passage birds = 55 m, SE = 8.2 m).

The degree of habitat change was also similar when comparing short-term and long-term winter residents. Results from the PCAr comparing the difference in variables of the 50-m plots from November to February showed that the first principal component (PC1r, which accounts for 54% of the total variation) was correlated with high vegetation values and human activities and with low bare ground and rock cover and presence of grazing (Fig. 5.10). The second principal component (PC2r, 22% of variation) was not strongly correlated to any specific habitat variable (Fig. 5.10). Clusters overlap completely showing that habitat changes are similar regardless of residency pattern. Furthermore, *t*-tests showed no significant differences between the change of habitat variables from November to February, between home ranges of short-term and long-term winter residents. Changes in PC1r and PC2r were similar for both residency categories; PC1r ~ res ($F_{(1,19)}$ = 0.28, *p* = 0.6), and PC2r ~ res ($F_{(1,19)}$ = 0.43, *p* = 0.52).



```
                  PC1           PC2
trees       0.3750074 -5.775701e-05
shrubs      0.4565350  4.452241e-01
herbs       0.1409782 -8.115870e-01
bare_rock  -0.5290943  1.909690e-01
grazing    -0.4533622  1.940769e-01
human_act   0.3815656  2.626158e-01
```

Bonferroni corrected *p*-values when residency~*PC1+PC2*:
PC1 (shrubs and trees with anthropogenic presence): *p* = 0.583
PC2 (all vegetation variables spread equally): *p* = 0.5

Figure 5.10. Habitat change differences between short-term and long-term winter residents. a) Results from the PCAr from the 50-m plots surveyed within territories and b) Differences in habitat variables between

November and February according to residency pattern. There were no differences in the degree of change between short-term and long-term winter residents.

When averaging the habitat variable values of the 50-m plots within territories, the first principal component (PC1hab, accounting for 30% of the total variation) correlated with a moderate presence of shrub and crop cover, grazing, and with a strong absence of bare ground and rock cover and presence of human activities. The second component (PC2hab, accounting for 23% of variation) was strongly correlated with herbs and the presence of grazing and with a strong absence of shrubs. The third component (PC3hab, accounting for 19% of variation) was mildly correlated with shrub and herb cover and grazing and human activity presence, and strongly negatively correlated with tree cover. Results from the model “MCP ~ PC1 + PC2 + PC3 + residency” showed that a positive PC2hab had a mild significant relation with home range sizes, meaning that larger home ranges had higher coverage of herb and grazing and had much lower shrub coverage, most likely indicating lower habitat quality (Table 5.5).

Table 5.5. Results from General Linear Models exploring predictors of home range size. Results from General Linear Models: MCP ~ PC1 + PC2 + PC3 + residency pattern, exploring predictors of home range size, and MCP ~ PC2*residency + PC3*residency, exploring whether habitat changes affected short-term and long-term individuals differently. PC2 was a mildly significant statistical predictor in the first model and habitat change did not affect short-term and long-term individuals differently.

Variable	**Estimate**	**SE**	***t*-value**	**Bonferroni *p*-value**
MCP ~ PC1 + PC2 + PC3 + residency				
Intercept	3590.9	1267.3	2.83	
PC1	-203.1	519	-0.39	1
PC2	1483.4	581.5	2.56	0.08
PC3	-945.8	641.9	-1.47	0.64
Residency	551.5	1563	0.35	1
*MCP ~ PC2*residency + PC3*residency*				
Intercept	3483.7	1075.7	3.24	
PC2	234.2	781.3	0.3	1
Resident	592.4	1318.5	0.5	1
PC3	-1959.5	682.5	-2.87	0.06
PC2:resident	1695.8	1039.5	1.63	0.62
Resident:PC3	2438.3	1225.2	1.99	0.33

We did not find strong evidence that habitat change affects short-term and long-term winter residents differently (Table 5.5 and Fig. 5.11a). The marginally significant interaction in the third component (Fig. 5.11b) is due to an outlier.

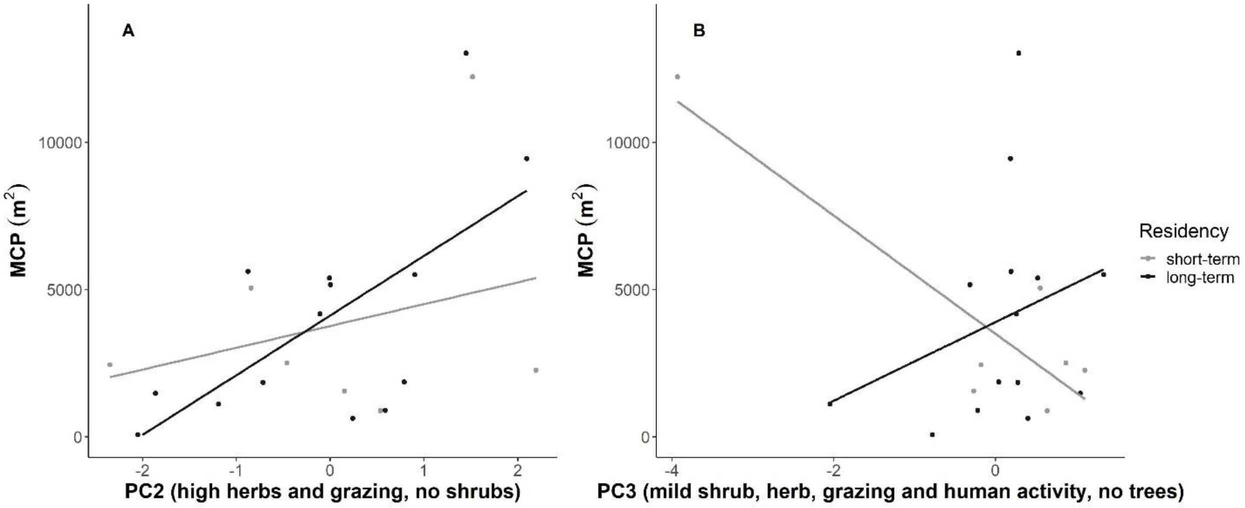


Figure 5.11. Relation between PC2 (a) and PC3 (b) with home range size amongst short-term and long-term winter residents. Scattered dots represent exact values from each individual. No evidence that habitat changes are different between residencies. Marginal significant interaction in (b) is due to an outlier.

5.5.5 Activity budgets

The proportion of time that individuals spent foraging, moving, perching, scanning and vocalising varied amongst stages (early = October – November, mid = December – February, and late = March – April) throughout the non-breeding season, whilst flying and preening did not (Fig. 5.12). Individuals spent a larger proportion of time perching and vocalising at the beginning of the season; this decreased as the season progressed. Foraging was more frequent during the mid-stage and individuals were seen moving and scanning for longer proportions of time at the end of the season (Fig. 5.12).

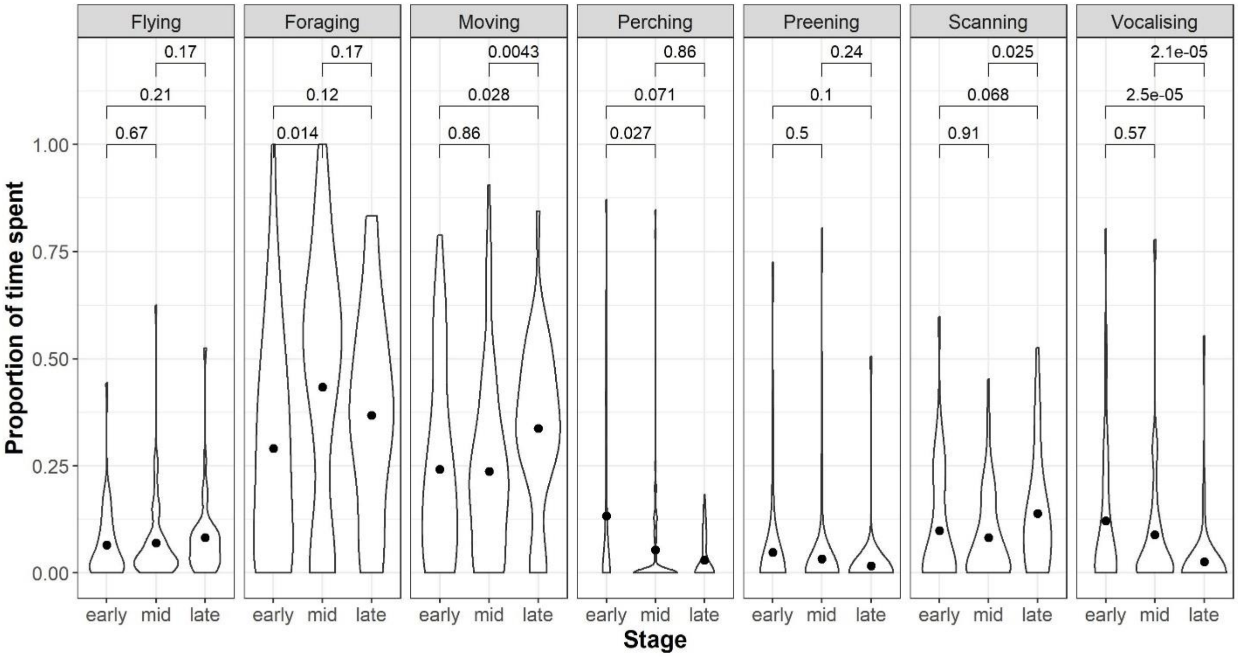


Figure 5.12. Time spent during each behavioural activity. The mean proportion of time spent during each behavioural activity during the early (October – November, *n* = 41), mid (December – February, *n* = 65), and late (March – April, *n* = 36) stage of the non-breeding season of years 2 and 3. Results from the Wilcoxon tests are shown in the graph.

5.6 Discussion

In this chapter, we describe Whitethroats' fine-scale spatial movements, habitat preference, and predictors of home range sizes during the non-breeding season and how these change throughout. Most of the results suggest few strong effects of habitat quality and seasonal habitat change on Whitethroat ranging behaviour. Our results suggest that the mean distance between all an individual's detections is, on average, 47 ± 3.4 m. First-years moved slightly longer distances than adults but there was no variation between years or between female and male adults. We found that both short-term and long-term winter residents established and maintained small home ranges (mean size = 3405 ± 435 m^2) and their size did not vary statistically across years or according to age or sex of individuals. Habitat characteristics within home ranges changed significantly between November and February: shrub cover decreased at the end of the season whilst bare ground/rock cover and anthropogenic activities increased, but the mean distance between all an individual's detections was similar throughout the period, even amongst individuals from different residency patterns. Although home range sizes were similar between autumn and spring short-term residents, long-term winter residents had larger home ranges at the beginning of the season, the opposite of what we expected. Mean distances were similar amongst individuals from different residency patterns. At a site-scale, individuals were more likely to occupy relatively open sites with shrubs, no trees, and some presence of anthropogenic activities and at a home range-scale, individuals seemed to prefer to use shrubby areas and avoid general open areas; this preference was stronger in November. First-years and adults seemed to show similar habitat preference during November but not in February as adults preferred areas with higher shrub cover, and lower bare ground cover and human activity presence. Adult females and males also show similar habitat preferences throughout the season, though females use areas with more shrub and herb cover. The degree of habitat change within home ranges of short-term winter residents was similar to long-term winter residents. Larger home ranges, however, had a greater degree of herb cover and grazing and had lower shrub cover. Moreover, the proportion of time spent carrying out certain behaviours changed throughout the period, suggesting some compensation to habitat quality did occur.

Here we discuss: (1) Whitethroats' spatial use of non-breeding grounds (2) habitat preference, flexibility to changing seasonal conditions and how this reflects broad requirements and demonstrates a generalist strategy, (3) the weak evidence of dominance-based habitat occupancy, (4) space use differences according to residency patterns, (5) habitat quality and habitat availability, and (6) how these results contribute to the conservation of the species.

5.6.1 Spatial use of non-breeding grounds

Our fine-scale movement results showed that Whitethroats used relatively small areas during their stay at our study site. Not only were individuals always detected at similar sites, but those that stayed for some time or throughout the non-breeding period (short-term and long-term individuals) occupied small home ranges of an average area of 0.34 ha (0.0031 – 2.2 ha). This supports the emerging evidence that many Afro-Palearctic migrants establish and defend small territories throughout the non-breeding season (*e.g*. Pied Flycatchers *Ficedula hypoleuca*; Salewski et al., 2002; Thorup et al., 2019, Common Redstarts *Phoenicurus phoenicurus*, Kristensen et al., 2013; Thorup et al., 2019, and Whinchats *Saxicola rubetra*, Blackburn & Cresswell, 2016b), though there are some exceptions, such as Willow Warblers *Phylloscopus trochilus* (Salewski et al., 2002; Willemoes et al., 2017), Garden Warblers *Sylvia borin* (Iwajomo et al., 2017) and Wood Warblers *Phylloscopus sibilatrix* (Mallord et al., 2016) that move over a much larger area.

Whitethroats' non-breeding home ranges varied from 0.0031 to 2.2 ha. These results coincide with those calculated by Ottosson et al. (*in prep*) who found that Nigerian Whitethroats, in April, had territories varying in area between 0.04 and 2 ha, with a mean of 0.5 ha. Wintering Whitethroats seem to have smaller (or in the case of the Whinchat, similar-sized) non-breeding home ranges than other

Afro-Palearctic migrants in West Africa such as Whinchats (mean size = 0.21 ha (0.04 – 0.47 ha) and 0.47 ha (0.23 – 0.77 ha); Barshep et al., 2012, 0.33 ha; Blackburn & Cresswell, 2015), Melodious Warblers (1.6 – 4.1 ha; Willemoes et al., 2017), and Pied Flycatchers (1.2 – 2.3 ha; Willemoes et al., 2017), and to Neotropical migrants such as Hermit Thrushes *Catharus guttatus* (0.55 ha; Brown & Long, 2006) and Ovenbirds *Seiurus aurocapilla* (0.69; Brown & Long, 2006) but direct comparisons should be taken with caution because home range estimations were calculated differently across studies.

On the other hand, Whitethroat wintering territories seem to be, in general, similar or even larger than breeding territories in diverse European locations: in Sweden, territories ranged from 0.6 to 1.6 ha (Persson, 1971), in Karelia < 0.1 ha (Matantseva & Simonov, 2012), in Poland 0.04 – 0.65 ha (Halupka et al., 2002), and in southern Germany 0.3 ha (Diesselhorst, 1968). Individuals seem to use similar areas during the breeding and non-breeding period, though during the non-breeding period, individuals have the advantage that they are not constrained to a specific location and can move to other locations if conditions become harsh. Maintaining a small home range during the non-breeding period, or during a part of it, may be beneficial for obtaining local knowledge regarding foraging locations, resource fluctuation, and competitor and predator densities (Latta & Faaborg, 2001; Catry et al., 2004; Brown & Long, 2006; Lind & Cresswell, 2006), and is a good strategy to ensure food availability throughout the period and for subsequent years (Greenberg, 1986; Kelsey, 1989; Cuadrado, 1995; Rolando, 2002; Zwarts et al., 2009).

We predicted that inexperienced individuals (*i.e*. first-years) would move longer distances and use larger home ranges than more experienced individuals (*i.e*. adults). This prediction was met when comparing mean distances, although the biological significance between the means of the groups (18 m) was not much, but was not met when comparing home range sizes. Even though first-years tended to have larger home ranges than adults (difference of 781 m^2), this was not significant. Longer distances moved may reflect unfamiliarity with the area. First-year birds arrive in Africa, for the first time, to unknown conditions and resources, so it is not surprising to find an individual scouting and moving around the area until a suitable spot is detected where it can satisfy its needs. As predicted, and because breeding pressures seem to be absent during this period, adult females and males moved similar distances and had similar home range sizes.

We predicted that years with better conditions, reflected with higher precipitation and therefore abundant resources, would result in individuals moving shorter distances and maintaining smaller home ranges. This was not the case in our study because distances and home ranges did not vary across years.

Even though the mean temperature from November to April was similar throughout all three non-breeding seasons (27.5°C between 2017 and 2018, 27.5°C between 2018 and 2019, and 26.5°C between 2019 and 2020[2]), summer precipitation (between July and September) was higher in year1 (658 mm; 2017) than in years 2 and 3 (563 and 576 mm in 2018 and 2019, respectively). Similar movement and home range sizes despite differences in precipitation could be because: (1) the difference in summer precipitation between years was not enough to generate strong effects in resource production and food availability, in other words, all years were particularly "good" and beneficial, (2) as individuals have a large tolerance and adaptability to whatever resources they find, they can cope even when resources are scarcer, and/or (3) precipitation does not directly reflect the quality of fine-scale habitats and there are other factors that should be considered (*i.e*. higher human activity in the presence of higher precipitation, reducing individuals' potential resources).

5.6.2 Habitat preference and flexibility to changing seasonal conditions: evidence of a generalist strategy

As we expected, habitats changed significantly throughout the non-breeding season. Whitethroats arrive at the end of the rainy season, between September and November, when vegetation is dense, and resources are abundant. During this period individuals settle at sites that are relatively open with good shrub cover, no trees, and with some presence of low-impact anthropogenic activities such as dead wood extraction. As the season progresses, precipitation and vegetation biomass decrease, and grazing, bushfires, and wood extraction increase. During this time, by February, the amount of bare ground and rock cover at the site and within home ranges increases significantly and individuals use open areas with no particular preference for a particular type of vegetation. Shrubs are still important though, as individuals were seen to utilise areas with more shrubs when compared to unoccupied areas. Overall, Whitethroats become less selective in their habitat use and tend to use all available scrubby habitats as the dry season progresses.

We also expected differences in spatial use throughout the season, to cope with seasonal habitat changes. Specifically, we expected individuals to move longer distances and increase their home ranges as the dry season progressed. This, however, was not the case: instead, we found no difference in distances travelled throughout the period and we found that autumn and spring short-term residents occupied similar-sized home ranges. Contrary to what we predicted, long-term winter residents reduced their home range size during the second half of the winter, when resources were likely to be more

---

[2] https://www.worldweatheronline.com/laminga-weather-averages/plateau/ng.aspx

limited. Because larger spaces are required to meet energy requirements when food resources are scarce (Harestad & Bunnell, 1979; Williams et al., 2016) home range size should have increased. This result may however be explained by the fact that during spring, when individuals are undergoing spring migration, the study site receives an influx of passage birds, thus winter resident birds may need to defend core areas from intruders. The behavioural change results, *i.e*. more moving and scanning later in the winter, are also consistent with this hypothesis. Alternatively, during this period long-term residents may be energy minimisers, using the bare minimum of energy just to survive at lowest risk period until they commence fattening for spring migration. Alternatively, despite the observed habitat change, there was little effect on available resources, or any changes acted in the Whitethroats favour. For example, invertebrate availability might increase because vegetation is reduced and they become easier to find.

Unsurprisingly, shrubs were found to be important to Whitethroats. Shrubs were the main vegetation type cover that positively affected Whitethroat preference at both spatial scales and throughout the season. Shrubs play an important role for foraging (for both insects and fruits), as a site to perch, scan, and vocalise to delimit territory, and to seek protection from predators. The key shrub species are likely to be highly specific to the location (Wilson & Cresswell, 2006). Species such as *Searsia natalensis*, *Lantana camara*, and *Acacia ataxacantha* were used very often and could be important shrub species at our study site. Low crops, (mainly cucumber) do not seem to be either beneficial or detrimental to the species but birds were rarely seen feeding in and utilising these spaces. As crops bordered many home ranges, however, we think crops could be an important aspect of the landscape, by creating open landscapes with retained shrubs along the field borders. Even though birds were detected within the forest woodland Reserve, densities were substantially lower. This could be due to a higher density of other resident and migratory birds that increases competition. Equally, structurally more complex vegetation may hinder movements for defending the space and foraging. Overall, individuals seem to require low, dense coverage with open space around them for defence displays and excursions across open ground to forage. Vegetation structure seems to be more important than vegetation type for non-breeding Whitethroats.

These vegetation structure results show strong similarities with observed preferences on breeding grounds: Whitethroats nest in scrub and thorny bushes, such as bramble and nettles (Persson, 1971; Mason, 1976; Tsiakiris et al., 2009; Meichtry-Stier et al., 2013; Szymański & Antczak, 2013), and highly modified agricultural environments, particularly where fields are surrounded by hedges and thorny thickets (Persson, 1971; Ekroos et al., 2019). In contrast to our findings, individuals at the breeding grounds are also seen to use grasslands and meadows with hedgerows (Persson, 1971; Mason, 1976; Ekroos et al., 2019; Denac & Kmecl, 2021) and woody vegetation (Halupka et al., 2002) with tall shrubs or trees (Tsiakiris et al., 2009). This supports the idea that, at least on a finer scale, migrants can use a wider range of different habitats in the non-breeding season compared to the breeding season (Lerche-Jørgensen et al., 2019), though still somewhat similar.

Previous studies of Whitethroats on non-breeding grounds reached similar conclusions. Individuals occupy dry savannahs and open woodland habitats and avoid closed canopies with dense tree growth (Moreau, 1972; Cramp, 1992) and areas with shrubs and trees beyond mean heights of 2.5 m (Wilson & Cresswell, 2006). It appears that, in northern Nigeria, the Whitethroat's preference is for relatively undegraded Sahelian woodland with high diversity rather than high tree density (Vickery et al., 1999). Unlike our findings, Vickery et al (1999) and Wilson and Cresswell (2006), both found that Whitethroats prefer habitats with diverse trees, but this could be due to the tree species, as they found *Salvadora persica* and *Balanites aegyptiaca* to be key species for food, which are not found at our study site.

We have many reasons to believe that Whitethroats have somewhat generalist traits during the non-breeding period (*i.e*. they feed on many resources and thrive in a range of habitats). We believe that habitat characteristics varied across home ranges between individuals. For example, tree cover varied from 0 – 35% amongst individuals, shrubs from 9 – 95%, herbs from 3 – 85%, bare ground and rock cover 0 – 77% and the presence and intensity of grazing and human activities were also very variable. We only found that shrub coverage was substantially influencing Whitethroats' preferences at both the site- and home range-scale. Individuals seemed to cope with strong habitat changes by the end of the season without strongly changing their spatial use, suggesting that birds can find enough food in a restricted area throughout the winter despite the seasonal changes in vegetation and food supply. We found that some individuals decide to remain at degraded or non-optimal habitats before spring migration, potentially more so than other migratory species (Moreau, 1972). They were seen to overcome not only environmental-related changes (*e.g*. decrease of precipitation and temperatures) but also support different intensities of anthropogenic activity changes (*e.g*. road building, bush fires, grazing, wood extraction). This is strongly supported when taking into account all the different habitats Whitethroats use throughout the annual cycle at different locations, from highly anthropogenically modified areas to conserved woodlands. A generalist strategy also allows Whitethroats to have a high degree of winter site fidelity across years, as was found with Whinchats at the same site (Blackburn & Cresswell, 2015).

Another indicator of the species' generalism is that it can exploit different resources whenever they are available and can modify its diet in accordance with these changes. The main dietary component of Whitethroats is insects (Stoate & Moreby, 1995; Jones et al., 1996). However, both at the end of the breeding season, in late summer, and before spring migration, individuals abruptly change their diet. Before the flight back to the breeding quarters, Whitethroats strongly rely on *Salvadora persica* berries to deposit fat reserves (Stoate & Moreby, 1995; Vickery et al., 1999; Wilson & Cresswell, 2006). Even though we did not directly measure diet, we observed individuals foraging on fruits at higher rates between February and April, especially on *Searsia natalensis* and *Lantana camara*.

Evidence suggests that a generalist strategy is relatively common amongst long-distance migrants (Marra & Holmes, 2001; Cresswell, 2014), though not necessarily more so than taxonomically similar African resident species (Ivande & Cresswell, 2016). This is not surprising given that migrants will encounter many different habitats at very spatially separated locations. Being a generalist confers many advantages. Increasing the type of resources and habitats that can be exploited increases the probability of arriving at suitable habitats after first migration, which reduces time spent moving through unfamiliar surroundings where mortality risk is higher (Cuadrado, 1997; Cresswell, 2014) and may reduce competition with African resident species and other migrants (Salewski et al., 2007). At the same time, being flexible to highly changing resource availability in short periods increases resilience to habitat change and loss both within and between years, especially in light of the many climate and anthropogenic changes that are occurring worldwide.

5.6.3 Weak evidence for dominance-based habitat occupancy

There is evidence suggesting that habitats with optimal resources tend to be occupied by dominant birds, mainly larger and more experienced individuals (*i.e*. adults and/or males), whilst subdominant individuals, smaller and inexperienced (*i.e*. first-years and/or females), are forced to occupy lower-quality habitats (Hutto, 1980; Mazerolle & Hobson, 2004; Brown & Long, 2006). This is especially true in territorial species. Yet habitat segregation is not always present for some of these species in other wintering areas (Holmes et al., 1989), so the degree of segregation can be species-specific, but also habitat-specific. Dominance-based habitat occupancy could be stronger in more specialist species. That habitats have not reached carrying capacity, as is likely the case in our study site, could also explain the lack of segregation because there is no need for competition. It is possible that in the future, once our sites become saturated, we would see further and more pronounced age and sex habitat segregation.

Our results suggest that there is only mild dominance-based habitat occupancy, but only during February, if at all. At this time, adults were found at sites with higher shrub cover and with less bare ground and rock cover and, to a lower degree, lower human activity intensity, though we only had data from one first-year. Our findings also suggest that, to some extent, females utilise areas with a higher cover of shrubs. These results are unexpected because males tend to have behaviour that is more dominant and are better competitors for higher quality areas. Age and/or sex segregation can have consequences on the body condition and fitness of individuals occupying different habitats (Marra & Holmes, 2001), which may ultimately be decisive in determining population dynamics (Marra et al., 1998). Here we did not directly compare densities or spatial use at different habitats, thus this should be further explored.

5.6.4 Space use differences across residency patterns

Fine-scale movements were similar among individuals from different residency patterns. Surprisingly, the degree of habitat change (*i.e*. how much each habitat characteristic changed throughout the non-breeding season) was similar between short-term and long-term winter residents: all individuals seemed to suffer the same degree of habitat deterioration. We predicted that individuals would leave the study site due to lack of resources once their requirements were not met, while the reason for individuals to remain in the area would be that their home range would provide the necessary resources throughout the season. This was not the case. Furthermore, there were still many suitable areas that could have been used at the study site (see below). We suggest that individuals leave the area not to continue south, but to go north, to a third non-breeding site (see Chapter 3) as early as January, to fatten up with *Salvadora persica* berries before spring migration. Cresswell and collaborators (2009) found that 33% of Whitethroats from the forest zone of southeast Nigeria moved to the Sudan savannah zone of northeast Nigeria by late February.

Whitethroats seem to have some flexibility in whether they decide to stay at suboptimal habitats versus risk moving elsewhere. Both strategies seem to be viable, largely due to their broad habitat requirements, but as generalists, we expected that remaining at suboptimal habitats and facing higher competition was preferable to the risk assumed when moving and discovering new terrain. Moving north early may represent a special case – in fact, the early onset of migration, putting some Whitethroats ready for migration just south of the Sahara, closer to the breeding area. Nevertheless, understanding the exact reason why some individuals decide to leave an available area and others decide to stay on needs to be further explored. Geolocators, or better still finer resolution tags, could solve the mystery if deployed between October and December.

5.6.5 Predictors of home range size and habitat availability

Home range size is predicted to correlate with resource availability, with animals occupying smaller home ranges to meet their needs. As resource availability determines habitat quality, home range size may function as a predictor of habitat quality (Harestad & Bunnell, 1979; Williams et al., 2016), though this may not always be the case (Lerche-Jørgensen et al., 2019). Our findings are consistent with this prediction: larger home ranges had higher coverage of herb and presence of grazing and lower shrub cover. Because shrubs are strongly preferred and used by Whitethroats, we suspect that larger home ranges are most likely an indicator of lower habitat quality at our study site, though sizes did not realistically vary strongly.

On the other hand, our presence/absence models as well as PCAs poorly predicted the presence of individuals – “present” clusters highly overlapped with “absent” clusters (Fig. 5.8). This shows that unoccupied plots (“absent” plots) have similar habitat characteristics to occupied and preferred plots (“present” plots), especially in February. This, along with only weak evidence for dominance-based habitat occupancy and strong evidence for a broad range of habitat tolerance, is consistent with a species below carrying capacity. We believe that there is still much suitable area available for Whitethroats at our study site yet to be occupied. If habitat conditions remain similar and Whitethroat populations increase, we expect to find a higher Whitethroat abundance, including long-term winter residents, at the study site in the coming years. However, this will depend strongly on habitats not deteriorating significantly so birds do not increase their home range to meet their needs. These results also suggest that the time when Whitethroats are in APLORI is unlikely to be a high mortality-risk period, and is unlikely to be affecting population trends at the moment.

5.6.6 Implications for conservation

Migrants spend over 70% of the year at the non-breeding grounds. For Afro-Palearctic migrants, this means that they spend more time in Africa than anywhere else. Recently, this area has been subject to major climatic and anthropogenic changes. It is now unlikely that truly pristine, unaltered habitats remain within the range of migratory species, with most landscapes showing some degree of modification (Sheehan & Sanderson, 2012). Drought and a strong increase in overgrazing, human populations, human activities, and agricultural practices have strongly affected African habitats, especially Sahelian savannah woodlands (Vickery et al., 1999), which are crucial staging grounds for all trans-Saharan migrants. Although these changes may result in the complete loss of suitable habitat in some areas, in other areas, degradation of woodland may improve habitats for Whitethroats at the expense of resident African species and other migratory species reliant on more mature wooded landscapes (Stoate et al., 2001; Mallord et al., 2016). In the event of an increase in agricultural practices and/or volume of crops to sustain human populations, these could benefit Whitethroats so long as it is not fulfilled through extreme monoculture conditions and hedgerows and shrubs remain present (Meichtry-Stier et al., 2013).

Whitethroats, in particular, appear to be able to survive in extremely degraded habitats (Moreau, 1972; Wilson & Cresswell, 2006) and may be more resilient to habitat loss and degradation than other migratory species (Mallord et al., 2016). However, Whitethroats are still heavily dependent on conditions in the Sahel region and are especially vulnerable to the disappearance of *Salvadora persica*, as it produces berries crucial for pre-migratory fattening (Vickery et al., 1999; Wilson & Cresswell, 2006; Zwarts et al., 2009) as evidenced after the 1960s population crash brought about by extreme drought conditions in the Sahel in the 1960s (Winstanley et al., 1974). At our study site, shrub species like *Searsia natalensis*, *Lantana camara*, and *Acacia ataxacantha* were crucial for providing shelter and food to individuals. These are also species with immense human value as they are used for fuelwood and timber. At lower human population densities this may mean that Whitethroats benefit as the landscape is managed for these resources, but at higher human densities, this may mean that Whitethroats are threatened as the landscape is denuded of these valuable resources.

Our results suggest that APLORI, our study site, can support large numbers of Whitethroats and still has enough suitable habitat to support more. Consequently, we extrapolate that core wintering sites are unlikely to strongly affect population trends of the species so long as shrubs are always present, both at the breeding and non-breeding grounds. We suggest that the conservation of Sahel woodlands should be prioritised for the long-term persistence of the species and to buffer the effects that extreme climatic events will have on the area. We provided evidence here that individuals at core wintering sites can overcome strong seasonal changes by either remaining at deteriorating sites or moving to other sites, suggesting great flexibility which is likely to buffer the effects of climate and habitat change in the region.

5.7 Appendices

Appendix 5.1. Fine-scale movements and home ranges.

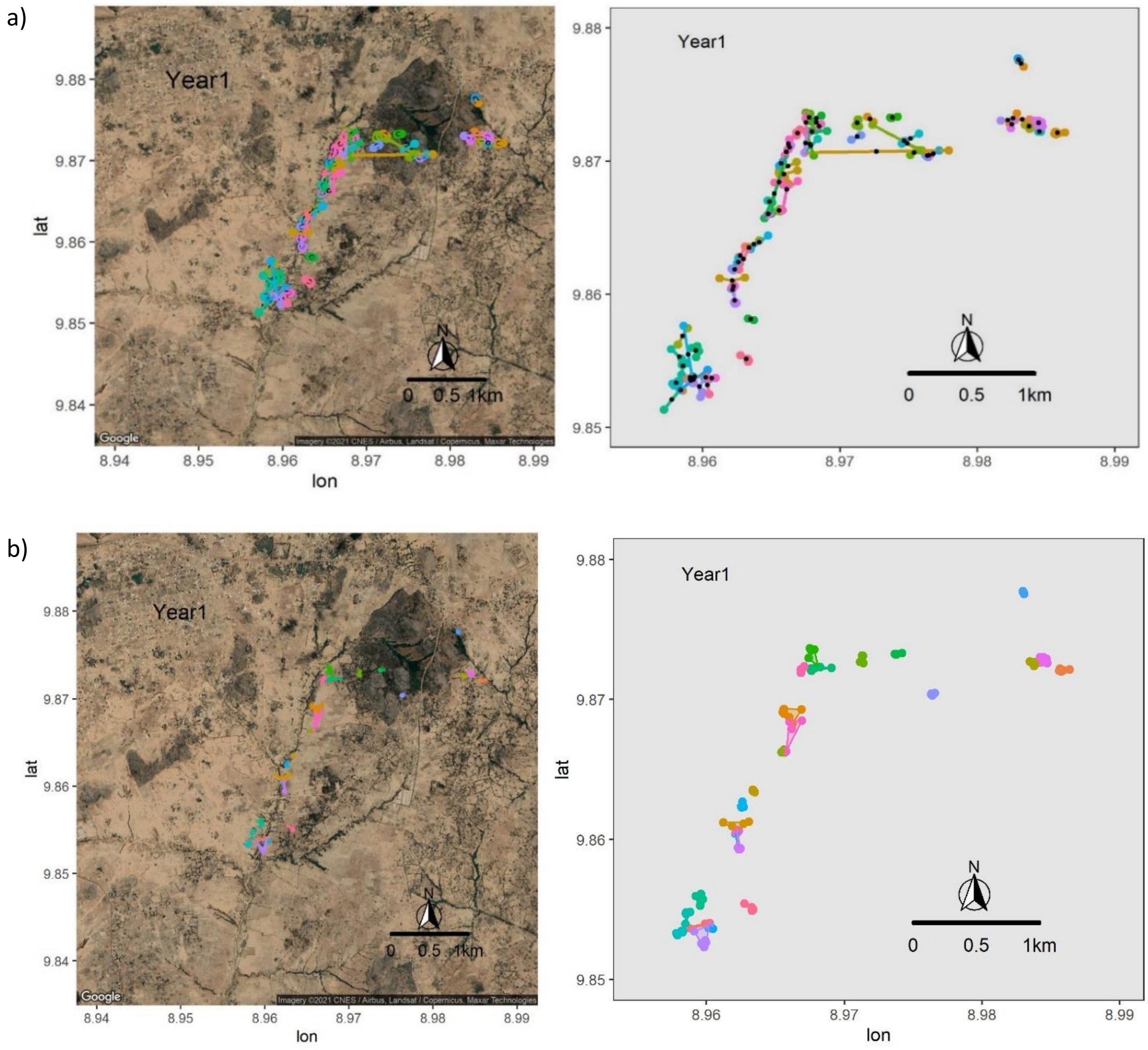


Figure A.5.1.1. a) Fine-scale movements of all individuals that were seen at least twice during year1. Black dots are centroids. b) Home ranges (Minimum Convex Polygons) of all individuals with at least five sightings during year1.

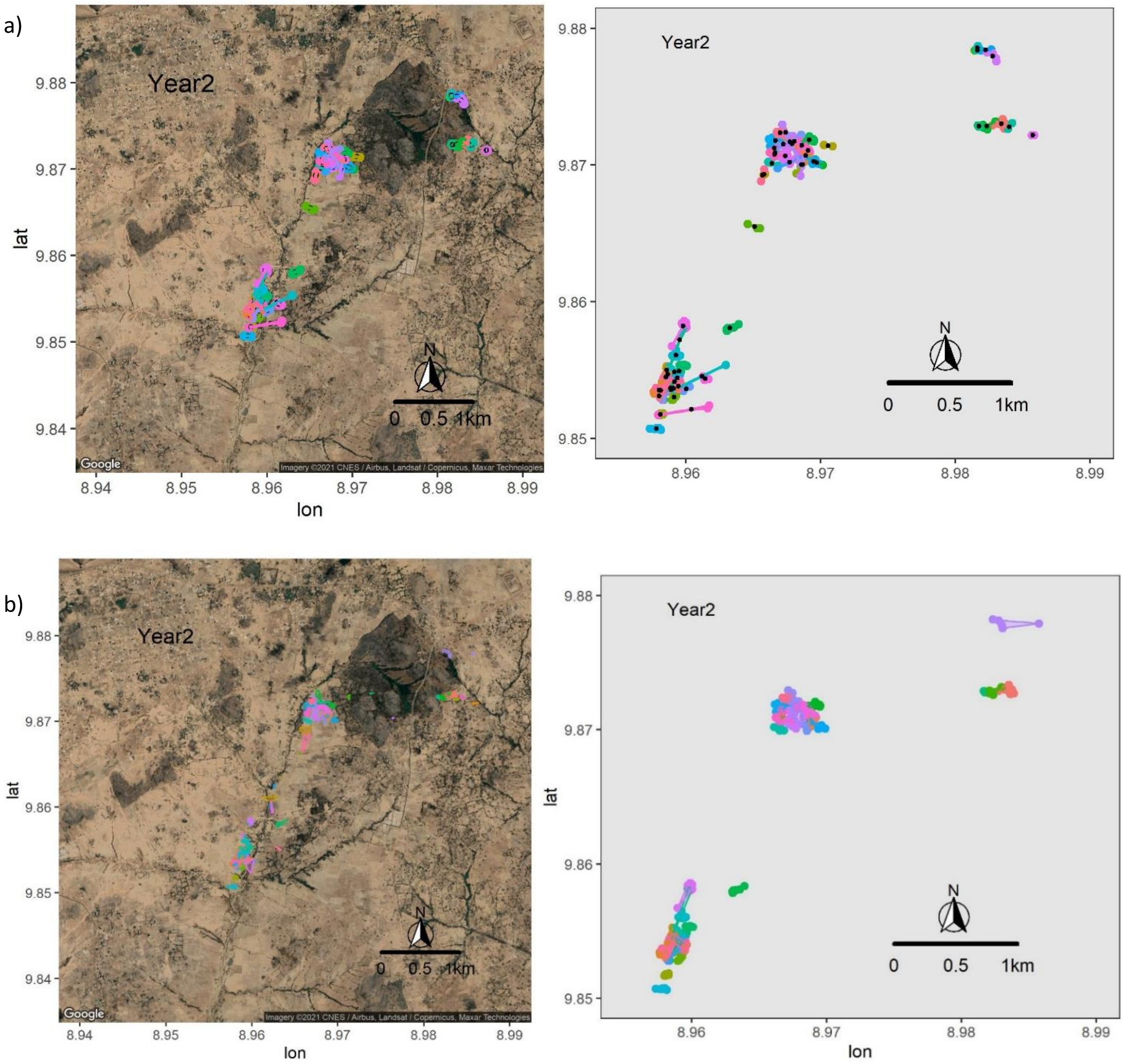


Figure A.5.1.2. a) Fine-scale movements of all individuals that were seen at least twice during year2. Black dots are centroids. b) Home ranges (Minimum Convex Polygons) of all individuals with at least five sightings during year2.

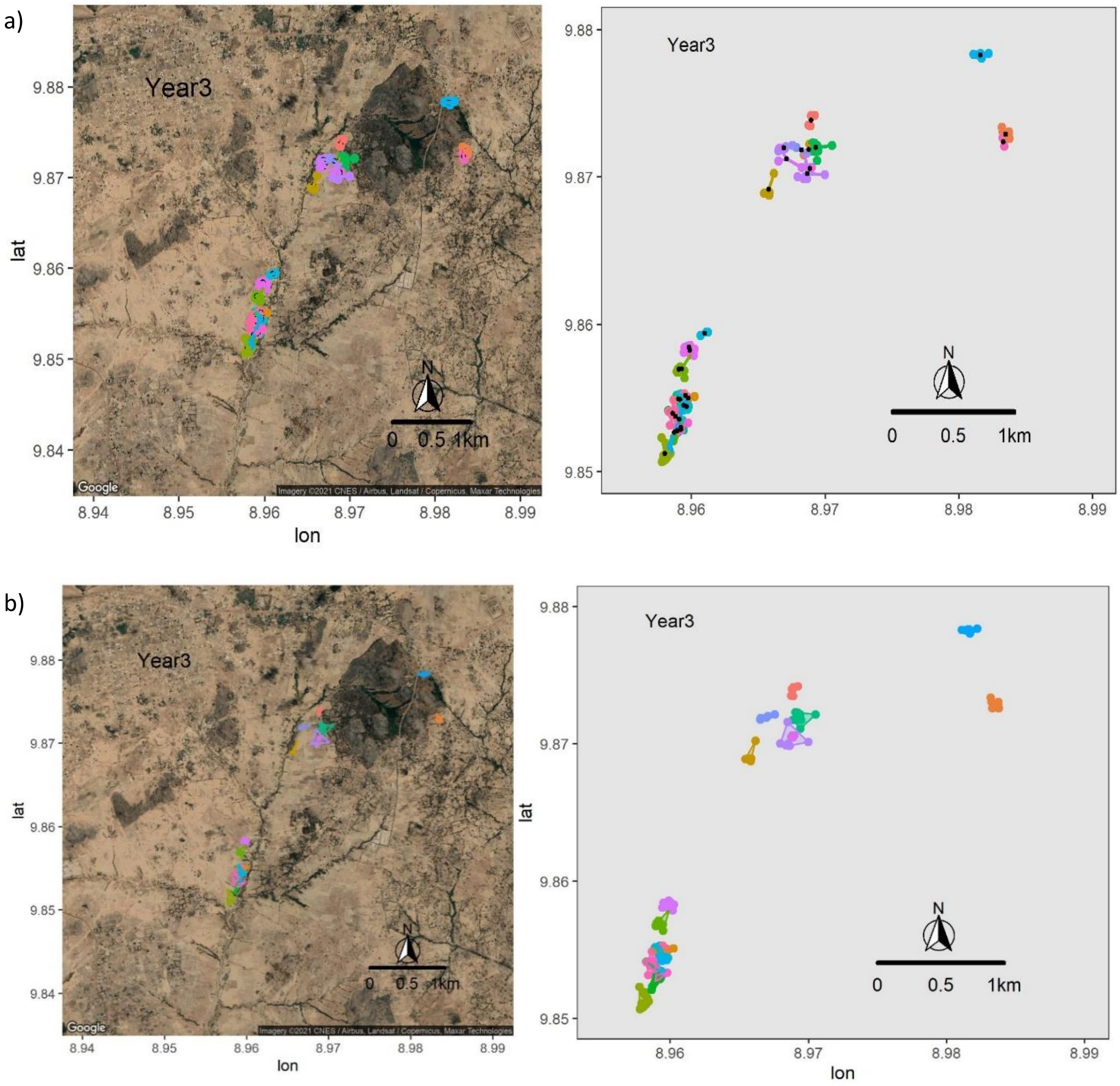


Figure A.5.1.3. a) Fine-scale movements of all individuals that were seen at least twice during year3. Black dots are centroids. b) Home ranges (Minimum Convex Polygons) of all individuals with at least five sightings during year3.

Appendix 5.2. Description of inter- and intra-specific interactions recorded during observations.

Throughout the observations, 33 interactions were recorded between Whitethroats. Ten seemed to be aggressive, mainly consisting of chases between birds without ever having direct contact amongst them, ten interactions consisted of individuals calling amongst themselves and 13 were passive, or non-aggressive, interactions that consisted of individuals seen at the same bush without obviously reacting to the other one's presence. Interspecific interactions were also observed. Birds were seen sharing bushes with Northern Red Bishops *Euplectes franciscanus*, Sun Larks *Galerida modesta*, Laughing Doves *Spilopelia senegalensis*, Rock Firefinches *Lagonosticta sanguinodorsalis*, Variable Sunbirds *Cinnyris venustus*, Vitelline Masked Weavers *Ploceus vitellinus*, and especially with Red-Cheeked Cordon Bleus *Uraeginthus bengalus*. A Whitethroat was seen being aggressive towards a Variable Sunbird, and Whitethroats were seen to be chased off by a Common Redstart *Phoenicurus phoenicurus*, Whinchat *Saxicola rubetra*, and Brown Babbler *Turdoides plebejus*.

Appendix 5.3. MCPs and 95% MCPs (m^2) between years, and between individuals of different age and sex categories.

Because the number of detections influenced home range sizes – the more detections, the larger the home ranges – we randomly selected five detections from each individual and calculated the MCPs and 95% MCPs by identifying and connecting the outermost points. There were no statistical differences amongst groups: home ranges did not vary between years and individuals from different age and sex cohorts.

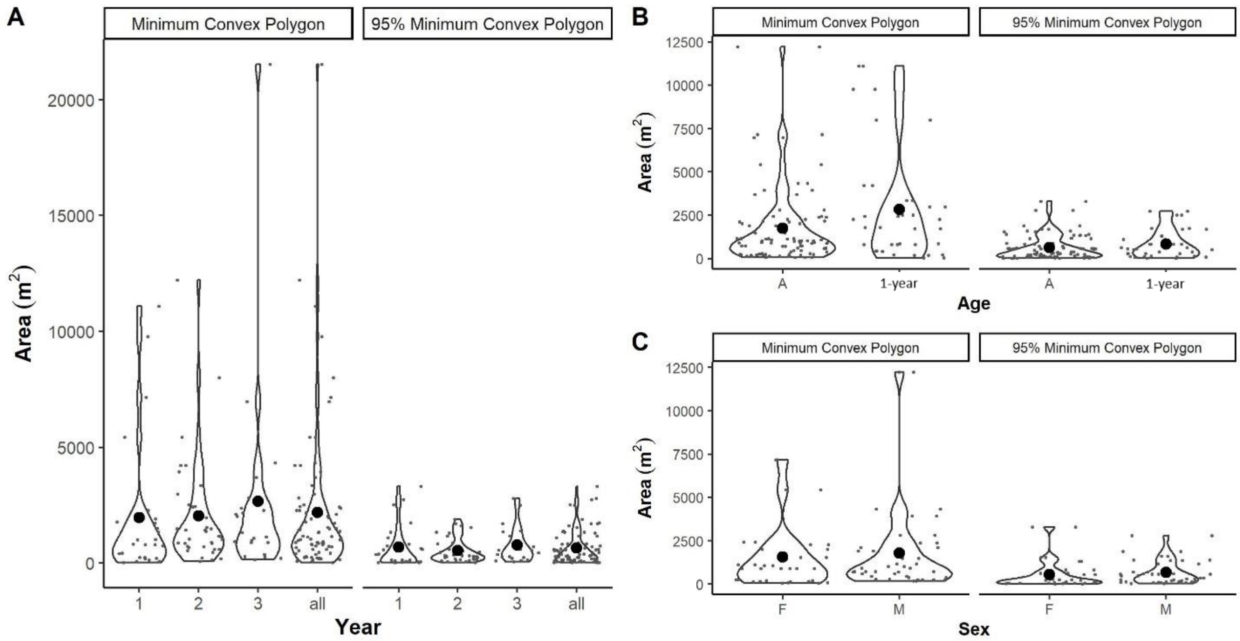


Figure A.5.3. Home ranges (m^2) obtained from MCPs and 95% MCPs between (a) years, (b) first-years and adults, and (c) adult females and males. The “all” category contains pooled data. Big black dots show means. Scattered dots represent exact values from each individual.

Appendix 5.4. Relation between the duration spent at the study site and home range size.

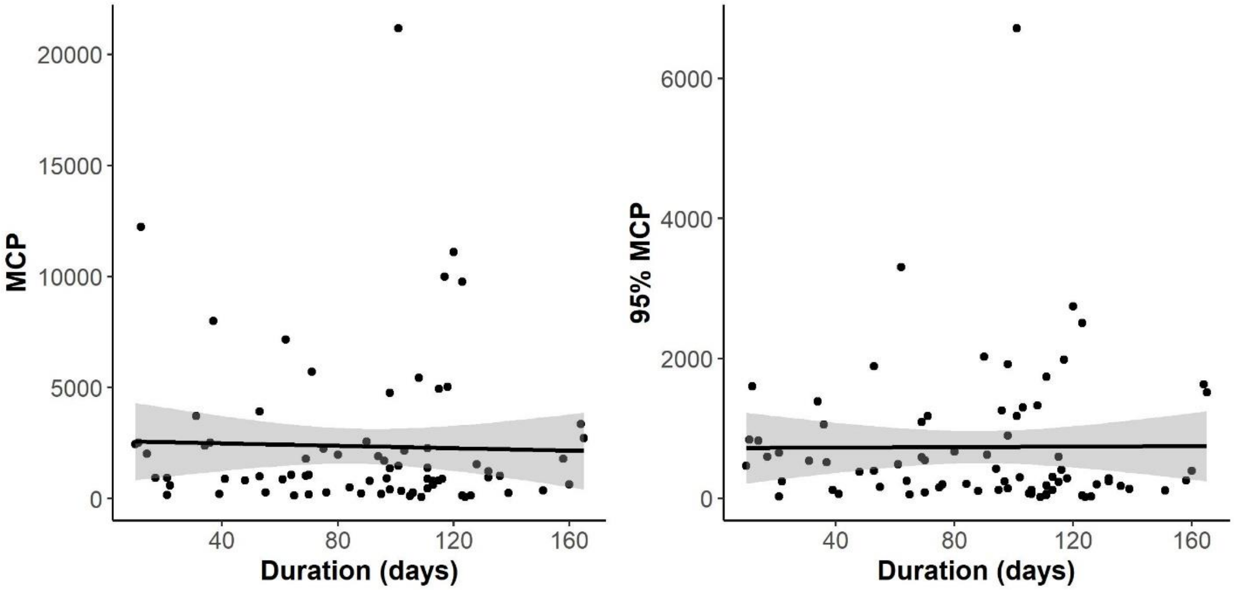


Figure A.5.4. Relation between the duration spent at the study site (in days) and home range size – (a) MCP and (b) 95% MCP – accounting for the total number of detections. Scattered dots represent exact values from each individual. The time spent at the study site did not have any effect on home range size when accounting for number of detections.

Chapter 6. High annual and overwinter survival suggest that the wintering stage is not likely to be the limiting part of the annual cycle of the Common Whitethroat

6.1 Abstract

Long-distance migratory birds spend significant periods of their annual cycle in areas exposed to many different ecological, energetic, and physiological pressures, potentially leading to differential survival rates throughout the year. Survival rates for each stage of the annual cycle are therefore key for understanding when and how populations of migratory animals are limited. Migration is, for example, an event with a high risk of mortality, particularly when considering preparations for and during spring and/or autumn migration; time spent in the non-breeding area, by comparison, likely represents a period of high survival given predictable resources and temperatures. In this chapter, we aim to estimate annual and overwinter survival rates and differences between demographic groups to determine whether the time spent at the non-breeding grounds represent a low-mortality period for the Common Whitethroat *Curruca communis*. Open-populations Cormack–Jolly–Seber (CJS) models were used to estimate annual and overwinter survival (φ) and detection probabilities (p) when needed. The annual survival rate, when averaging all datasets and considering all individuals, was 0.41 (0.33 – 0.47). However, when most transients were removed, the mean annual survival rate increased up to 0.61 (0.58 – 0.67). We did not find clear differences in the annual survival rates between adult and first-year birds: adult annual survival rates ranged between 0.38 and 0.45 (mean = 0.41) and first-years' survival between 0.35 and 0.61 (mean = 0.47). Overwinter survival was high and much greater than between-winter survival, averaging 0.94 (0.82 – 1) and 0.37 (0.36 – 0.39), respectively. In this case, adults seem to have higher overwinter survival rates than first-years (mean adults' overwinter survival = 1 and mean first-years' overwinter survival = 0.79). Our results confirm that the stationary period on non-breeding grounds is a low-mortality period for the species. We suggest that Whitethroat conservation efforts should focus on the active migration period and stopover sites, both during autumn and spring migration, when we assume the highest mortality rates occur and when they are likely to be more susceptible to extreme weather changes.

6.2 Introduction

For long-distance migration to confer an evolutionary advantage, survival and reproduction must increase when moving between locations when compared to remaining at a same place over the course of the year, outweighing the benefits of residency and shorter distance movements (Biber & Salathé, 1991; Zúñiga et al., 2017). Migratory birds' annual survival rate is influenced by conditions at their breeding and wintering grounds, as well as along migratory routes, since birds spend different periods of their annual cycle in geographically and ecologically disparate locations (Berthold & Terrill, 1991; Walther & Pirsig, 2017). Estimating these rates for each stage of the annual cycle is key in understanding when and how populations of migratory birds are limited, ultimately enabling one to pinpoint when higher mortality rates occur. It also enables further study in population ecology and the evolution of life-history traits. Their complex annual cycle, however, makes it challenging to estimate accurate annual survival rates. Nevertheless, identifying these "dangerous periods" is essential for implementing and directing more appropriate conservation measures (Wilcove & Wikelski, 2008), especially considering recent global population declines (Sanderson et al., 2006; Vickery et al., 2014; Bairlein, 2016).

Different ecological, energetic, and physiological pressures occur during each stage of a migrant's annual cycle, leading to differential survival throughout the year (Sillett & Holmes, 2002; Newton, 2010; Rockwell et al., 2017; Buechley et al., 2021). During the breeding season, for example, searching and competing for mates and territories, nest building, egg-laying and incubation, chick-rearing, and, in some cases, moulting, are energetically demanding activities that strongly influence survival during this period (Newton, 2010; Klaassen et al., 2014). During the wintering season, birds' survival is regulated by competition for suitable habitat, resources, and territories against both resident bird species and other long-distance migrants during a period with progressively deteriorating conditions (Sillett & Holmes, 2002; Marra et al., 2015). Finally, during migratory periods, birds are affected by events and conditions that occur during the migratory flight and at stopover sites. During the long journey, birds cross extreme barriers (*e*.*g*. the Mediterranean Sea and Sahara Desert), are hunted and may encounter heavy winds, collisions, storms, and other extreme weather events (Bairlein, 2016), greatly increasing mortality rates. At stopover sites, a large number of individuals and species gather to rest and refuel usually in small areas, thus survival is limited by high competition, predation, and pathogen and parasite exchange (Flegg, 2004; Newton, 2010). Even though the migratory period is the shortest stage of the annual cycle, it seems that migratory songbird mortality rates may be up to 15 times higher during migration than during stationary periods (Sillett & Holmes, 2002; Klaassen et al., 2014), mostly because of multifactorial unpredictability and major energetic costs during this period.

Furthermore, events within one stage of the migratory bird's annual cycle may have an effect on events in subsequent stages (Webster et al., 2002; Rockwell et al., 2017). Not finding suitable habitat at the stationary wintering grounds, for example, could have a significant impact on spring migration departure dates and consequently on arrival dates at the breeding grounds. The clearest example of this is termed the phenological mismatch between migratory birds and their prey (Cotton, 2003; Both et al., 2006; Visser et al., 2006; Møller et al., 2008): birds that arrive at the breeding grounds either too early or too late miss the peak spring phenological events, such as flowering and fruiting in plants and emergence of insects (Menzel et al., 2006), significantly decreasing their breeding success and survival (Both et al., 2006; Saino et al., 2010).

Differential survival not only depends on temporal and spatial aspects. Certain annual strategies often vary with sex and age, thus survival rates throughout the annual cycle can also vary according to different demographic groups (Newton, 2010; McKim-Louder et al., 2013; Rockwell et al., 2017). Different parental roles, physical aspects, and territorial behaviours across individuals may lead to differential survival between males and females and first-years and adults (Sillett & Holmes, 2002). Because fledged chicks have little experience foraging, escaping predators, and generally being independent, post-fledging survival tends to be particularly low (Berthold, 1993; Anders et al., 1997; McKim-Louder et al., 2013; Grüebler et al., 2014). Similarly, mortality rates are likely to be higher during migration for inexperienced individuals, and first-years are more likely to arrive at lower quality non-breeding habitats due to the stochastic nature of first migrations (Cresswell, 2014). At the wintering grounds, differences in dominance according to age and sex may result in sub-dominant individuals (first-years and/or females) being forced to occupy lower-quality habitats compared to dominant individuals (adults and/or males; Hutto, 1980; Mazerolle & Hobson, 2004; Brown & Long, 2006). These individuals often have reduced survival as a result (Jones et al., 1996; Marra & Holmes, 2001; Norris et al., 2004), and carry-over effects may influence future breeding success (Marra & Holmes, 2001; Both et al., 2016).

Finally, survival can also vary across years. Survival is expected to be higher when weather conditions are favourable and Afro-Palearctic migrants are known to be influenced by weather conditions in Africa. Correspondingly, dry years and severe drought have been identified as the cause for severe population declines in many migratory species. Resource availability during one stage will also directly impact the subsequent stages. Seasonality, such as spring migration and autumn migration can also impact survival differently because in autumn, populations are large and first-years are carrying out their first migration, lacking detailed knowledge of the route (Cresswell, 2014) or potential corrections to wind drift, whilst in spring all individuals have experienced at least one journey and are heading for their known natal destination (Newton, 2010).

Whilst there has been much interest and effort in estimating annual survival rates, only more recent studies have begun to examine the patterns of survival at different stages of the annual cycle. These studies have been based on resightings of marked individuals and long-term CES ringing programmes that can estimate "apparent" survival during different annual stages (*e*.*g*. Boano et al., 2004; Johnston et al., 2016; Rockwell et al., 2017) by recapturing or resighting marked individuals over multiple years at the same study sites (Lebreton et al., 1992). This, however, is extremely biased to studies carried out at the breeding grounds. Arguably, one of the best methods to estimate accurate survival rates is the use of global-scale remote-tracking systems to track individuals live and with great precision, thus enabling the determination of the timing and location of mortalities and, in turn, the estimation of "true" survival throughout the full annual cycle (Klaassen et al., 2014; Cheng et al., 2019; Sergio et al., 2019), at least in large birds that can carry the weight of the devices.

Despite the importance of survival rates however, these are difficult to measure, particularly in small birds that cannot be tracked in real-time. To estimate survival parameters of small birds in the field under natural conditions, resightings or recaptures of individually marked animals throughout and after some time are needed (Lebreton et al., 1992; Hammond, 2018). Return rates, or the proportion of individuals that are recaptured in a subsequent year, are then often used as an index of survival in migratory birds. However, annual return rates to a wintering or breeding site are the product of four independent probabilities: (1) true survival, (2) site fidelity (*i*.*e*. 1–probability of permanent emigration), (3) annual variation in local site use or residency duration (*i*.*e*. 1–probability of temporary emigration), and, (4) detection rates. Detection rates (p) directly influence survival estimates and, in natural populations, are nearly always less than one. Perfect detection is hardly ever achieved, and dispersal (and therefore apparent disappearance) can easily be confused with mortality, making true survival rates hard to estimate (Marshall et al., 2000; Gardali et al., 2003; Lettink & Armstrong, 2003). How accurate an estimate is depends mainly on the size of the study area, the dispersal behaviour of the species (Schaub & Royle, 2014), and the probability of detecting individuals. For example, the higher the degree of site fidelity and the easier individuals are to detect, the easier it is to differentiate dispersal from mortality and thus, to estimate real survival rates (Lettink & Armstrong, 2003; Schaub & Royle, 2014; Blackburn & Cresswell, 2016c).

The Common Whitethroat *Curruca communis* is a widely distributed small warbler (Shirihai et al., 2001). It has been well studied at its breeding grounds (Persson, 1971; Mason, 1976; da Prato & da Prato, 1983; Boddy, 1993; Stoate & Szczur, 2001; Tsiakiris et al., 2009; Meichtry-Stier et al., 2013), but information regarding its non-breeding ecology, especially data as basic as overwinter survival rates have not been previously estimated. We have shown that ~20% of individuals return to the site every year and that residency duration varies according to individuals (Chapter 4). Also in Chapter 4, we estimated that Whitethroats have low to medium detection rates (a 33% probability of detection per visit through resightings). Thus, return rates can only be considered as minimal (or "apparent") survival rates and this chapter will lead to better, or "truer" survival estimates.

6.3 Aims

Migratory birds spend at least two-thirds of their annual cycle away from the breeding grounds yet estimates of winter survival are hard to come by. The main aim of this chapter is to estimate overwinter and annual survival rates to determine whether the time spent at the non-breeding grounds represents a high-mortality period for the Whitethroat. The specific aims and corresponding predictions are:

1) To estimate annual survival rates (probability of surviving from one non-breeding season to the next) and differences between cohort groups (age/sex). We predict high mortality rates during migration, and thus annual survival rates to be lower than overwinter survival. As we do not consider a first-year's first migration (autumn migration from breeding site to non-breeding site), we do not expect to find strong differences between age groups. Similarly, as the non-breeding period does not seem to involve segregation or behaviours specific to sex, we do not expect to find significant variation by sex. Lastly, even when controlling for age and sex, we expect to find higher Whitethroat annual survival rates when estimated from data collected from non-breeding grounds compared to data from breeding grounds, as any individuals sighted in non-breeding grounds will have more experience.
2) To estimate overwinter survival rates (probability of surviving the "stationary" non-breeding period) and differences between cohort groups (age/sex). We do not expect the stationary wintering period to have a strong negative effect on Whitethroat survival. Breeding pressures are absent during this period, all birds have migrated successfully (including first-year birds) and, as Whitethroats seem to be generalists in their wintering requirements, we expect high overwinter survival rates, similar or higher to survival rates at the breeding grounds. We expect

higher survival rates in adults, because of their previous experience. We do not expect differences in survival between females and adults due to the absence of breeding pressures.

6.4 Methods

6.4.1 Study site, mist-netting, and resighting efforts

See Chapter 2 for general methods.

6.4.2 Data collection

APLORI’s long-term ringing CES database

Birds included in this study were captured as part of the APLORI Constant Effort Sites (CES) ringing long-term programme. A CES ringing scheme consists of mist-netting at the same locations over the same period at regular intervals throughout the year to measure species richness, abundance, and overall changes over time. APLORI has been carrying out the CES ringing programme within the Amurum Forest Reserve (9°52’ N, 8°58’ E) since 2000, though for logistic reasons and improvements to the scheme sites changed and ringing has not been undertaken at regular intervals throughout all years: it took place twice a year until 2009, five times a year from 2010 to 2016, and has occurred six times a year since 2017.

For this study, we analysed data pertaining to birds caught using understory mist-nets from two sites – site1 and site2. Birds in site1 were caught between December 2002 and February 2020 and birds from site2 were caught between March 2010 and February 2020. We analysed data obtained from two sampling efforts a year. During each sampling effort, mist-netting occurred between 0600 and 1100 hrs for three days within a ten-day period. From 2010, when the sites coincided, ringing was carried out for six consecutive days alternating between both sites. The first sample effort of the year occurred between February and March, when birds were preparing for spring migration, and the second sample effort between September and December when individuals were arriving at the area to spend the winter. We extracted 202 records from 154 individuals on site1 and 97 records from 81 individuals on site2 (Table 6.1). Note that year 2002 comprises data from November/December 2002 and February/March 2003, year 2003 comprises data from November/December 2003 and February/March 2004, and so on.

Table 6.1. Number of Whitethroats ringed each year and subsequently recaptured.

Site 1		**Year of recapture**																	
Year	*n*	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	Total
2002	29	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4
2003	10	.	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
2004	16	.	.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
2005	9	.	.	.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
2006	14	.	.	.	.	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2007	12	.	.	.	.	.	0	0	0	0	0	0	0	0	0	0	0	0	0
2008	16	.	.	.	.	.	.	0	0	0	0	0	0	0	0	0	0	0	0
2009	11	.	.	.	.	.	.	.	0	0	0	0	0	0	0	0	0	0	0
2010	4	.	.	.	.	.	.	.	.	1	0	0	0	0	0	0	0	0	1
2011	3	.	.	.	.	.	.	.	.	.	0	0	0	0	0	0	0	0	0
2012	2	.	.	.	.	.	.	.	.	.	.	0	0	0	0	0	0	0	0
2013	3	.	.	.	.	.	.	.	.	.	.	.	0	0	0	0	0	0	0
2014	5	.	.	.	.	.	.	.	.	.	.	.	.	0	0	0	0	0	0
2015	1	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0	0	0	0
2016	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0	0	0
2017	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	0	1
2018	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0
2019	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	

Both sites																			
Year	*n*																		
2009	14	.	.	.	.	.	.	.	0	0	0	0	0	0	0	0	0	0	0
2010	7	.	.	.	.	.	.	.	.	0	1	0	0	0	0	0	0	0	1
2011	10	.	.	.	.	.	.	.	.	.	0	1	0	0	0	0	0	0	1
2012	5	.	.	.	.	.	.	.	.	.	.	0	0	0	0	0	0	0	0
2013	4	.	.	.	.	.	.	.	.	.	.	.	0	0	0	0	0	0	0
2014	15	.	.	.	.	.	.	.	.	.	.	.	.	0	0	1	1	0	2
2015	3	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0	0	0	0
2016	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0	0	0
2017	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0	0
2018	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0
2019	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	

Detailed study

In this chapter, we also used data obtained from resightings and mist-netting carried out throughout the fieldwork period (Chapter 2). Because survival estimates require similar sampling effort, we only used and compiled data collected during (1) November and December, and (2) February, March, and April (Table 6.2). All individuals ringed after December of year3 were excluded from the analyses and were used only for overwinter survival estimates. Birds that could not be confidently aged or sexed were excluded from models including age and sex as predictors.

Table 6.2. Number of ringed and detected birds, across years.

		Year of detection	
Year	***n***	**2018**	**2019**
2017	182	38	18
2018	110	.	9
2019	10	.	.

6.4.3 Data analyses

Cormack–Jolly–Seber (CJS) models

Here we used capture-recapture data in association with open-population models Cormack-Jolly-Seber (CJS) and associated model-selection criteria to estimate apparent (or "true") annual and overwinter survival rates. An animal that is not recaptured on a particular sampling occasion may either have died or still be alive but simply not recaptured. The basic task in the analysis is thus to simultaneously estimate two parameters: survival and detection. The Cormack-Jolly-Seber (CJS) models estimate apparent survival $\varphi(i)$ – the probability that an individual survives from year i to year $i + 1$ and returns to the sampling area, and the encounter probability $p(i)$ – the probability that an animal in the sampling area at time i is encountered at time i, *i.e.* the probability that given that the individual is alive and in the sample, that it is in fact encountered. In these models, the encounter probability (p) is explicitly modelled to correct for possible biases in survival estimates (Pradel et al., 1997; Schaub & Royle, 2014). These models produce survival estimates that are not influenced by variations in recapture probability and are therefore more reliable than those based on return rates only (Martin et al., 1995). To obtain unbiased estimates for the parameters of interest, some basic assumptions should be met: (1) that all individuals have the same survival probability, (2) that all individuals have the same capture probability, (3) that marks are not lost or overlooked, and that (4) the duration of each capture occasion is instantaneous in relation to the intervals between sessions (Seber, 1982; Hammond, 2018). Some of these assumptions are difficult to meet, especially assumption #2, as we have provided evidence that individuals have different residency periods throughout the wintering period (see Chapter 4).

Several CJS models were used to estimate annual and overwinter survival with several datasets. All analyses were performed using MARK software (White & Burnham, 2009). In MARK, various models can be tested, such as allowing for changes in $\varphi(i)$ and $p(i)$ between different sample efforts (*e.g*. different years) or constancy between them. For some examples of possible models, the nomenclature and the description of the models are defined in Table 6.3. The model with the lowest Akaike's Information

Criterion (AIC) values was taken as the best representation of the data. The type of model that was used most often was $\varphi(.)p(.)$ (see Table 6.3).

Table 6.3. Description of potential survival models.

Model	Description
$\varphi(.)p(.)$	Both survival and detection probability are constant across sample efforts
$\varphi(t)p(.)$	Survival is different across sample efforts, but detection probability is constant
$\varphi(.)p(t)$	Survival is constant across sample efforts, but detection probability varies across sample efforts
$\varphi(t)p(t)$	Both survival and detection probability vary across sample efforts
$\varphi(.)p(0.5)$	Both survival and detection probability are constant across sample efforts, however, the detection probability value is set to 0.5
$\varphi(g)p(g)$	Both survival and detection probability are constant across sample efforts but vary according to group category (*e.g*. sex, age, or season)
$\varphi(g{*}t)p(g{*}t)$	Both survival and detection probability are time-dependent but also vary according to group category (*e.g*. sex, age or season)

Annual survival rates

For a migratory bird, the annual survival rate is the product of survival probabilities during the stationary and migratory periods of the annual cycle, that is, φannual = φwintering × φmigration × φbreeding (*e.g*. the probability of surviving from January year *i* to January year *i* + 1). To estimate annual survival rates, we used several datasets. The first dataset comprised capture-recapture data collected from 114 individuals caught in February and March from site1 of the CES, between 2003 and 2020 (*i.e*. Formula 1 below; Table 6.4). The second dataset comprised data collected from 65 individuals caught in February and March at both CES sites (*i.e*. captures at site1 + captures at site2) between 2009 and 2020 (Table 6.4). For both cases, the best model was "$\varphi(.)p(.)$", where survival and detection probability were constant across sample efforts.

Formula 1: $Feb/Apr\ 2003 \xrightarrow{\varphi} Feb/Apr\ 2004 \xrightarrow{\boldsymbol{\varphi}} \ldots \xrightarrow{\boldsymbol{\varphi}} Feb/Apr2020$

Additionally, we used a third dataset comprising data collected from 213 individuals caught and resighted in November and December between year1 and year3 and a fourth dataset with data collected from 159 individuals caught and resighted in February and March between year1 and year3

(Table 6.4). For the latter two datasets, the best models were also “$\varphi(.)p(.)$”, but because we previously estimated that detection probability was, on average, 0.33 (Chapter 4), we set the constant p-value to 0.33 (“$\varphi(.)p(0.33)$”).

Table 6.4. Summary explanation of used datasets to obtain annual and overwinter survival rates. *n* = total sample size, ad = adults, fy = first-years, F = adult females, and M = adult males.

Survival period estimated	Dataset	Details
Annual survival The probability of surviving from year *i* to year *i* + 1. e.*g*. surviving from January 2003 to January 2004.	CES site 1	Data collected between February and March of 2003 – 2020 by mist-netting 3 days per sample effort, 18 sample efforts *n* = 114; by residency: individuals seen at least once after capture = 21; by age: ad = 57, fy = 56; by sex: F = 17, M = 32
	CES sites 1 and 2	Data collected between February and March of 2009 – 2020 by mist-netting 6 days per sample effort (3 days per site), 11 sample efforts *n* = 65; by age: ad = 51, fy = 12; by sex: F = 16, M = 19
	Detailed study	Data collected between November and December of 2017 – 2019 by resightings and mist-netting Individuals were sought out at least once a week, 3 sample efforts *n* = 213; by residency: individuals seen at least once after capture = 89; by age: ad = 76, fy = 107; by sex: F = 27, M = 36
		Data collected between February and March of 2018 – 2020 by resightings and mist-netting Individuals were sought out at least once a week, 3 sample efforts *n* = 159; by residency: individuals seen at least once after capture = 96; by age: ad = 76, fy = 74; by sex: F = 27, M = 41
Overwinter survival The probability of surviving the winter season (~4.5 months). e.*g*. surviving from November 2003 to March 2004.	CES site 1	Data collected between November/December and February/March of 2002 – 2020 by mist-netting 3 days per sample effort, 36 sample efforts *n* = 154; by age: ad = 71, fy = 79; F = 48, M = 61
	CES sites 1 and 2	Data collected between November/December and February/March of 2009 – 2020 by mist-netting 6 days per sample effort (3 days per site), 21 sample efforts *n* = 81; by age: ad = 59, fy = 20; by sex: F = 20, M = 23
	Detailed study	Data collected between November/December and February/March of 2017 – 2019 by resightings and mist-netting Individuals were sought out at least once a week, 6 sample efforts *n* = 302; by age: ad = 121, fy = 146; by sex: F = 85, M = 36

Eliminating transients

As mentioned above, CJS models assume that “all individuals have the same capture probability”. However, we know for a fact that within the Whitethroat population of our study site individuals show many residency patterns, from individuals passing through to individuals that remain for most of the winter (Chapter 4) thus violating this assumption, as resident birds will have higher detection probabilities than transient birds. Pradel et al. (1997), as cited by Ruiz-Gutierrez et al. (2016), defined transients as ‘captured and marked individuals that have a zero probability of returning to be recaptured in future sampling events’, so by not taking transients into account, we might underestimate annual survival rates, because many individuals that were never detected after capture are most likely alive but outside our study site.

To account for transients, and to obtain more realistic survival rates, we used data from individuals that were seen at least once after first capture. We carried out CJS models with three datasets. The first dataset comprised data collected from 21 individuals caught in February and March (2003 – 2020) from site1 of the CES (Table 6.4). The best model for this data was constant survival and detection probabilities through time (“$\varphi(.)p(.)$”). Note: we did not use $p = 0.07$ because that estimation came from information collected with transients and is not fit for purpose. The second dataset comprised data collected from 89 individuals caught and resighted in November and December between year1 and year3 and a third dataset with data collected from 96 individuals caught and resighted in February and March between year1 and year3 (Table 6.4). For both cases, we only tested the model “$\varphi(.)p(0.33)$”, where survival and detection probability were constant across sample efforts and detection probability was set to 0.33.

Differences between first-year and adult birds

To understand whether annual rates differed amongst individuals of different age groups (*i.e*. between first-years and adults) we analysed three similar datasets. The first dataset comprised data collected from 113 individuals caught in February and March (2003 – 2020) from site1 of the CES (Table 6.4). The best model for this data was survival different between age groups but constant through time, and a 0.07 detection probability obtained from the mean of the previous analysis (“$\varphi(\text{age})p(0.07)$”). The second dataset comprised data collected from 183 individuals caught and resighted in November and December between year1 and year3 and the third dataset, data collected from 150 individuals caught and resighted in February and March between year1 and year3 (Table 6.4). For the latter two datasets, the best model was “$\varphi(\text{age})p(0.33)$”. All individuals were grouped either as individuals caught as adults or as first-years. For individuals caught as adults, survival rates were constant across sample efforts

(φad; Table 6.5). For first-years, however, survival rates were estimated separately for the first year after an individual was caught (φfy; Table 6.5) but was then φad for subsequent years (Table 6.5).

Table 6.5. Estimation of adult survival (φad) and first-year survival (φfy) according to the age they were caught.

When caught as an adult				
Year when caught	Survival year1	Survival year2	Survival year3	Survival year4
1	φad	φad	φad	φad
2		φad	φad	φad
3			φad	φad
4				φad
When caught as a first-year				
Year when caught	Survival year1	Survival year2	Survival year3	Survival year4
1	φfy	φad	φad	φad
2		φfy	φad	φad
3			φfy	φad
4				φfy

We also repeated these analyses with data collected from individuals at both CES sites, but the sample size was too small to obtain any reliable results. Similarly, sample sizes were too small to estimate annual rate differences between adult females and males.

Overwinter survival rates

We also estimated survival probabilities during the stationary non-breeding period ($\varphi wint$; *i.e*. survival between November/December and February/March or survival between autumn and spring migrations, ~4.5 months) and the remainder of the annual cycle ($\varphi rest$; *i.e*. survival between February/March and November/December or survival between spring and autumn migrations, including breeding season ~7.5 months; Formula 2).

Formula 2: $$Nov/Dec2003 \xrightarrow{\boldsymbol{\varphi}\mathbf{wint}} Feb/Mar2004 \xrightarrow{\boldsymbol{\varphi}\mathbf{rest}} Nov/Dec2004 \xrightarrow{\boldsymbol{\varphi}\mathbf{wint}} \dots \xrightarrow{\boldsymbol{\varphi}\mathbf{rest}} Feb/\ Mar2020$$

To do this, we used larger versions of the previously described datasets, as each dataset had data from November, December, February and March – a total of two sample efforts per year: (1) November and December, and (2) February and March. The first dataset comprised capture-recapture data collected from 154 individuals from site1 of the CES (2003 – 2020). The best model for this dataset was

"φ(season)p(0.07)" (Table 6.4). The second dataset comprised data collected from 81 individuals from sites 1 and 2 of the CES (2009 – 2020). The best model for this dataset was also "φ(season)p(0.07)" (Table 6.4). The third and final dataset comprised data collected from 302 individuals between year1 and year3 of the detailed study. The best model for this dataset was "φ(season)p(0.33)" (Table 6.4).

Differences between first-year and adult birds

To understand differences in overwinter survival between individuals of different age groups (*i.e*. between first-years and adults) we analysed three similar datasets. The first dataset comprised data collected from 150 individuals caught in November, December, February and March (2002 – 2020) from site1 of the CES (Table 6.4). We used the model "φ(season*age)p(0.07)", where survival differed between seasons (overwinter and the rest) and amongst age groups, and the detection probability was set to 0.07. The second dataset comprised data collected from 267 individuals caught and resighted in November, December, February, and March of years 1, 2, and 3 (Table 6.4). For the latter dataset, the model was similar to above, but the detection probability was set to 0.33 "φ(season*age)p(0.33)". As in the calculation of annual survival rates, all individuals were grouped either as individuals caught as adults or as first-years (see Table 6.5).

Due to small samples sizes, overwinter differences amongst adult females and males were impossible to estimate reliably.

6.5 Results

6.5.1 Annual survival rates

In general, the best models, based on AICc values, were those where both survival rates and detectability rates were constant across sample efforts (Table 6.6).

Table 6.6. Annual survival model selection results. Cormack–Jolly–Seber models used to estimate apparent annual survival rates (φ) and capture probabilities (p) using different datasets. Models were tested either to remain constant "(.)" or to vary "(t)" across sample efforts, and by age "(a)" when applicable (see Table 6.3 for further details). Given the resighting detection probability was known *a priori*, we tested models with p set to "(0.33)" when appropriate. From left to right: Model, AICc = small sample sizes corrected Akaike values; ΔAICc = difference of models' AICc values in relation to the first model; Model likelihood; Deviance = model deviance; N Par = number of estimated parameters; sample efforts = number of sampled years; n = sample size; ad = number of adults; fy = number of first-years. The best-fitting models are highlighted in bold.

ANNUAL SURVIVAL RATES					
Model	**AICc**	**ΔAICc**	**Model Likelihood**	**Deviance**	**N Par**
CES site1, sample efforts = 18, *n* = 114					
φ(.)p(.)	73.3	0	1	29.8	2

φ(t)*p*(.)	98.8	25.5	0	16.7	18
φ(.)*p*(t)	99.7	26.4	0	17.6	18
φ(t)*p*(t)	109.5	36.2	0	15.7	22
CES site1 + site2, sample efforts = 11, *n* = 65					
_φ_(.)_p_(.)	25.6	0	1	9.9	2
φ(t)*p*(.)	41.1	15.5	0	2.6	11
φ(.)*p*(t)	42.3	16.7	0	3.8	11
φ(t)*p*(t)	43.2	17.6	0	1.7	12
Nov/Dec this study, sample efforts = 3, *n* = 213					
_φ_(.)_p_(0.33)	179.2	0	1	2.1	1
φ(.)*p*(.)	181.1	1.9	0.4	1.9	2
φ(.)*p*(t)	182.7	3.5	0.2	1.5	3
φ(t)*p*(.)	182.7	3.5	0.2	1.5	3
φ(t)*p*(t)	184.8	5.6	0.1	1.5	4
Feb/Mar this study, sample efforts = 3, *n* = 159					
_φ_(.)_p_(0.33)	158.01	0	1	8.6	1
φ(.)*p*(.)	158.04	0.03	0.98	6.6	2
φ(.)*p*(t)	159.2	1.2	0.5	5.7	3
φ(t)*p*(.)	159.2	1.2	0.5	5.7	3
φ(t)*p*(t)	159.2	1.2	0.5	5.7	3
RESIDENTS					
CES site1, sample efforts = 18, *n* = 21					
_φ_(.)_p_(.)	51.7	0	1	30.62	2
φ(.)*p*(0.07)	54.4	2.65	0.27	35.59	1
Nov/Dec this study, sample efforts = 3, *n* = 89					
_φ_(.)_p_(0.33)	129.9	0	1	0.7	1
Feb/Mar this study, sample efforts = 3, *n* = 96					
_φ_(.)_p_(0.33)	132.7	3.4	0.18	6.6	1
FIRST-YEARS *vs*. ADULTS					
CES site1, sample efforts = 18, *n* = 113; ad = 57, fy = 56					
_φ_(a)_p_(0.07)	73	0	1	35.9	2
φ(.)*p*(.)	73.2	0.2	0.9	36.1	2
φ(a)*p*(.)	75	2.1	0	35.9	3
φ(a)*p*(a)	76.4	3.5	0.2	35.1	4
φ(.)*p*(a)	79	6	0.1	40	3
Nov/Dec, sample efforts = 3, *n* = 183; ad = 76, fy = 107					
φ(a)*p*(a)*	168	0	1	2.8	4
_φ_(a)_p_(0.33)	168	0.3	0.9	7.2	2
φ(a)*p*(.)	170	2.2	0.3	7.1	3
Feb/Mar, sample efforts = 3, *n* = 150; ad = 76, fy = 74					
_φ_(a)_p_(0.33)	152.9	0	1	12.6	2

$\varphi(a)p(.)$	153.4	0.5		0.8	11	3
$\varphi(a)p(a)$	154	1.1		0.6	9.6	4

*The p suggested for this model was "1" for adults, which is not realistic. Because "$\varphi(a)p(0.33)$" had a similar AICc value, we opted to use results from this model instead.

For Whitethroats wintering in Nigeria, the annual survival rate, *i.e*. the probability of an individual surviving from one given month to the same month the following year, is between 0.33 and 0.47 (Table 6.7; Fig 6.1a; Appendix 6.1). Data obtained from the CES long-term ringing database shows that individuals have between a 0.40 and 0.47 probability of surviving from February/March of year *i* to February/March of year *i* + 1 when considering a capture probability of 0.05 and 0.07, respectively. Similar results were estimated when using results collected during the detailed study, through resightings, and with an estimated detection probability set to 0.33, during February/March ($\varphi = 0.42$). When estimating annual survival rate from November/December of year *i* to November/December of year *i* + 1, we found similar, though slightly lower, annual survival rates (0.33), but this difference is not significant and is probably due to not all individuals having returned to the study site by November or December.

Table 6.7. Annual survival (φ) and detection probabilities (p). Annual survival (φ) and detection probabilities (p) estimated according to the best model for each dataset (see Table 6.6). Annual survival rates are highlighted in bold. Standard errors and 95% confidence intervals are also shown. φFy = annual survival of first-years and φAd = annual survival of adults.

Dataset	Best Model	Parameter	Estimate	SE	95% CI	
CES site1	$\varphi(.)p(.)$	φ	**0.47**	0.14	0.23	0.73
		p	0.07	0.05	0.02	0.231
CES site1 + 2	$\varphi(.)p(.)$	φ	**0.4**	0.3	0.05	0.89
		p	0.05	0.07	0.003	0.46
Nov/Dec: detailed study	$\varphi(.)p(0.33)$	φ	**0.33**	0.05	0.24	0.44
		p	0.33	-	-	-
Feb/Mar: detailed study	$\varphi(.)p(0.33)$	φ	**0.42**	0.07	0.3	0.55
		p	0.33	-	-	-
RESIDENTS						
CES site1	$\varphi(.)p(.)$	Phi	**0.58**	0.12	0.35	0.78
		p	0.26	0.13	0.09	0.56
Nov/Dec: detailed study	$\varphi(.)p(0.33)$	Phi	**0.59**	0.09	0.42	0.75
		p	0.33	.	.	.
Feb/Mar: detailed study	$\varphi(.)p(0.33)$	Phi	**0.67**	0.09	0.48	0.82
		p	0.33	.	.	.
FIRST-YEARS *vs*. ADULTS						
CES site1	$\varphi(a)p(0.07)$	φFy	**0.61**	0.31	0.11	0.95

		φAd	**0.45**	0.1	0.26	0.65
		p	0.07	-	-	-
Nov/Dec: detailed study	$\varphi(a)p(0.33)$	φFy	**0.35**	0.09	0.2	0.53
		φAd	**0.38**	0.09	0.24	0.56
		p	0.33	-	-	-
Feb/Mar: detailed study	$\varphi(a)p(0.33)$	φFy	**0.46**	0.12	0.25	0.69
		φAd	**0.4**	0.09	0.25	0.59
		p	0.33	-	-	-

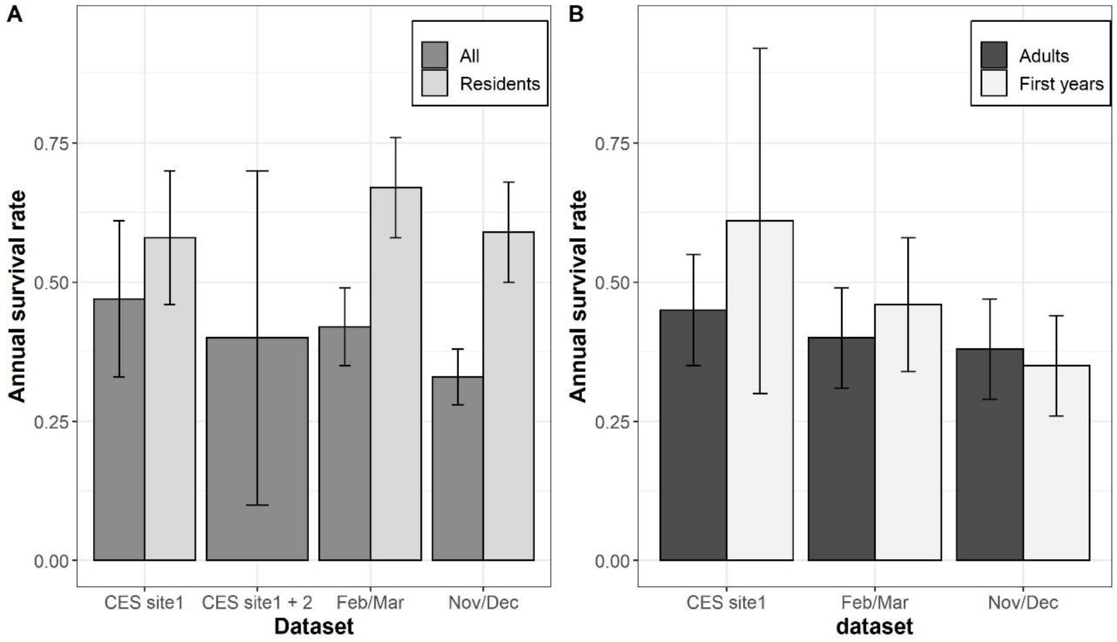


Figure 6.1. Annual survival rates. Annual survival rates ± a standard error for each dataset. a) Shows the annual survival rates of all individuals and residents. b) Illustrates the annual survival rates of adult and first-year birds.

Eliminating transients

When eliminating individuals that were not detected after first capture (transients), annual survival rates increased considerably (Table 6.7; Fig. 6.1a). When using the CES site1 dataset we estimated that the annual survival rate was 0.58, 0.11 higher than when transients were considered (Fig. 6.1a). The detailed study showed similar results: for November/December the estimated annual rate was 0.59 and for February/March it was even higher (0.67), 0.26 and 0.25 higher, respectively, than when considering all individuals (Fig. 6.1a).

Difference between first-year and adult birds

There were no clear differences in the annual survival rates between adult and first-year birds (Table 6.7; Fig. 6.1b). Estimated annual survival rates ranged between 0.38 and 0.45 for adults and between 0.35 and 0.61 for first-years, depending on the dataset. Even though the CES site1 dataset estimated higher survival rates for first-years compared to adults, standard errors were also larger, suggesting that even with this apparently large difference between groups (0.45 *vs* 0.61), many adults and first-years have similar annual survival rates.

6.5.2 Overwinter survival rates

When estimating overwinter survival rates, the best models, based on AICc values, were those where seasonal survival was constant across years and when detectability rates were set (0.07 for CES data and 0.33 for detailed study) and constant across sample efforts (Table 6.8).

Table 6.8. Seasonal survival model selection results. Cormack–Jolly–Seber models used to estimate apparent seasonal survival rates (*φ*) and capture probabilities (*p*) using different datasets. Models were tested to vary by season "(season)" or to remain constant "(.)" across sample efforts, and by age "(a)", when applicable. Detection probabilities were known *a priori* so we tested models with a *p* set to "(0.07)" when using CES data and to "(0.33)" when using results from the detailed study. From left to right: Model, AICc = small sample sizes corrected Akaike values; ΔAICc = difference of models' AICc values in relation to the first model; Model likelihood; Deviance = model deviance; *N* Par = number of estimated parameters; sample efforts = number of sampled years; *n* = sample size; ad = number of adults; fy = number of first-years. The best-fitting models are highlighted in bold.

SEASONAL SURVIVAL RATES					
Model	**AICc**	**ΔAICc**	**Model Likelihood**	**Deviance**	***N* Par**
CES site1, sample efforts = 36, *n* = 154					
_φ_(season)_p_(0.07)	163	0	1	82.3	2
φ(season)*p*(season)	163.5	0.5	0.8	78.6	4
φ(season)*p*(.)	164	1.1	0.6	81.3	3
CES site1 + site2, sample efforts = 21, *n* = 81					
_φ_ (season)_p_(0.07)	78	0	1	52.4	2
φ(season)*p*(season)	79.1	1.1	0.6	49.1	4
φ(season)*p*(.)	80.1	2	0.4	52.3	3
Detailed study, sample efforts = 6, *n* = 302					
_φ_(season)_p_(0.33)	380.8	0	1	85.6	2
φ(season)*p*(.)	682.7	1.9	0.4	85.4	3
φ(season)*p*(season)	684	3.2	0.2	0.2	4
FIRST-YEARS *vs*. ADULTS					
CES site1, sample efforts = 36, *n* = 150; ad = 71, fy = 79					
_φ_(season*a)_p_(0.07)	166.6	0	1	105.4	3
φ(season*a)*p*(.)	167.1	0.4	0.8	103.7	4
φ(season*a)*p*(a)	168.9	2.3	0.3	103.4	5
Detailed study, sample efforts = 6, *n* = 267; ad = 121, fy = 146					
_φ_(season*a)_p_(0.33)	630.5	0	1	126.7	3
φ(season*a)*p*(.)	632.1	1.6	0.5	126.2	4
φ(season*a)*p*(a)	633.9	3.4	0.2	126	5

For all datasets, overwinter survival was high and much greater than between-winter survival (Table 6.9; Fig. 6.2a; Appendix 6.2), even though the overwintering period consists of up to 5 months, while the period between winters consists of at least 7 months. When using data collected from the CES ringing programme the estimated overwinter survival (*i.e*. the probability of surviving from November to February) was one, meaning that no or few deaths occur during this period. Results obtained from the detailed study, however, indicate that the estimated overwinter survival is lower, approximately 0.82 (Table 6.9, Fig. 6.2a). On the other hand, between-winter survival was substantially lower, ranging from an estimated survival rate between 0.36 and 0.39, depending on the analysed dataset (Table 6.9; Fig 6.2a) – this period contains spring migration, breeding, and autumn migration survival periods.

Table 6.9. Seasonal survival rates (φ) and detection probabilities (p). Seasonal survival rates (*φ*) and detection probabilities (*p*) estimated according to the best model for each dataset (see Table 6.8). Overwinter survival rates (*φ*(Nov-Feb)) are highlighted in bold while between-winter survival (*φ*(Feb-Nov)) are underlined. Standard errors and 95% confidence intervals are shown for each estimate. *φ*(Nov-Feb) Fy = overwinter survival of first-years, *φ*(Nov-Feb) Ad = overwinter survival of adults, and *φ*(Feb-Nov) All = survival between February and November of both first-years and adults.

Dataset	Best Model	Parameter	Estimate	SE	95%CI	
CES site1	*φ*(season)*p*(0.07)	*φ*(Nov-Feb)	**1**	0	1	1
		φ(Feb-Nov)	0.39	0.07	0.27	0.52
		p	0.07	.	.	.
CES site1 + 2	*φ*(season)*p*(0.07)	*φ*(Nov-Feb)	**1**	0	1	1
		φ(Feb-Nov)	0.37	0.09	0.21	0.56
		p	0.07	.	.	.
Detailed study	*φ*(season)*p*(0.33)	*φ*(Nov-Feb)	**0.82**	0.07	0.64	0.92
		φ(Feb-Nov)	0.36	0.05	0.27	0.47
		p	0.33	.	.	.
FIRST-YEARS *vs*. ADULTS						
CES site1	*φ*(season*age)*p*(0.07)	*φ*(Nov-Feb) Fy	**0.87**	0.49	0.001	0.99
		φ(Nov-Feb) Ad	**1**	0	1	1
		φ(Feb-Nov) All	0.38	0.07	0.26	0.51
		p	0.07	.	.	.
Detailed study	*φ*(season*age)*p*(0.33)	*φ*(Nov-Feb) Fy	**0.7**	0.1	0.48	0.86
		φ(Nov-Feb) Ad	**1**	0	1	1
		φ(Feb-Nov) All	0.36	0.04	0.28	0.44
		p	0.33	.	.	.

Difference between first-year and adult birds

Adults have a higher overwinter apparent survival rate than first-years (Table 6.9; Fig. 6.2b), especially when analysing results collected through the detailed study. Results from both datasets show that adults have a probability of one of surviving the winter. First-years, however, have lower probabilities, between 0.7 and 0.87 (Table 6.9; Fig. 6.2b).

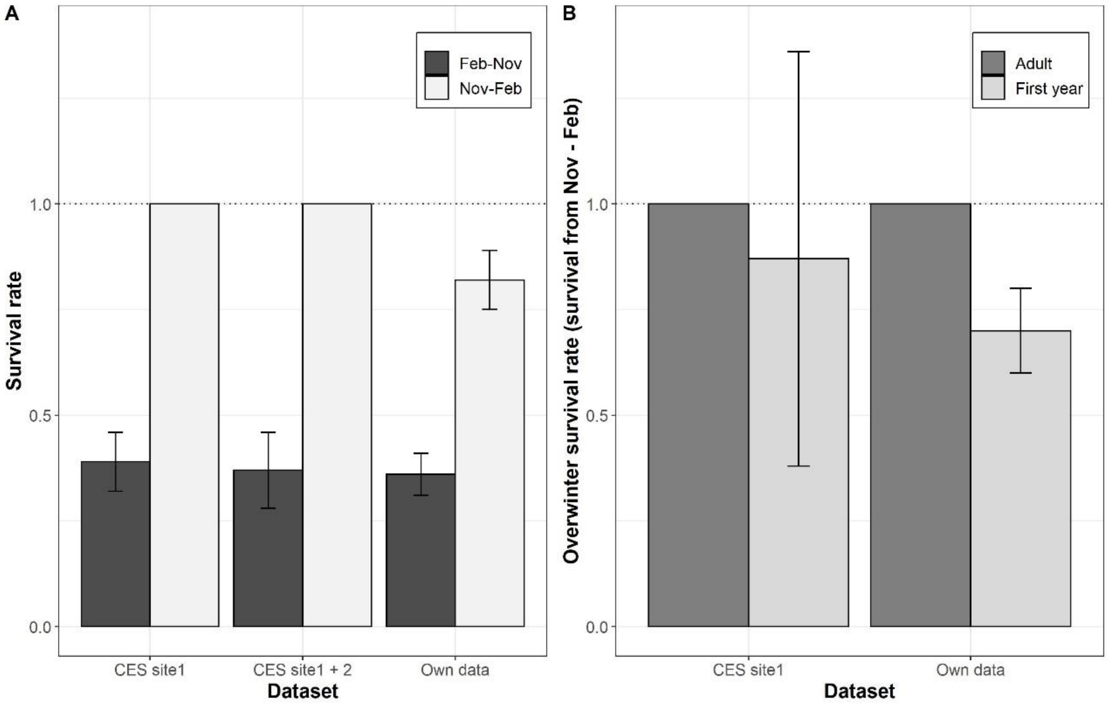


Figure 6.2. Seasonal and overwinter survival rates. a) Seasonal survival rates ± standard errors for each dataset. b) Overwinter survival rates of adults and first-year birds calculated for each dataset. The dotted line represents survival = one. No standard errors were calculated on occasions when survival = one.

6.6 Discussion

In this chapter, we calculated the annual and overwinter survival rates of Whitethroats wintering in central Nigeria. The mean annual survival rate, when averaging all datasets and considering all individuals, is 0.41 (0.33 – 0.47). However, when most transients were removed, the mean annual survival rate increased to 0.61 (0.58 – 0.67). Our results did not show clear differences in annual survival rates between adult and first-year birds: adult annual survival rates ranged between 0.38 and 0.45 (mean = 0.41) and first-years' survival between 0.35 and 0.61 (mean = 0.47), depending on the dataset. Our results also show that overwinter survival was high and much greater than between-winter survival, averaging 0.94 (0.82 – 1) and 0.37 (0.36 – 0.39), respectively. Finally, adults seem to have higher overwinter survival rates than first-years: mean adults' overwinter survival = 1 and mean first-years' overwinter survival = 0.79 (0.7 – 0.87). During this section, we will: (1) discuss the limitations and potential biases of our study, (2) compare annual and overwinter survival rates obtained in this study with those obtained from other Whitethroat studies and other migratory species, and (3) discuss what these results mean for the conservation of Whitethroats.

6.6.1 Methodological considerations

To estimate true survival rates of migratory species under ideal conditions, without the use of remote-tracking devices, all studied individuals should be marked at the same time, be highly conspicuous, and have small, established territories or home ranges where they remain throughout the entirety of the sampling period and to which they return every year. In reality, this is rarely the case, especially in the case of Whitethroats. We found that while some Whitethroats remain at the study site throughout the winter, many remain for shorter periods throughout different parts of the season or are simply passing through. We also detected that some individuals do not necessarily return to the site every year and those that do, do not necessarily repeat the same residency pattern as previous years. This highlights how individually- and yearly-dependent non-breeding behaviour is and not only poses logistical problems for estimating survival but also violates CJS model assumptions and therefore makes true annual and overwinter survival rates difficult to calculate. For these reasons, and because no analytical method can distinguish between dispersal and mortality, we acknowledge that at least some birds that failed to return to our study site in the following year may have survived and wintered in other locations, and some birds that remained at the study site could have been missed altogether, potentially underestimating survival rates.

However, to overcome these obstacles, we used different datasets, each with its advantages and limitations. The CES dataset from APLORI is one of the few long-term ringing programmes in West Africa. Even though it is not carried out in a preferred habitat for Whitethroats and modifications and improvements have been made to it over time, it provides valuable standardised information since 2002 and comprises one of the longest-running programmes on the continent. On the other hand, the detailed study was a short-term project but with high precision and intensive data collection at a small spatial- and temporal-scale. As all datasets provided similar estimates and because we removed most of the potential transients whose presence would underestimate survival rates (Abadi et al., 2013), we believe that the results obtained here represent a good attempt at estimating true annual and overwinter survival rates.

A limitation to this study was that, even though we estimated what we consider appropriate overall survival rates, small sample sizes mean we did not manage to identify and estimate differences amongst adult sex groups, and we have weak statistical power for age-related models. Further exploration of these differences would lead to a better understanding of population dynamics but could be challenging to undertake as sexing and ageing Whitethroats in the field can be difficult (Waldenström & Ottosson, 2000).

6.6.2 Annual survival rates

The mean apparent annual survival rate estimated from the non-breeding grounds for Whitethroats was at least 0.41 and 0.61 when eliminating most potential transients. These values are similar, or slightly higher, than annual survival rates estimated from the breeding grounds (range between 0.09 and 0.55, but approximate mean = 0.33; Fig. 6.3, see references within) though it is important to consider that all studies estimated survival using different methods and during different periods, and most studies only estimated adult male survival rates. However, it is not surprising that different breeding populations have distinct survival rates, because different pressures may be occurring at different scales (*i.e*. differences in the quality of breeding sites or varying selective pressures operating along different migratory routes). For example, the low annual survival rate in Russia (9%) is suggested to be due to high emigration rates (breeding dispersal) or a reflection of a sub-optimal site (Shitikov et al., 2013), while higher survival rates in the UK of up to 68% reflect a period of recovery after a sharp population decline (Boddy, 1993).

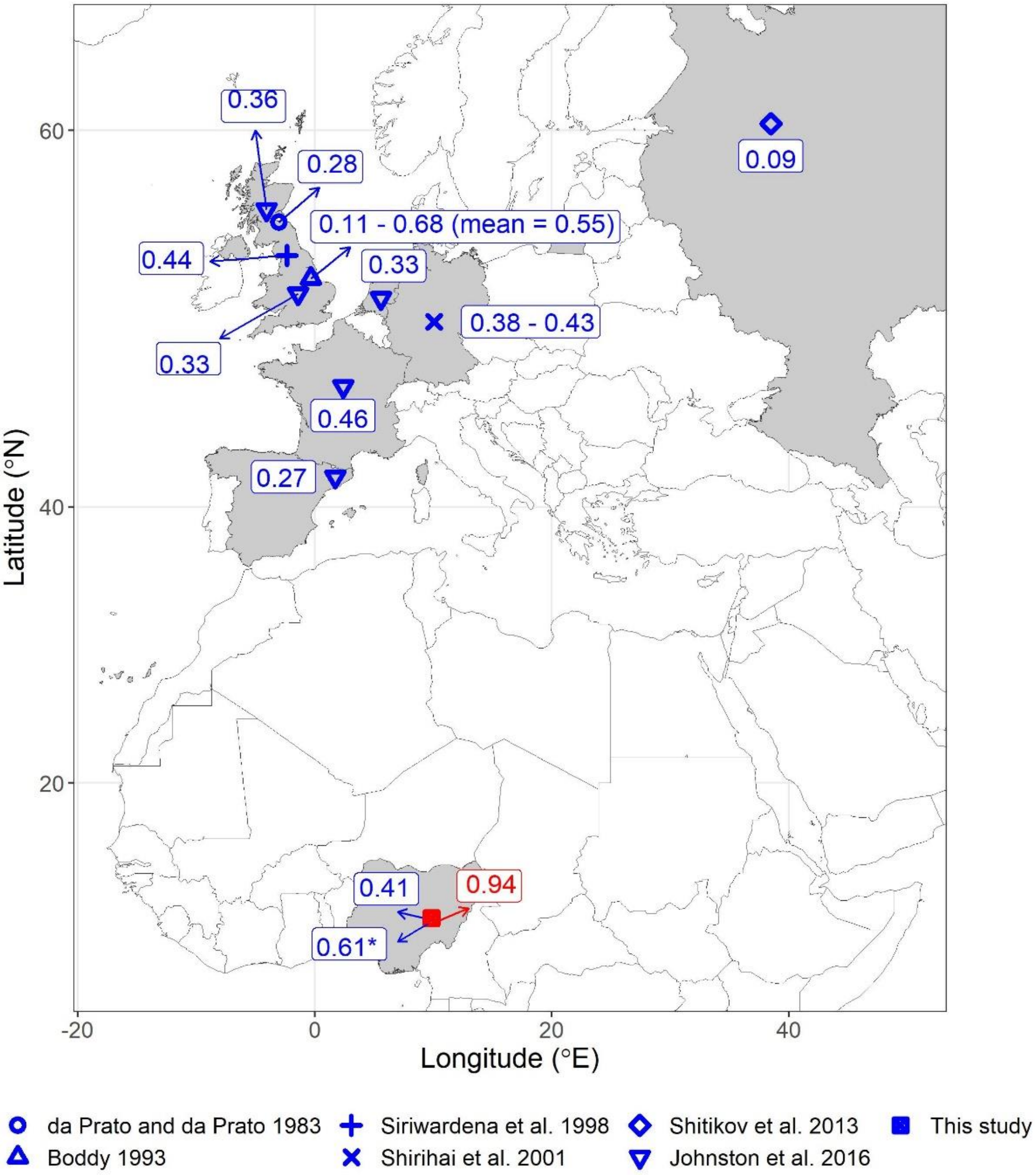


Figure 6.3. Annual and overwinter survival rates of Common Whitethroats. Annual (blue) and overwinter (red) survival rates of Whitethroats throughout its distribution. * = survival rate estimations when eliminating potential transients. Estimations were obtained from different studies (illustrated with different shapes, key is below map). Studies were undertaken using different methods during different periods. Most studies estimated survival rates of adult male birds.

By eliminating many potential transients, the annual survival rate increased by 20%. It is well documented that ignoring individual capture heterogeneity between residents and transients generally leads to a small negative bias in survival estimates (Pradel et al., 1997; Hines et al., 2003; Abadi et al., 2013), and thus we believe 0.61 to be the most realistic value. The slightly higher estimated survival rates on the wintering grounds compared to those estimated at the breeding grounds also suggests that mortality rates could be higher during the breeding period and/or autumn migration, compared to the wintering period and/or spring migration, especially for first-year individuals. In other words, although annual survival rates represent survival during 12 months independent of where and when it's estimated from, then even if age is controlled for, sampling in the non-breeding grounds means that there has already been some sort of selection during migration, as all birds are four to six months older and more experienced than birds sampled in the breeding season, for any age class. Additionally, there may be lower dispersal rates and higher site fidelity between years at the wintering grounds compared to the breeding grounds, even if residency patterns change. Because Whitethroats are generalists, and potentially more so outside of the breeding period, individuals may return to the same wintering sites even if conditions are not optimal, whereas at the breeding grounds return rates are lower if previous breeding attempts fail (Haas, 1998), and thus dispersal and mortality are harder to differentiate. Alternatively, differences could be due to different data collection and analysis methods between studies. Not only did we account for transients, but we also included data obtained through high resighting and mist-netting efforts. Most European estimates are derived solely from mist-netting live-capture-recapture sampling. Two disadvantages to this could lead to underestimation of survival rates: (1) recapture rates tend to decrease with time due to net-shyness – once a bird has been captured, marked, and released, it tends to avoid nets in the future (MacArthur & MacArthur, 1974; Marques et al., 2013), and (2) most passerines that hit the nets are captured, regardless of their residency or territorial behaviour, making transients difficult to differentiate from residents.

Our annual survival estimates were also similar to or higher than those reported for other Afro-Palaearctic migrants that were estimated from the breeding grounds, ranging from 0.3 for Chiffchaffs *Phylloscopus collybita* (Robinson et al., 2008), Sand Martins *Riparia riparia* (Cowley & Siriwardena, 2005) and House Martins *Delichon urbicum* (Johnston et al., 2016), to at least 0.77 for Cyprus Wheatears *Oenanthe cypriaca* (Xenophontos & Cresswell, 2016; but see Appendix 6.3 for more examples) and from the wintering grounds in Malawi: 0.54 for Garden Warblers *Sylvia borin* and 0.59 for Great Reed Warblers *Acrocephalus arundinaceus* (Peach et al., 2001; Appendix 6.3), and for Neotropical migrants (Holmes et al., 1989; Conway et al., 1995; Sandercock & Jaramillo, 2002; Drake et al., 2014; Paxton et al., 2017). This again could reflect differences in population trends or be due to methodological reasons.

Female survival rates appear to be frequently lower than those of males (Donald, 2007) when estimated at the breeding grounds. This is thought to be caused by stronger breeding dispersal in females resulting in permanent emigration from study sites, higher female reproductive effort, different parental roles, physical traits, and territorial behaviour (Sillett & Holmes, 2002; Donald, 2007) and, in some cases, females having longer migration routes (Catry et al., 2005). On the contrary, survival does not appear to vary by sex at the non-breeding grounds in Whinchats *Saxicola rubetra* (Blackburn & Cresswell, 2016c) nor in Eurasian Reed Warblers *Acrocephalus scirpaceus* at a stopover site (Halupka et al., 2017), suggesting that these pressures and differences do not apply outside of the breeding grounds. Unfortunately, small sample sizes and difficulties in sexing individuals did not allow for estimation of differences in annual survival between females and males in this study, but because breeding pressures do not act during this period and as there was no clear habitat segregation between them (see Chapter 5), we do not expect there to be any strong differences.

Similarly, and as predicted, there were no differences between adult and first-year birds' annual survival rates. Many studies carried out at the breeding grounds have shown that the survival of Afro-Palearctic birds varies significantly by age groups, first-years showing significantly lower survival rates than older birds (Siriwardena et al., 1998; Sandercock & Jaramillo, 2002; Xenophontos & Cresswell, 2016; Kiss et al., 2020; Fay et al., 2021). Similar to results found in this study, however, studies that estimated annual survival rates from the wintering grounds did not find these differences, either in the Palearctic (Blackburn & Cresswell, 2016c), or in the Neotropic (Sillett & Holmes, 2002). These results support the conclusion that post-fledging and first migration is the period with the highest mortality for first-years (Grüebler et al., 2014; Fay et al., 2021), because of inexperience in migration, and because first-years are more likely to arrive at lower quality non-breeding habitats due to the stochastic nature of first migrations (Cresswell, 2014) as well as their decreased ability to correct for significant changes during the migratory routes, lowering their survival. However, some studies suggest that mortality during the non-breeding period, including first migration, is low compared with that just after fledging (Grüebler et al., 2014), mainly due to mortality during the first month after hatching as first-years are inexperienced, not very mobile, are highly dependent on their parents, and are highly vulnerable to predators (McKim-Louder et al., 2013). When survival rates are calculated based on data from wintering grounds they cannot include the higher mortality of the first 4–6 months of life.

6.6.3 Overwinter survival

Results suggest a very high overwinter survival rate in Nigeria from 0.82, obtained from the detailed study data, up to a survival rate of one when analysing the CES data, indicating that no, or very low, mortality occurs during this period. Though recent studies using remote-tracking systems to track individuals with great precision are becoming more common to estimate accurate survival rates throughout the year (*e.g*. Klaassen et al., 2014; Cheng et al., 2019; Sergio et al., 2019; Buechley et al., 2021), studies that estimate passerine overwinter survival rates are still rare and mainly focused on Neotropical migrants (Appendix 6.4).

Overall, many studies have estimated high overwinter survival rates, ranging between 0.56 up to 0.95 (Appendix 6.4), including a study carried out at the same study site for a similar Afro-Palearctic migrant, the Whinchat, with an overwinter survival of over 0.90 (Blackburn & Cresswell, 2016c). Similar to above, however, estimates and comparisons need to be taken with caution as few studies have been undertaken throughout the entirety of the wintering period, many used different methods, and some use site persistence (*e.g*. Sherry & Holmes, 1996; Thorup et al., 2019) as a means to estimate apparent survival (see Chapter 4 for detailed discussion), which would severely underestimate true overwinter survival rates.

High overwinter survival rates, close to one, are not surprising. Whitethroats, for example, are generalists during the wintering period: they feed on diverse resources, thrive in a range of habitats, seem to be able to occupy several locations throughout the non-breeding period and can cope with significant habitat changes (Chapter 5). These characteristics confer an advantage over the breeding grounds because individuals do not need to remain at a single site to rear young, where they are exposed to higher predation rates but can move to other locations if required. Their energetic requirements are low, both in terms of the need to only maintain their body condition rather than feeding many young, and in terms of their greater propensity to inhabit areas with higher temperatures. Additionally, because the evolution of a migratory over a residency strategy demands at least an equal annual survival rate (assuming similar productivity), high overwinter survival rates at stationary sites might be compensating for increased mortality associated with migration (Dokter et al., 2018) and migration may yield equal or greater fitness benefits compared with year-round residency (Zúñiga et al., 2017).

In some species, there is evidence of winter habitat segregation according to sex and age, where dominant individuals (larger and with more experience), mainly males, winter at higher quality habitats, while sub-dominant birds, females and first-years, occupy poor quality habitats, resulting in differential survival (Holmes et al., 1989; López-Ornat & Greenberg, 1990; Marra & Holmes, 2001; Catry et al., 2004). Here, we found that adults exhibited higher overwinter survival rates than first-years but, because they both indicated similar habitat preferences (Chapter 5), we suspect that this difference is due to the lower residency durations and lower winter site fidelity of first-years (Chapter 4) than as a result of true survival differences. Other studies have also not found differences amongst age groups

(Sillett & Holmes, 2002; Grüebler et al., 2014; Blackburn & Cresswell, 2016c). Sex differences could not be calculated but, as mentioned above, they are not expected.

Even though many studies have found very high overwinter survival rates, this might differ among habitat types and quality, populations, species and periods (Conway et al., 1995; Sherry & Holmes, 1996; Catry et al., 2004; Allen et al., 2019; Boano et al., 2020), and a general conclusion might be misleading. For example, annual variation in first-year survival depends on population growth rates (Grüebler et al., 2014) and several strong populations declines of Afro-Palearctic migrants, such as Whitethroats (Winstanley et al., 1974), Sedge Warblers *Acrocephalus schoenobaenus* (Peach et al., 1991), Sand Martins (Szép, 1995), amongst others, have been associated with an increasing frequency of drought conditions in the Sahel region in Africa, showing survival variability through time, depending on weather conditions. For example, the Sahel rainfall index best explains the survival of the Pallid Swift *Apus pallidus*, with the driest season resulting in reduced survival, while the El Niño-Southern Oscillation (ENSO) best explains mortality in Common Swifts *Apus apus* (Boano et al., 2020). Likewise, the Kirtland's Warbler *Setophaga kirtlandii* annual survival probability, in the Neotropics, was predicted by rainfall in its wintering grounds, in the Bahamas, suggesting that the effects of winter precipitation carried over to influence the survival probability of individuals in later seasons (Rockwell et al., 2017). Here we did not have sufficient data to find yearly differences and results may not reflect either previous or future survival rates.

6.6.4 Implications for conservation

Higher annual survival rates calculated at the wintering grounds compared to the breeding grounds, extremely high overwinter survival rates, an absence of variation in annual survival between age and sex groups, and a generalist strategy during the wintering period all strongly indicate that the wintering period is a low-mortality period for Whitethroats. This also suggests that mortality is higher during the post-fledging period at the breeding grounds and/or during the first autumn migration. These results are consistent with contemporary literature.

Grüebler and collaborators (2014) provide clear evidence that the major bottleneck for Barn Swallows *Hirundo rustica*, where the highest mortality occurs, is during a very short time of the year, during the post-fledging period. During this time chicks are vulnerable, inexperienced, and have little experience foraging and escaping predators, making them susceptible to predation and starvation. Many other studies, however, agree that the highest mortality period for a long-distance migrant occurs during active migration (Sillett & Holmes, 2002; Paxton et al., 2017; Rockwell et al., 2017; Buechley et al., 2021). Mortality during this period may be directly related to events encountered during migration (*e.g*. crossing of extreme barriers, navigation errors, hunting pressures, degradation or loss of suitable habitat for stopovers, unpredictable weather; Newton, 2010), or may be a delayed carry-over effect of conditions experienced during the stationary periods (Marra & Holmes, 2001), or a combination of both. Paxton *et al*. (2017) estimated that the migratory period accounted for 62% of the estimated annual mortality of Willow Flycatchers *Empidonax traillii* even though this period comprises less than a quarter of its annual cycle. In particular, the first migration towards the wintering grounds represents a risky journey because first-years lack detailed knowledge of the route and wind corrections (Cresswell, 2014; Buechley et al., 2021). Many first-year Egyptian vultures *Neophron percnopterus* for example drown in the Mediterranean Sea on their first autumn migration (Buechley et al., 2021).

We suggest that Whitethroat conservation efforts should focus on the active migration period and stopover sites, both during autumn and spring migration, when we assume the highest mortality rates occur and during which time we believe they are more susceptible to extreme weather changes. However, detailed survival studies need to be carried out to estimate true mortality rates at the breeding grounds and at other wintering sites, to ensure that population trends are not population-specific. Studies at the non-breeding grounds should, however, consider that individuals might be more mobile and year-dependent than previously thought, *i.e*. individuals might have several important stationary wintering grounds.

6.6.5 Conclusions

Studies to understand how, where, and why long-distance migrants die are important for recognising and mitigating threats that occur throughout the annual cycle, and for identifying conservation priorities of long-distance migratory birds, especially in light of recent global population declines. Understanding survival patterns across the entire annual cycle is especially important for migratory species because one period will have a strong effect on the next and studying one part without the other could lead to biased and incorrect conclusions. For example, conservation efforts aimed only at breeding and/or wintering sites may not sustain populations if high mortality rates occur during migration. Increasingly, more studies are undertaking the “full-annual cycle” approach, but overwinter and active migration survival estimates have been largely overlooked, remain scarce, and are mainly focused on large non-passerine birds and Neotropical migrants. Full annual cycle information is important for understanding how populations of migratory animals are limited throughout the year and are crucial in predicting how a population will respond to future climate changes. Unfortunately, for passerines, this will only arrive when non-archival tags, which can truly distinguish between death and dispersal, such as satellite transmitters and/or GPS devices, are lightweight enough to be fitted on small birds throughout the year.

6.7 Appendices

Appendix 6.1. Annual survival rates.

Table A.6.1. Annual survival rates from all models with an AICc weight > 20.

ANNUAL SURVIVAL RATES							
Dataset	Model	AICc Weight	Parameter	Estimate	SE	95% CI	
CES site1	$\varphi(.)p(.)$	1	φ	**0.47**	0.14	0.23	0.73
			p	0.07	0.05	0.02	0.231
CES site1 + 2	$\varphi(.)p(.)$	1	φ	**0.4**	0.3	0.05	0.89
			p	0.05	0.07	0.003	0.46
Nov/Dec: detailed study	$\varphi(.)p(0.33)$	0.56	φ	**0.33**	0.05	0.24	0.44
			p	0.33	-	-	-
	$\varphi(.)p(.)$	0.22	φ	**0.38**	0.14	0.16	0.67
			p	0.27	0.13	0.1	0.57
Feb/Mar: detailed study	$\varphi(.)p(0.33)$	0.28	φ	**0.42**	0.07	0.3	0.55
			p	0.33	-	-	-
	$\varphi(.)p(.)$	0.27	φ	**0.25**	0.09	0.11	0.45
			p	0.64	0.25	0.18	0.94
FIRST-YEARS *vs*. ADULTS							
CES site1	$\varphi(a)p(0.07)$	0.63	φFy	**0.61**	0.31	0.11	0.95
			φAd	**0.45**	0.1	0.26	0.65
			p	0.07	-	-	-
	$\varphi(a)p(.)$	0.22	φFy	**0.67**	0.52	0.02	0.99
			φAd	**0.46**	0.14	0.22	0.72
			p	0.06	0.05	0.01	0.24
CES site1 + 2	$\varphi(a)p(0.07)$	0.6	φFy	**0**	0	0	0
			φAd	**0.39**	0.16	0.15	0.7
			p	0.07	-	-	-
Nov/Dec: detailed study	$\varphi(a)p(a)$	0.46	φFy	**0.5**	0.23	0.15	0.86
			φAd	**0.14**	0.04	0.08	0.23
			pFy	0.19	0.1	0.06	0.46
			pAd	1	0	1	1
	$\varphi(a)p(0.33)$	0.4	φFy	**0.35**	0.09	0.2	0.53
			φAd	**0.38**	0.09	0.24	0.56
			p	0.33	-	-	-
Feb/Mar: detailed study	$\varphi(a)p(0.33)$	0.43	φFy	**0.46**	0.12	0.25	0.69
			φAd	**0.4**	0.09	0.25	0.59
			p	0.33	-	-	-
	$\varphi(a)p(.)$	0.33	φFy	**0.27**	0.12	0.01	0.55
			φAd	**0.25**	0.1	0.12	0.49
			p	0.62	0.26	0.16	0.93

	φ(a)p(a)	0.24	φFy	**0.36**	0.2	0.09	0.76
			φAd	**0.16**	0.04	0.1	0.26
			pFy	0.44	0.26	0.09	0.86
			pAd	1	0	1	1

Appendix 6.2. Seasonal survival rates.

Table A.6.2. Seasonal survival rates from all models with an AICc weight > 20.

SEASONAL SURVIVAL RATES							
Dataset	Best Model	AICc Weight	Parameter	Estimate	SE	95%CI	
CES site1	φ(season)p(0.07)	0.43	φ(Nov-Feb)	**1**	0	1	1
			φ(Feb-Nov)	**0.39**	0.07	0.27	0.52
			p	0.07	.	.	.
	φ(season)p(season)	0.32	φ(Nov-Feb)	**0.91**	0.43	0	0.999
			φ(Feb-Nov)	**0.39**	0.17	0.13	0.7
			p(Nov-Feb)	0.12	0.06	0.05	0.29
			p(Feb-Nov)	0.04	0.03	0.01	0.15
	φ(season)p(.)	0.25	φ(Nov-Feb)	**1**	0	0.99	1
			φ(Feb-Nov)	**0.32**	0.08	0.2	0.5
			p	0.1	0.03	0.05	0.18
CES site1 + 2	φ(season)p(0.07)	0.52	φ(Nov-Feb)	**1**	0	1	1
			φ(Feb-Nov)	**0.37**	0.09	0.21	0.56
			p	0.07	.	.	.
	φ(season)p(season)	0.3	φ(Nov-Feb)	**1**	0	0.99	1
			φ(Feb-Nov)	**0.38**	0.13	0.17	0.64
			p(Nov-Feb)	0.11	0.05	0.04	0.26
			p(Feb-Nov)	0.02	0.03	0.003	0.18
Detailed study	φ(season)p(0.33)	0.6	φ(Nov-Feb)	**0.82**	0.07	0.64	0.92
			φ(Feb-Nov)	**0.36**	0.05	0.27	0.47
			p	0.33	.	.	.
	φ(season)p(.)	0.23	φ(Nov-Feb)	**0.79**	0.09	0.56	0.92
			φ(Feb-Nov)	**0.36**	0.05	0.27	0.46
			p	0.35	0.05	0.26	0.44
FIRST-YEARS *vs*. ADULTS							
CES site1	φ(season*age)p(0.07)	0.63	φ(Nov-Feb) Fy	**0.87**	0.49	0.001	0.99
			φ(Nov-Feb) Ad	**1**	0	1	1
			φ(Feb-Nov) All	**0.38**	0.07	0.26	0.51
			p	0.07	.	.	.
Detailed study	φ(season*age)p(0.33)	0.43	φ(Nov-Feb) Fy	**0.7**	0.1	0.48	0.86
			φ(Nov-Feb) Ad	**1**	0	1	1
			φ(Feb-Nov) All	**0.36**	0.04	0.28	0.44
			p	0.33	.	.	.

Appendix 6.3. Annual survival rates of small Afro-Palearctic migrants.

Table A.6.3. Annual survival rates of small Afro-Palearctic migrants. Most annual rates were estimated from the breeding grounds, except studies marked with an "*" and "**", which were estimated from the wintering grounds and a stopover site, respectively. Table is arranged from lowest to highest survival rate values. Data of Whitethroats are italicised.

Authors	**Region**	**Species**	**Survival rates**
Johnston *et al*. 2016	Western Europe	Chiffchaff *Phylloscopus collybita*	0.3
Cowley & Siriwardena, 2005	England	Sand Martin *Riparia riparia*	0.3
Johnston *et al*. 2016	Western Europe	Lesser Whitethroat *Curruca curruca*	0.31
Johnston *et al*. 2016	Western Europe	Sedge Warbler *Acrocephalus schoenobaenus*	0.31
See Fig. 6.3 for references	*Europe*	*Common Whitethroat* *Curruca communis*	*mean = 0.33*
Johnston *et al*. 2016	Western Europe	Willow Warbler *Phylloscopus trochilus*	0.37
Johnston *et al*. 2016	Western Europe	Blackcap *Sylvia atricapilla*	0.39
Johnston *et al*. 2016	Western Europe	Garden Warbler *Sylvia borin*	0.4
Johnston *et al*. 2016	Western Europe	Eurasian Reed Warbler *Acrocephalus scirpaceus*	0.42
Boddy, 1994	England	Lesser Whitethroat *Curruca curruca*	0.45
Schaub & von Hirschheydt, 2009	Switzerland	Barn Swallow *Hirundo rustica*	0.48
Fay *et al*. 2021	Europe	Whinchat *Saxicola rubetra*	0.5
Blackburn & Cresswell, 2016c*	Nigeria	Whinchat *Saxicola rubetra*	0.52
Peach *et al*. 2001*	Malawi	Garden Warbler *Sylvia borin*	0.54
Peach *et al*. 2001*	Malawi	Great Reed Warbler *Acrocephalus arundinaceus*	0.59
Boano *et al*. 2020	Italy	Common Swift *Apus apus*	0.78
Robinson *et al*. 2008	Great Britain	Barn Swallow *Hirundo rustica*	0.404 (0.028)
Robinson *et al*. 2008	Great Britain	House Martin *Delichon urbicum*	0.303 (0.014)
Robinson *et al*. 2008	Great Britain	Sand Martin *Riparia riparia*	0.367 (0.053)
Halupka *et al*. 2017	Poland	Eurasian Reed Warbler *Acrocephalus scirpaceus*	0.4–0.6
Boano *et al*. 2004	Italy	Nightingale *Luscinia megarhynchos*	0.44 (0.04)
*This study **	*Nigeria*	*Common Whitethroat* *Curruca communis*	*0.61*

Boano *et al*. 2020	Italy	Pallid Swift *Apus pallidus*	0.71–0.76
Xenophontos & Cresswell, 2016	Cyprus	Cyprus Wheatear *Oenanthe cypriaca*	< 0.77

Appendix 6.4. Overwinter survival rates of small passerine migrants.

Table A.6.4. Overwinter survival rates of small passerine migrants. "*" represent monthly survival rates so overwinter survival rates were calculated for five months to reflect overwinter survival and are shown in brackets. "**" shows survival rates obtained by calculating site persistence. Table is arranged from lowest to highest overwinter survival rate values. Data of Whitethroats are italicised.

Authors	**Neotropic/ Palearctic**	**Country**	**Species**	**Overwinter survival rates**
Thorup *et al*. 2019	Palearctic	Ghana	Willow Warbler *Phylloscopus trochilus*	0.29**
Thorup *et al*. 2019	Palearctic	Ghana	Melodious Warbler *Hippolais polyglotta*	0.49**
Sherry & Holmes, 1996	Neotropic	Jamaica	American Redstart *Setophaga ruticilla*	0.50-0.80**
Conway *et al*. 1995	Neotropic	Belize	Kentucky Warbler *Geothlypis formosa*	0.89* [0.56]
Conway *et al*. 1995	Neotropic	Belize	Ovenbird *Seiurus aurocapilla*	0.89* [0.56]
Conway *et al*. 1995	Neotropic	Belize	Wood Thrush *Hylocichla mustelina*	0.90* [0.59]
Holmes *et al*. 1989	Neotropic	Jamaica	Black-Throated Blue Warbler *Setophaga caerulescens*	0.66
Conway *et al*. 1995	Neotropic	Belize	Hooded Warbler *Setophaga citrina*	0.93* [0.7]
Holmes *et al*. 1989	Neotropic	Jamaica	American Redstart *Setophaga ruticilla*	0.8
Grüebler *et al*. 2014	Palearctic	from Switzerland	Barn Swallow *Hirundo rustica*	0.8
Thorup *et al*. 2019	Palearctic	Ghana	Common Redstart *Phoenicurus phoenicurus*	0.87
Paxton *et al*. 2017	Neotropic	Costa Rica	Willow Flycatcher *Empidonax traillii*	0.88
Blackburn & Cresswell, 2016c	Palearctic	Nigeria	Whinchat *Saxicola rubetra*	0.98* [0.90]
Rockwell *et al*. 2017	Neotropic	Bahamas	Kirtland's Warbler *Setophaga kirtlandii*	0.98* [0.90]
Thorup *et al*. 2019	Palearctic	Ghana	Pied Flycatcher *Ficedula hypoleuca*	0.91
This study	*Palearctic*	*Nigeria*	*Common Whitethroat* *Curruca communis*	*0.94 (0.81-1)*
Sillett & Holmes, 2002	Neotropic	Jamaica	Black-Throated Blue Warbler *Setophaga caerulescens*	0.99* [0.95]

Chapter 7. General discussion

Globally, many bird species are in rapid decline and long-distance migrants seem to be at more risk than short-distance migrants and residents (Sanderson et al., 2006; Vickery et al., 2014; Bairlein, 2016; Maggini et al., 2021). The complex annual cycle of long-distance migrants makes it difficult to pinpoint the causes of these declines, because limiting factors may operate at breeding or non-breeding grounds, during active migration, or due to interactions or carry-over effects between stages (Newton, 2004; Morrison et al., 2013; Vickery et al., 2014; Bairlein, 2016). Despite spending most of their annual cycle at locations other than at breeding grounds, the study and hence our understanding of the non-breeding period has been limited, with what little has been possible focused particularly on the Neotropical system (Salewski & Jones, 2006). In this thesis, we studied the winter and migration ecology of Whitethroats, a common and fairly typical Afro-Palearctic migrant, and sought to understand how events outside of the breeding period may influence their population dynamics. Whitethroats are especially susceptible to changes in conditions in Africa (Winstanley et al., 1974), and so understanding their complete annual cycle, particularly the non-breeding period, could help understand the recovery and, potentially, the prevention of future declines in the population of this and other similar species of Afro-Palearctic migrants wintering in West Africa.

7.1 Summary of findings

Results obtained from geolocators show that Whitethroats wintering in central Nigeria breed across eastern Europe, as previously proposed by Escandell & García (2011) and Waldenström & Ottosson (2002) and supported by “EURING’s” long-term ringing database, suggesting a somewhat high migratory spread defined by a north-easterly flight pattern in spring and a south-westerly flight in autumn (Chapter 3). Results also indicate the locations and duration of important stopover sites across North Africa and southern and central Europe and highlight small differences between spring and autumn migration, the latter being longer and faster (Chapter 3). Results also show that individuals undergo loop migration and occupy a first non-breeding site in the Sahel region for a prolonged period before arriving at APLORI (Chapter 3). Results obtained through intensive mist-netting and resighting efforts as well as through habitat sampling at non-breeding grounds suggest that, once at APLORI, Whitethroats show great individual variation regarding temporal and spatial behaviour (Chapters 4 and 5). Results show that individuals have different residency periods, spanning from individuals simply passing through, to individuals remaining for most of the season (Chapter 4). Furthermore, an individual’s previous residency duration does not seem to determine its residency duration the following year (Chapter 4). Individuals also show a high degree of between- and within-winter site fidelity, as many individuals return to the same location year after year (Chapter 4) and individuals establish small home ranges regardless of residency duration, even while the dry season progresses and habitat conditions deteriorate (Chapter 5). Shrubs were identified as the preferred main vegetation type and seem to be highly important for Whitethroats (Chapter 5). Finally, we document very high overwinter and annual survival rates, which are similar, or higher, than those recorded for the breeding grounds and other small Afro-Palearctic migrants (Chapter 6). Altogether, these findings suggest that Whitethroats are highly likely to be generalists and their populations are probably not limited by the stationary wintering period.

7.2 The annual cycle of Common Whitethroats

My results show that the mean proportions of time an individual allocates to the stationary non-breeding sites, spring migration, breeding, and autumn migration are 55%, 9%, 22%, and 14%, respectively (Fig. 7.1). This means that individuals spend >80% of the annual cycle away from breeding grounds, either actively migrating or stationary at stopover or wintering sites. In this thesis, we studied the annual cycle of Whitethroats wintering in a small three km^2 site in APLORI focusing on the non-breeding period. We found that these individuals breed in a large area throughout central, northern, and eastern Europe. Populations that rely on several non-breeding sites and that show high migratory spread, like Whitethroats, are proposed to have generalist-associated traits, a greater potential to track shifting habitats and be, overall, more resilient to changes (Webster et al., 2002; Cresswell, 2014).

Results suggest that the highest mortality occurs while moving between breeding and wintering grounds. The strategy used during this phase therefore strongly defines the annual cycle of long-distance migrants. Migrants either accumulate enough body reserves to carry out a single, long flight to cross the Sahara Desert and the Mediterranean Sea, or divide the journey into sections, resting and refuelling along the way (Moreau, 1972; Bairlein, 1988; Alerstam, 2011). We believe that, even though Whitethroats are capable of undertaking both strategies, they prefer to fly intermittently before and after crossing a major barrier to restore their body condition (Eraud et al., 2013). In extreme situations, however, when they are strongly constrained by time, they can cross both the Sahara Desert and the Mediterranean Sea in a single flight, as showed by one of the geolocated birds and as proposed by Ottosson et al., (2001). The use of both strategies has also been detected in Whinchats *Saxicola rubetra* tracked from APLORI (Blackburn et al., 2019).

Spring migration was faster than autumn migration, despite spring migration following a longer path – spring migration was calculated from the breeding grounds to APLORI, while autumn migration was calculated from the breeding grounds to the first stationary non-breeding grounds, which are located further north than APLORI, and closer to the breeding grounds. This supports the optimal migration theory (or time-minimising strategy), where birds exhibit quicker spring migrations to ensure timely arrival at the breeding grounds to occupy and establish better territories and find mates (Fransson, 1995; Drent et al., 2003; Yohannes et al., 2009; Karlsson et al., 2012), contrasted with the comparatively fewer fitness consequences associated with a late arrival at non-breeding grounds (McNamara et al., 1998). Not only were timing and duration different between spring and autumn, but individuals followed disparate routes in each direction, a trait referred to as “loop migration”. Loop migration is common amongst migrants and is thought to emerge from a combination of adaptations to dominant wind systems, ecological barriers, spatiotemporal distribution of resources and suitable habitats, and historical aspects of the species’ distribution (Klaassen et al., 2010; Schmaljohann et al., 2012; Tøttrup et al., 2012; Briedis et al., 2018). Surprisingly, all tracked individuals utilised a first non-breeding site before arriving at APLORI, where they remained for an average of two months. The use of multiple non-breeding sites could be part of a strategy in which birds temporarily suspend migration to optimise resource use during the non-breeding season, based on the availability of predictable food sources in the region (McKinnon et al., 2013; Arlt et al., 2015), and is a behaviour strongly related to environmental conditions (Heckscher et al., 2011). It also seems to be a common behaviour for several migrants in the Palearctic system (Stach et al., 2012; Lemke et al., 2013; Koleček et al., 2016; Burgess et al., 2020) and might well be the rule rather than the exception.

Once at the second and/or main wintering grounds (APLORI), Whitethroats exhibited high individual variation in many aspects and strategies of their ecology. My results show that individuals spend different periods in the area, from a couple of days up to five months during all three years. A continuum of residency duration is commonly found at other wintering sites, though not many studies have researched it in detail (King & Hutchinson, 2001). The proportion of individuals in each residency pattern, however, is likely to depend on the location of the sites: the most southerly sites may host a higher proportion of winter residents than sites located along the migratory routes. Results also show that individuals utilise relatively small areas during their stay, regardless of their duration, and that individuals return to the same sites year after year. This supports emerging evidence indicating that many Afro-Palearctic migrants establish and defend small territories throughout the non-breeding season (Salewski et al., 2002; Kristensen et al., 2013; Blackburn & Cresswell, 2016b; Thorup et al., 2019) and suggests that maintaining a small home range during the non-breeding period, or at least a part of it, as well as returning to it every year, may be beneficial in obtaining local knowledge regarding foraging locations, resource fluctuation, and competitor and predator densities (Latta & Faaborg, 2001; Catry et al., 2004; Brown & Long, 2006; Lind & Cresswell, 2006), and therefore ensures food availability throughout the period and for subsequent years (Greenberg, 1986; Kelsey, 1989; Cuadrado, 1995; Rolando, 2002; Zwarts et al., 2009).

In summary, the annual cycle of Whitethroats found wintering in Nigeria seems to be as follows (Figs. 7.1 and 7.2): Individuals breed across eastern Europe between May and August (Figs. 7.2a and b). In August, individuals commence migration and fly in a south-westerly direction, crossing the Black Sea and/or the Mediterranean Sea, and the Sahara Desert (Fig. 7.2a). Most individuals will rest for long periods within Europe. Whitethroats arrive at a first non-breeding site in the Sahel savannah, in central-eastern Africa at the end of the summer rains (Figs. 7.2a and b); one geolocated individual spent more time at the first non-breeding site than at the main breeding site in Europe. This is the first migration for individuals born during that breeding season: these individuals lack knowledge of small- and medium-scale locations and will arrive at the non-breeding ground stochastically and look for a suitable wintering area (Cresswell, 2014). This migration may be a high-mortality period, especially for first-years. During this period, habitats are productive and insect abundance is high, representing favourable foraging conditions (Stach et al., 2012; Tøttrup et al., 2012). Over time, habitats dry and conditions become harsh (Moreau, 1972; Morel, 1973; Jones, 1995; Ottosson et al., 2005) causing birds to move to other non-breeding grounds between November and December — in this case, APLORI — where rainfall ends later and resources are available for longer. This may only, however, apply to individuals that did not secure a good first site.

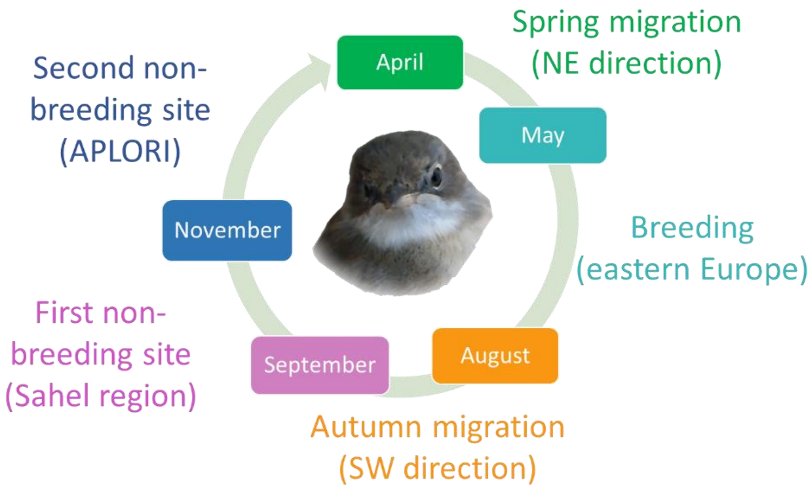


Figure 7.1. The annual cycle of a Common Whitethroat wintering in central Nigeria.

Once at APLORI, some individuals will use the site as a quick stopover site to rest and refuel, and will continue migration further south, or close by, whilst others will remain for a significant period (Figs. 7.2c and d). Those birds will most likely remain within a small home range. As the season progresses, habitats continue to deteriorate, and some individuals will opt to leave the area (Figs. 7.2c and d). Surprisingly, the degree of habitat change (*i.e*. how much habitats change throughout the non-breeding season) was similar between short-term and long-term winter residents: all individuals seemed to suffer the same degree of habitat deterioration. This may suggest that individuals either continue further south in search of better conditions, or may leave the area not to continue south, but to go north, to a third non-breeding site as early as January, to fatten up with *Salvadora persica* berries before spring migration (Vickery et al., 1999; Cresswell et al., 2009). Moving north early may represent a special case – in fact, the early onset of migration – putting some Whitethroats ready for migration just south of the Sahara, closer to the breeding area. Individuals that remain at APLORI will use smaller home ranges and will commence spring migration between February and April. Most individuals will fly north and spend some time in the Sahel region until they acquire the necessary fat reserves to carry out a successful journey to their breeding grounds. Individuals will fly in a north-easterly direction and will fly faster than during autumn until they reach the breeding grounds (Fig. 7.2b). Individuals with later departures will undertake faster migrations to compensate for lost time.

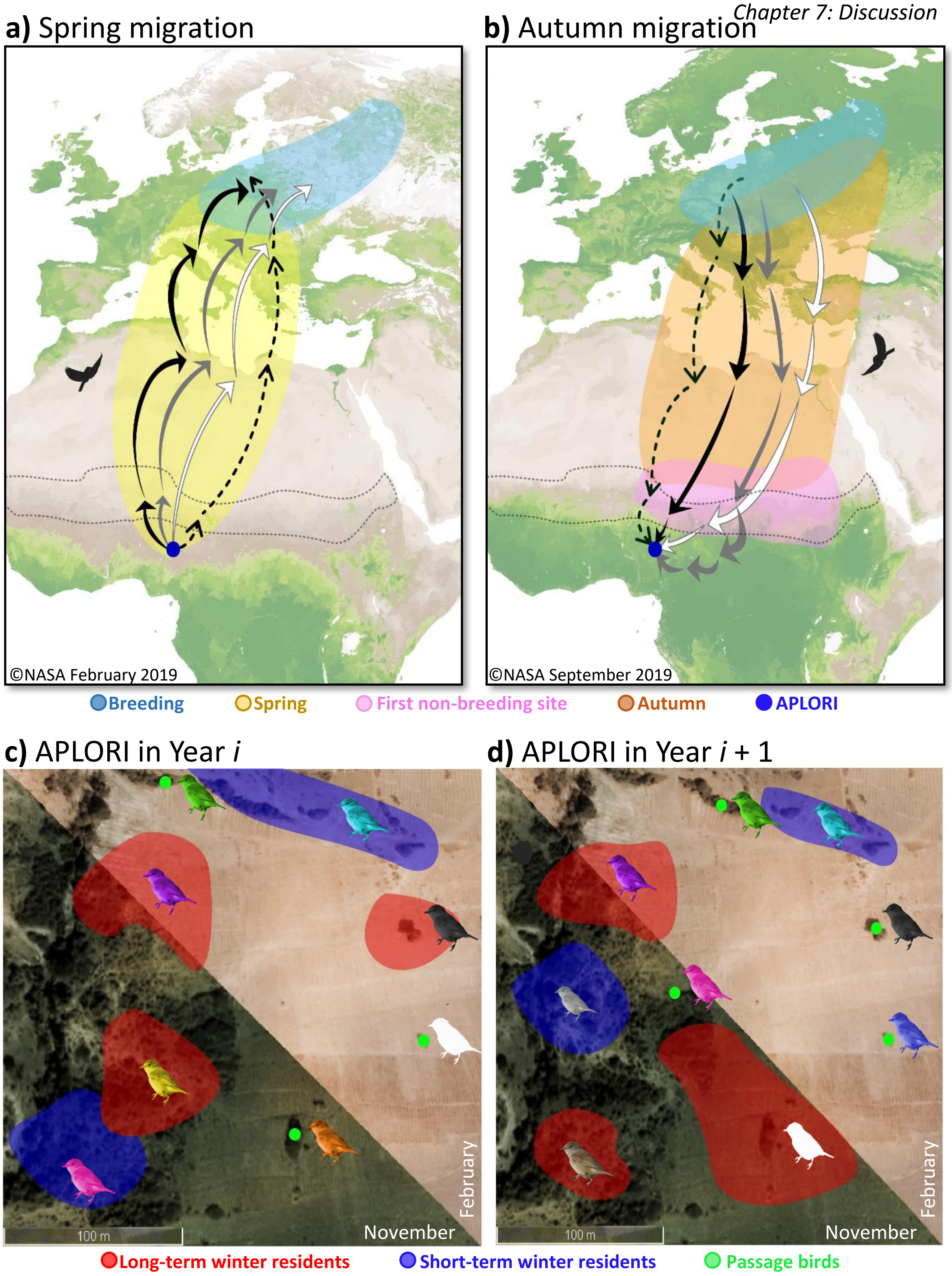


Figure 7.2. Migratory routes and spatiotemporal use of the wintering grounds. Migratory routes (a, b) and spatiotemporal use of the wintering grounds (c, d) by Common Whitethroats wintering in Nigeria and surrounding areas. a) Migratory routes during spring migration by an average adult (continuous black arrow), a first-year bird (grey arrow), an adult that departed APLORI later than average (white arrow), and an adult flying in an anticlockwise loop direction (dotted black arrow). All birds show a similar north-easterly flight, a breeding area across central-eastern Europe, and a similar number of stopovers, except the late-departed individual that did not

spend much time in the Sahel region before migration and undertook a faster migration with fewer stopover sites. Here, adults and first-years carry out similar migrations. b) Migratory routes during autumn migration by an average adult (continuous black arrow), a first-year bird (grey arrow), the adult who left late during spring migration (white arrow), and an adult flying in an opposite loop direction (dotted black arrow). Here, individuals fly in a south-westerly direction and arrive at a first non-breeding site in the Sahel region, prior to APLORI. During autumn migration, first-year birds are experiencing their first migration and will potentially scout other areas before arriving at APLORI. Different colours represent the expected areas used by Whitethroats during spring migration (yellow area) the breeding period (light blue area), autumn migration (orange area), first non-breeding grounds (pink area), and APLORI (dark blue dot). Vegetation base maps of figures a and b were downloaded from the database "MODIS/Terra Vegetation Indices Daily Rolling-8-Day L3 Global 250m SIN" from *NASA* and represent vegetation during February 2019 and September 2019, respectively. In both figures, the Sahel region is traced with a dotted line (note the strong vegetation difference between months). Figures c and d represent individuals' spatial use in APLORI during year *i* and the following year (year *i* + 1), respectively. Shaded areas represent residency patterns: red = long-term winter residents, blue = short-term winter residents, and green dots = passage birds. Same colour birds represent the same individuals. Triangles show habitat differences between seasons: the lower-left triangles represent habitats during November, at the end of the wet season (green, productive, presence of crops), while the upper-right triangles represent the same habitats during February, at the end of the dry season (less vegetation, crops are dry). These maps show distinct residency patterns, different degrees of between-year site fidelity, and changes of residency patterns across years. For example, the white bird was a passage bird during year *i*; the following year it shifted 100 m in a south-westerly direction, where it remained throughout the wintering period. The yellow long-term winter resident in year *i* did not return to the area because it died, it shifted to another site close by or did return to the area but was not detected. Base maps were obtained from Google Earth™ from November 2016 and February 2021. For better contrast, images were modified using infrared images of foliage/soil obtained from the "Copernicus Sentinel-2 mission" of *ESA*. Note that the same base map was used for both years – in reality, habitats may have changed.

To explain the high degree of between-year site fidelity but a low degree of residency repeatability through years, as well as the high individual variation, we proposed that the best strategy for a long-distance migrant, or at least for Whitethroats, might be to remain stationary at a suitable site for as long as possible. During the first autumn migration, individuals arrive stochastically at the first non-breeding site and explore the area in pursuit of a suitable location. Individuals will remain at the site for as long as possible. Some proportion of the population will remain through the winter, most likely those that are better competitors, have better territories, or are able to find better environmental conditions (*e.g.* higher rainfall and lower anthropogenic impacts), whilst others will move to a second site. Through the course of their life, some individuals may never move to a second site, and some may only do so in their second or third autumn non-breeding season, depending on that year's conditions. The following year the same first site will be revisited; if conditions are stable and the site secures an individual's survival then there would be no need to migrate elsewhere. Otherwise, it would migrate to the same second site, and so on. If the first site is only suitable for a short time, it will remain until resources are inadequate and then it will go to the second site, even if it would arrive earlier than the previous year. When individuals are reaching the limits of their potential distribution, such as at APLORI, they will return only in occasional years of widespread food shortage or suboptimal conditions at previous sites

(Newton, 2008), so a proportion of individuals would not arrive at APLORI year after year. Some individuals would decide to commence spring migration before others to have an advantage on securing good *Salvadora persica* sites and to have shorter migrations towards the breeding grounds. Some individuals may get unlucky and will need to change sites several times, which makes them appear itinerant, whilst others will remain as long-term winter residents at a few sites. Regardless of any particular year's conditions, the number of migration steps and migration distance is minimised and matched to environmental conditions. Of note, some individuals seemed to occupy similar home ranges as others, yet some decided to remain whilst the others left. This may be attributable to variable competitive ability, where birds in poorer condition (poorer competitors) may have been forced to move.

Frequently, small long-distance passerine migrants are treated as a relatively homogeneous group, and more so individuals from the same species. Perhaps the most important result from this thesis is that the non-breeding period may be a more complex and more mobile period than previously suspected (Hiemer et al., 2018; Bulluck et al., 2019), with high individual variation and decisions varying according to yearly environmental conditions. Therefore, these generalisations may not apply for all individuals and/or populations of the species. These findings, coupled with other recent studies (Stutchbury et al., 2016; Hiemer et al., 2018; Bulluck et al., 2019) are leading to a paradigm shift in how we think about the non-breeding period, largely influenced by a focus on stationary and territorial species, anecdotal evidence, and results from ring recoveries and geolocated birds that may be biased to individuals with high site fidelity.

7.3 Whitethroats as a model species

Migrant species clearly vary within and between each other, especially considering that different species require different habitats, that habitats change seasonally and that similar habitats in different regions may offer different resources that require adaptations to local conditions (Salewski & Jones, 2006). It would therefore be erroneous to assume a one-for-all strategy for hundreds of migrants that vary in size, geographical locations, evolutionary origins, behaviours, physiology, etc. Nonetheless, generalisations can be made for the behaviours and decisions of Afro-Palearctic migrants in Africa, and Whitethroats, especially, seem to be a typical long-distance passerine migrant that can provide important information that may apply to many, if not most, migratory passerine species.

Whitethroats show a degree of migratory spread consistent with the general pattern of other Afro-Palearctic migratory species: a high migratory spread and low connectivity (Finch et al., 2017), though there are exceptions to this (Schmaljohann et al., 2012; Hahn et al., 2013; Ouwehand et al., 2016). Individuals also seem to be able to undertake both an intermittent and a non-stop strategy, depending on resource availability and constraints of the moment, but in optimal conditions would undertake an intermittent strategy, as would most songbirds during the crossing of the Sahara Desert (Bairlein, 1988, 1992; Schmaljohann et al., 2007; Salewski et al., 2010; Maggini & Bairlein, 2011). These results also support the increasing evidence of loop migration (Klaassen et al., 2010; Schmaljohann et al., 2012; Tøttrup et al., 2012; Briedis et al., 2018) and the use of multiple core wintering sites (Stach et al., 2012; Lemke et al., 2013; McKinnon et al., 2014; Koleček et al., 2016; McKinnon & Love, 2018; Burgess et al., 2020). At non-breeding grounds, my results show similar patterns to other Afro-Palearctic migrants: high site fidelity between-years (Kelsey, 1989; Cuadrado, 1992; Salewski et al., 2000; Koronkiewicz et al., 2006; Belda et al., 2007; Cresswell et al., 2009; Blackburn & Cresswell, 2016b; Thorup et al., 2019), home range establishment (Salewski et al., 2002; Barshep et al., 2012; Kristensen et al., 2013; Blackburn & Cresswell, 2016c; Thorup et al., 2019), ability to cope with changing conditions (Salewski & Jones, 2006; Blackburn & Cresswell, 2015), and overall generalist traits (see below; Devictor et al., 2008; Ivande & Cresswell, 2016). Most importantly, however, Whitethroats show a high degree of individual variation and a range of behaviours.

In the Palearctic system, migration may have evolved in response to climate becoming increasingly seasonal, cold, and arid (around 30 mya; Finlayson, 2011) and, since its origins, migratory populations have fluctuated in response to environmental and habitat conditions (Cox, 1985; Bell, 2000; Finlayson, 2011). Migratory species have therefore adapted to become resilient, and there is no clearer example of this than in the slow recovery of Whitethroat populations since their sharp decline due to a drought in the 1960s. The ability to cope with changing and deteriorating conditions throughout the non-breeding period and to make decisions accordingly, as well as a wide distribution and array of individual variation suggest that Whitethroats have a high degree of flexibility and plasticity, traits that migrants should have in order to flourish in a changing world (Salewski & Jones, 2006; Cresswell, 2014). This plasticity and flexibility are what confer evolutionary advantages of migratory species over more restricted, resident, and/or specialist species (Moreau, 1972; Finlayson, 2011).

7.4 Whitethroats show a generalist strategy

Whether individuals are generalists (*i.e*. feed on a variety of resources and thrive in a range of habitats) or specialists (*i.e*. feed on limited resources and have stricter habitat requirements) has strong implications for the ecology of migrants and defines how species respond to future climate and anthropogenic changes (Julliard et al., 2006; Lerche-Jørgensen et al., 2019). Results from this thesis show that during active migration individuals use different migratory routes, arrive at different breeding grounds, and adjust strategies according to conditions along the journey and/or across years. During the stationary wintering period, individuals feed on diverse resources, have several foraging strategies (*e.g*. on the ground and moving within a bush), occupy several locations and habitats, and manage to cope with deteriorating habitat conditions as the dry season progresses. Their ability to cope with significant habitat changes by the end of the season without substantially changing their home range size, in some cases decreasing the area of their home range, suggests that some birds find sufficient food in a small area despite seasonal changes in environmental conditions, vegetation and food supply, and a significant increase in anthropogenic activities (*e.g*. wood extraction, bush fires, grazing). Summarily, these traits, as well as high individual variation within- and between-years and a high degree of winter site fidelity across years, strongly suggest that Whitethroats are generalists during the non-breeding period, if not for the entirety of their annual cycle.

A generalist strategy seems to be relatively common amongst long-distance migrants (Marra & Holmes, 2001; Cresswell, 2014). Having generalist traits confers several advantages. Generalists are more likely to remain in suboptimal habitats than more specialist species and face higher competition as the season progresses, but avoid the risks of moving and discovering new terrain (Salewski et al., 2002; Julliard et al., 2006; Devictor et al., 2008), whilst specialists tolerate a smaller range of resource levels, and are expected to be less able to cope with environmental and habitat changes. Thus, habitat specialists should be more negatively affected by unpredictable and rapid global changes than generalists (Kassen, 2002; Gregory et al., 2007; Devictor et al., 2008; Colles et al., 2009). In the Whitethroat, for example, a small home range may only provide the minimum resources necessary to survive the winter, if certain requirements are met like the presence of shrubs. Being flexible to highly changing resource availability in short periods increases resilience to habitat change and loss both within and between years, especially considering the numerous global climate and anthropogenic changes. Furthermore, increasing the type of resources and habitats that can be exploited increases the probability of arriving at suitable habitats after first migration, which reduces time spent moving through unfamiliar surroundings where mortality risk is higher (Cuadrado, 1997; Cresswell, 2014) and may reduce competition with African resident species and other migrants (Salewski et al., 2007). These traits seem to confer more advantages at the non-breeding grounds as an individual can move to other locations if required and are not constrained to a single site to rear chicks. Additionally, because there are no energetical breeding pressures during this period and individuals have overall lower energetical requirements, only undertaking basic activities such as foraging and avoiding predators and/or unfavourable weather (Cuadrado, 1995; Salewski et al., 2002; Blackburn & Cresswell, 2015; Williams et al., 2016; Thorup et al., 2019), maintaining an adequate body condition is easier than compared to when at breeding grounds and actively migrating.

Whether resident species are more likely to be habitat specialists than migratory species remains open to debate. Resident species can select breeding habitats before migrants return, so migrants who can take advantage of multiple landscapes can minimise direct competition for resources with resident species (Pérez-Tris & Tellería, 2002) and/or resident species may adapt to fluctuations in resource availability by becoming habitat generalists, whereas migrants do not have to become generalists because they avoid declines in local resource availability through migration (Cox, 1985). In a savannah in central Africa, however, Afro-Palearctic migrants and African resident species showed similar degrees of generalism (Ivande & Cresswell, 2016) and a high degree of habitat overlap and habitat occupancy, suggesting that migrants may be an integral rather than marginal component of tropical avian communities (Salewski & Jones, 2006; Ivande & Cresswell, 2016). Migrants did, however, show stronger dispersal capabilities and greater flexibility in the use of habitats, as they were detected over a wider latitudinal range than residents (Ivande & Cresswell, 2016).

7.5 How does the non-breeding period affect population dynamics?

Higher annual survival rates calculated at the wintering grounds compared to the breeding grounds, extremely high overwinter survival rates, an absence of variation in annual survival between age groups, a generalist strategy during the non-breeding period, a high degree of between-year site fidelity, a lack of dominance-based habitat occupancy and evidence of suitable unoccupied habitat within the study site all strongly indicate that the wintering period is likely to be a low-mortality period for Whitethroats. As long as sites have shrubs where individuals can forage and rest, the stationary wintering grounds seem unlikely to limit populations. The evolution of any migratory strategy over one of residency demands at least an equal annual survival rate (assuming similar productivity). Thus, high overwinter survival rates at stationary sites might be compensating for increased mortality associated with migration (Dokter et al., 2018) and migration, overall, may yield equal or greater fitness benefits compared with year-round residency (Zúñiga et al., 2017). My findings support this and suggest that the highest mortality period for Whitethroats throughout their annual cycle is highly likely to be during active migration (Sillett & Holmes, 2002; Blackburn & Cresswell, 2016c; Paxton et al., 2017; Rockwell et al., 2017; Buechley et al., 2021); either during first migration, from the breeding grounds to the non-breeding grounds as a first-year and/or during spring migration regardless of age. Mortality during both migrations is also greatly dependant on events encountered along the way (*e.g*. crossing extreme barriers, navigation errors, hunting pressures, degradation or loss of suitable habitat for stopovers, unpredictable weather; Newton, 2010).

Age-related differential survival rates are common and occur in many Afro-Palearctic passerine species (Boddy, 1994; Newton, 2010; Cresswell, 2014; Johnston et al., 2016; Buechley et al., 2021; Fay et al., 2021); first-year birds tend to have lower annual survival rates when estimated from the breeding grounds (McKim-Louder et al., 2013; Blackburn & Cresswell, 2016c). First-year birds lack knowledge of small and medium scale locations concerning where to arrive and many individuals are bound to arrive at low-quality sites, thus their first non-breeding period is a period of high uncertainty and stochasticity (Brown & Long, 2006; Newton, 2008; Strandberg et al., 2010; Cresswell, 2014). This uncertainty, as well as less experience in correcting for wind drift and other harsh and unexpected weather conditions that occur along the journey, may increase mortality rates for this age group during this period (Thorup et al., 2003; McKinnon et al., 2014). Because annual survival rates were estimated from the non-breeding grounds, first migration is not considered, and this could explain why there were no differences in annual survival rates between age groups. Annual survival rates for migrants are ~0.30 when estimated from the breeding grounds. In this research, annual survival rates were as high as 0.61 when eliminating potential transients. The higher rates may be explained by high mortality during first migration, especially for first-year birds – although lower first-year survival at the breeding grounds may also reflect apparent survival because of lower natal site fidelity.

On the other hand, by the time spring migration commences all individuals are essentially adults; first-years have experienced a first migration and survived the stationary non-breeding season so age differences should not be strong, especially when there is no evidence of dominance-based habitat occupancy. Spring migration is more time-constrained than autumn migration, as individuals need to arrive at the breeding grounds to exploit peak insect abundance and to secure and establish high-quality territories to increase breeding success. Additionally, spring migration is longer and faster, thus to arrive successfully at the breeding grounds, individuals need to have elevated fat stores. Because this period coincides with the end of the dry season, and even though rains may have already commenced, habitats are recuperating and continue to be suboptimal, contrasted with autumn migration where resources are more abundant; preparing for spring migration is thus highly challenging. The ability to deposit sufficient nutrient stores depends on a species' morphology, physiology, ecological conditions at departure and stopover sites, and on the distances between suitable staging sites: less favourable conditions to refuel may increase mortality during spring migration (Lok et al., 2015). Hence, spring migration is a highly challenging period and it is highly likely that it represents a high mortality period, both for adults and first-year birds. Whitethroats, in particular, have been associated with the presence and availability of *Salvadora persica* berries in the Sahel region as it represents the main refuelling resource for the Sahara crossing (Moreau, 1972; Stoate & Moreby, 1995; Vickery et al., 1999; Wilson & Cresswell, 2006; Zwarts et al., 2009): the sharp population decline in the 1970s was strongly associated with a severe drought that decreased available resources during this stage (Winstanley et al., 1974; Hjort & Lindholm, 1978; Baillie & Peach, 1992).

Other periods such as the breeding season may also play an important role in shaping population dynamics (Fay et al., 2021). Over the past few decades, the increase in agricultural lands, the homogenisation of the landscape due to monocultures, the drainage of water bodies for irrigation, and the intensification of crop management (*e*.*g*. increase of fertilisers, pesticides, grazing) have reduced the number of suitable habitats for breeding, nesting and foraging of birds in Europe (Chamberlain et al., 2000; Donald et al., 2001; Vickery et al., 2004; Hewson & Noble, 2009; Thaxter et al., 2010). In the case of Whitethroats in particular, if human settlements and/or intensive agricultural lands do not retain hedgerows and/or shrubs, crucial for an individuals' survival and during the post-fledgling period, then this will likely increase an individuals' susceptibility to predation and starvation (Butler et al., 2010; Meichtry-Stier et al., 2013; Grüebler et al., 2014; Ekroos et al., 2019).

High overwinter survival rates and high suitable habitat availability at APLORI, during both the beginning and end of the period, suggest that the site is not at carrying capacity. This strong degree of habitat availability may be because populations are still low compared to those before 1970 and populations are still in the process of recovering. Most migrants have declined because of problems in Europe and during migration (Vickery et al., 2004, 2014; Sanderson et al., 2006; Strandberg et al., 2010; Fay et al., 2021). Migrants are likely generalists that can use a range of different habitats of different qualities, so in as expansive a continent as Africa there is unlikely to have been much habitat shortage ever, even more so now. As populations and anthropogenic activities increase in the area, however, and habitats start to saturate, core wintering grounds are likely to have stronger negative effects on population dynamics in the future.

7.6 Implications for the conservation of Common Whitethroats and other migrants

It is well established that the survival of long-distance migratory birds depends on what occurs throughout different stages of their annual cycle. As a species, Whitethroats are increasing and listed as “least concern” according to the IUCN Red List (BirdLife International, 2019). However, whether breeding populations are decreasing, increasing, or are stable is highly site-specific (Baillie et al., 2007; Hewson & Noble, 2009; European Environment Agency, 2019; Woodward et al., 2020; Kamp et al., 2021; Maggini et al., 2021)but overall, populations have yet to recover from the devastating crash after the 1960s Sahel drought (Winstanley et al., 1974; Zwarts et al., 2009). In particular, Eastern European populations, where most Nigerian individuals are likely to breed, are either stable or decreasing, or there is not enough data to infer population trends (European Environment Agency, 2019).

Africa, where individuals spend <70% of the year, is subject to major climatic and anthropogenic changes that have had strong impacts on their resources and natural habitats. It is now unlikely that truly pristine, unaltered habitats remain within the range of migratory species, with most landscapes showing some degree of modification (Sheehan & Sanderson, 2012). Drought and a strong increase in overgrazing, human populations, human activities, and agricultural practices have strongly affected African habitats, especially Sahelian savannah woodlands (Vickery et al., 1999). The potential generalist traits, their use of a wide variety of resources throughout the year, from highly anthropogenically modified areas to conserved woodlands, strong site fidelity year after year, and some degree of flexibility to adjust according to yearly and seasonal conditions, suggest that Whitethroats can survive in extremely degraded habitats (Moreau, 1972; Wilson & Cresswell, 2006) and may be more resilient to interannual habitat, climate, and anthropogenic changes than other migratory species (Mallord et al., 2016).

Hence, some changes may result in the complete loss of suitable habitat in some areas but in other areas woodland degradation may improve habitats for Whitethroats at the expense of resident African species and other migratory species reliant on more mature wooded landscapes (Stoate et al., 2001; Mallord et al., 2016). In the event of an increase in agricultural practices and/or volume of crops to sustain human populations, these changes could benefit Whitethroats so long as they are not achieved through extreme monoculture conditions and, most importantly, that hedgerows and shrubs remain present (Persson, 1971; Meichtry-Stier et al., 2013; Ekroos et al., 2019). Additionally, strong land-use changes across the non-breeding grounds in Africa will have a diffuse impact on many Whitethroat breeding populations. For example, changes in central sub-Saharan Africa, where our study site is located, will have a severe effect on a subset of individuals of specific central-eastern European breeding populations (*e.g*. Polish, Belarussian, Lithuanian, western Russian), but due to the large distribution of the species, the most western and eastern populations may not be as severely affected (Koleček et al., 2016). Therefore, for alarming impacts to occur at a species level, changes would need to occur at a very large scale.

The strong population decline in the 1960s showed how susceptible the species can be to major climate changes in the region, despite their ability to overcome harsh conditions (Winstanley et al., 1974), but also demonstrated the species' ability to recuperate and adapt (Ottosson et al., 2002). Although Whitethroats seem to currently be at an overall low risk of decline compared to other migrants, it is important to understand the threshold of what types of changes and to what degree these changes will have catastrophic effects. Two good anecdotal examples illustrate this point: (1) at our study site, shrub species like *Searsia natalensis*, *Lantana camara*, and *Acacia ataxacantha* were crucial for providing shelter and food to individuals. These are also species with high human value as they are used for fuelwood and timber (*pers obs*). At lower human population densities this may mean that Whitethroats benefit as the landscape is managed for these resources, but at higher human densities, this may mean that Whitethroats are threatened as the landscape is denuded of these valuable resources. (2) The harsh drought in the Sahel zone of West Africa in the late 1960s that decreased food availability just before the start of spring migration and consequently killed >70% of some European Whitethroat populations (Moreau, 1972; Winstanley et al., 1974). We suspect that individuals were revisiting previously known sites as they moved northwards but were met with extreme unfavourable conditions. In this case, their plasticity could not compensate for the lack of food and resources at a site because there were no further sites available, with only the desert further north.

I thus suggest that conservation efforts should be directed along migratory routes, especially at the Sahel region in spring and/or the breeding grounds (Vickery et al., 1999; Zwarts et al., 2009; Wilson & Cresswell, 2010). During the wintering stationary period, efforts should be made to retain scattered bushes throughout habitats, particularly at those habitats with high anthropogenic activities. Were another drought to occur, the best way to avoid the total collapse of the species is by securing bushes and a range of plant species with different hydric stress tolerance that would provide Whitethroats with enough food and shelter.

Many long-distance migrants can cope with fluctuating conditions and overcome harsh conditions (Adams et al., 2014; Blackburn & Cresswell, 2015). The degree of this flexibility, however, is likely to be population- and species-specific as was observed after the severe drought that occurred in West Africa, when only certain species were severely affected (Winstanley et al., 1974; Peach et al., 1991; Szép, 1995; Adams et al., 2014). The effect that future changes will have on species will greatly depend on the degree of the change, at what spatial scale it occurs, the frequency between events, and the species' strategies to adapt and/or recuperate. Individuals with strong site fidelity, for example, may be more threatened by habitat loss and changes at wintering sites and could be more susceptible than more itinerant individuals (Cohen et al., 2018). The degree of specialism and degree of migratory spread will also determine what the impact, positive or negative, of habitat loss and extreme weather conditions will be for the species and how well they recuperate (Kassen, 2002; Devictor et al., 2008; Colles et al., 2009; Finch et al., 2017; Lerche-Jørgensen et al., 2019).

The future of a species depends not only on its ability to adapt but on efficient conservation strategies at both the breeding and non-breeding grounds that will buffer the impact of future climatic and anthropogenic changes (Doswald et al., 2009; Lerche-Jørgensen et al., 2019). Studying the full annual cycle, and what challenges a species may face throughout the different periods, will help identify where species are more susceptible so that conservation efforts can be directed accordingly (Ådahl et al., 2006; Holmes, 2007; Martin et al., 2007; Klaassen et al., 2014; Marra et al., 2015; Sergio et al., 2019), either by protecting one large area or focusing on several small ones. With extreme events increasing both in frequency and intensity and the significant increase of monocultures and human settlements (IPCC, 2021), especially at the non-breeding grounds (Walther, 2016), strong declines could impact many species regardless of their degree of specialism, migratory spread, and resilience. Not only should efforts be directed at stopping declines, but also on buffering catastrophic events so that in case a catastrophic event occurs, species have time to either recuperate or adapt.

7.7 Novel contributions and study limitations

Although perhaps a typical migrant species, Whitethroats may not be the ideal study species. Their low detection probabilities, high mobility, and their tendency to hide inside bushes, making reading full colour-combinations difficult at times, result in generally small sample sizes and an increased probability that some individuals may have been overlooked and/or misidentified. To account for this, however, I undertook long periods of *in-situ* fieldwork with intense sampling efforts. To my knowledge, this is the first study to research, at a very fine scale, the ecology of Whitethroats throughout the entirety of the non-breeding season. This research is also the first to ever deploy geolocators on the species to reveal migratory routes and strategies, and to describe a complete annual cycle of a set of individuals. Moreover, it is one of the few studies that has fitted geolocators on any migrant from the wintering grounds. By studying a migrant in detail from the non-breeding grounds, this thesis also presents novel findings regarding residency patterns, site fidelity, habitat use, and overwinter survival, and is the first study to estimate annual survival rates from the non-breeding grounds. It is important to highlight, however, that individuals sampled during this thesis represent a small fraction of all individuals, and my samples may be biased towards those that are easier to catch or more resident. A high presence of anthropogenic activities at the study site may have influenced individuals' behaviour in an atypical way, but this probably reflects the true situation of African habitats where Whitethroats winter. The most difficult challenge of this research, however, that was not overcome and should be further explored, was studying the differences between individuals of different age (first-years *vs* adults) and sex (females *vs* males) groups. Sexing and aging Whitethroats is particularly challenging (Waldenström & Ottosson, 2000). Throughout this research, age- and sex-related comparisons should be interpreted with caution and in many instances, are lacking due to small sample sizes. Further exploration of these differences would lead to a better understanding of population dynamics.

7.8 Future research

Many studies have concluded that the non-breeding period of long-distance migrants has been neglected in terms of research (Morel, 1973; Sherry & Holmes, 1996; Walther & Rahbek, 2002; Newton, 2004; Salewski & Jones, 2006; Holmes, 2007; Kirby et al., 2008; Zwarts et al., 2009; Faaborg et al., 2010; Ockendon et al., 2012; Adams et al., 2014; Vickery et al., 2014; Marra et al., 2015; Walther & Pirsig, 2017). On a global scale, the breeding ecology of long-distance migratory birds has been studied to a greater extent than the wintering ecology, and most research carried out during the non-breeding period has been undertaken in the Neotropics and/or has focused on large non-passerine birds (Kelsey, 1992; Sherry & Holmes, 1996; Salewski & Jones, 2006; Holmes, 2007; Faaborg et al., 2010; Heckscher et al., 2011; Fraser et al., 2012; Klaassen et al., 2014; Cooper et al., 2017; Cheng et al., 2019; Sergio et al., 2019). Although much has been suggested, assumed, and indirectly explored with the use of new tracking technologies over the past years (Bridge et al., 2013; McKinnon et al., 2013; Briedis et al., 2019; Brlík et al., 2020) much information regarding this period is still lacking and, as long as this gap in knowledge persists, we will never fully understand the basic biology and ecology of long-distance migratory birds (Faaborg et al., 2010; Marra et al., 2015). Understanding survival patterns across the entirety of the annual cycle is especially important for migratory species because one period will have a strong effect on the next (Sillett & Holmes, 2002; Both et al., 2006; Morrison et al., 2013; Mayor et al., 2017; Buechley et al., 2021) and studying one part without the other could lead to biased and incorrect conclusions. Additionally, capturing the full annual cycle is important for understanding how populations of migratory animals are limited throughout the year and is crucial for predicting how populations will respond to future climate changes. In turn, this assists in directing successful conservation efforts – especially for understanding the thresholds at which species cannot recuperate from extreme habitat loss, habitat degradation and climate change (Ådahl et al., 2006; Klaassen et al., 2014; Marra et al., 2015; Burgess et al., 2020). Thus, further research at large spatial and temporal scales is needed, as well as basic knowledge of the functioning of the intercontinental systems, in addition to – above all – transnational research collaborations (Berthold & Terrill, 1991; Sheehan & Sanderson, 2012).

Key to identifying where, when, and how populations of long-distance migrants are limited is understanding the routes individuals take from breeding to non-breeding grounds and back, and how different breeding populations mix once at the non-breeding grounds (Webster et al., 2002; Webster & Marra, 2005; Cresswell, 2014; Finch et al., 2017). Hence, individuals must be tracked throughout many complete annual cycles. This is particularly complicated to study, especially in small passerine birds, as presently the only method for tracking active migration is using geolocators. Even though these devices are an increasingly useful tool for the general study of small passerine migration they have a series of disadvantages, such as the need to recapture individuals to download data, low resolution, and high error margins during the equinoxes (Lisovski et al., 2012). Therefore, understanding small-scale spatiotemporal movements through them is unreliable and conclusions regarding migratory connectivity drawn from a single deployment location with a small sample size may be misleading. Multiple deployment locations throughout a species' range, appropriate sample sizes, and deployment across multiple years is vital to determine the correct degree of migratory connectivity and how breeding populations mix in non-breeding grounds. Future research will need repeated tracks of the same individual to show yearly migratory differences, if any, and to better understand how constrained or flexible long-distance migrants are in their migration routes and timings.

Similarly, detailed studies to estimate true mortality/survival rates throughout different periods of the annual cycle, especially from the breeding grounds and from other wintering sites and across multiple years, should also be a priority for the research of Afro-Palearctic migrants. Results from these studies will provide a better understanding of population trends and will highlight where individuals and which populations are more at risk.

Moreover, generating detailed information on fine-scale movement and temporal patterns at non-breeding grounds, as well as between-years site fidelity, is crucial. To do so, however, many aspects should be considered:

1. Most importantly, that concepts and methods are not homogenised between studies, as they vary according to the researcher's particular objectives. For example, when analysing geolocator data, the researcher defines sun elevation angles and the duration of a stopover. While we defined a stopover as a site where birds spent at least three days, many other studies may have used (and did use) other parameters. Similarly, survival rates were estimated using resightings data across the non-breeding period, while many studies used results from mist-netting during a short period. One last example is the comparison of residency periods: itineracy and residency are, in practical terms, subjective and depend greatly on the duration of the study as well as how these terms are defined – a study that lasted one month may define a resident individual differently than a study that was carried out for a longer period, and whether studies were carried out at the beginning, mid, or end of the non-breeding period would also generate different results. It is therefore vital to standardise methods and definitions.
2. When working with long-distance migrants it is important to consider that within one population there can be a mixture of passage birds, short-term residents, and long-term residents. Failure to account for this dynamic, or to account for detection rates, could lead to biased estimates of abundance, population trends, and survival (Cohen et al., 2018).
3. Study comparisons are not straightforward. Because site fidelity varies by site and across years, and where in the species' distribution studies are carried out will elicit different results (even when working with the same species), it is difficult to make meaningful comparisons. The only way to overcome this is by increasing efforts to study the non-breeding period across many species and populations.

The lack of appropriate tagging tools, small sample sizes, and studying at only a single site has left many unresolved questions. Some of which are: Why did individuals carry out a loop migration in different directions? Do other individuals from central Nigeria undertake the same migratory routes? Because we are highly confident that differences in residency patterns are due to movement and not mortality, where do these individuals go and why do some individuals remain at some sites whilst others move, despite both groups occupying similar deteriorating sites? Why do different individuals have a different number of core wintering sites? Many of these current limitations and unanswered questions can, however, only be overcome and solved when non-archival tags such as satellite transmitters and/or GPS devices, which can truly distinguish between death and dispersal, are light enough in weight to be fitted on small birds throughout the year.

7.9 Conclusion

The conservation of migratory species is challenging because their shifting distributions make it difficult to identify diverse factors limiting populations at different points throughout the annual cycle. Understanding the life history of long-distance migratory species and assessing the potential reasons for recent global population declines helps direct general conservation and management priorities more appropriately and efficiently. This thesis presents in-depth research regarding the non-breeding ecology of a small Afro-Palearctic migrant, much of which is likely to apply to other small migrants wintering in Sub-Saharan Africa. Results from this research suggest that the study site at APLORI, a typical African landscape with a large, increasing human population that is affected by many anthropogenic pressures, can sustain large numbers of Whitethroats and still have enough suitable habitat to support more. Consequently, we extrapolate that core wintering sites are unlikely to strongly affect population trends of the species so long as shrubs are always present, both at the breeding and non-breeding grounds. It is therefore likely that Whitethroats, and potentially other Afro-Palearctic migrants, are limited elsewhere, most likely in the Sahel zone. This region represents the final phase of fattening for Whitethroats and the region’s deterioration, and consequently, lack of *Salvadora persica* berries, is thought to have caused the sharp population declines in the 1970s. Dry conditions in the Sahel region at the end of autumn migration, however, could also have had strong detrimental effects for refuelling and may have been an additional cause of these declines. Nevertheless, the conservation of Sahel woodlands should be prioritised for the long-term persistence of the species and to buffer the effects that extreme climatic events will have on the area.

Despite studies at the non-breeding grounds being crucial for fully understanding the ecology of long-distance migrants, working at the non-breeding grounds represents a series of challenges: not only is it logistically difficult, but it also takes a lot of time and resources to study the entirety of the period. For this reason, results presented in this work, though basic and limited, represent a large and important percentage of what is known about Whitethroats at non-breeding grounds. While the scale of this study is too small to draw firm conclusions about a species so largely distributed as the Whitethroat, our results highlight the complexity of the annual cycle of a single species and the importance of carrying out *in situ*, small-scale research throughout a migrant’s annual cycle over several years.

References

Abadi, F., Botha, A., & Altwegg, R. (2013). Revisiting the effect of capture heterogeneity on survival estimates in Capture-Mark-Recapture studies: does it matter? *PLoS ONE*, *8*(4), 20–22. https://doi.org/10.1371/journal.pone.0062636

Aborn, D. A., & Moore, F. R. (2004). Activity budgets of Summer Tanagers during spring migratory stopover. *The Wilson Bulletin*, *116*(1), 64–68. https://doi.org/10.1676/0043-5643(2004)116[0064:ABOSTD]2.0.CO;2

Ådahl, E., Lundberg, P., & Jonzén, N. (2006). From climate change to population change: the need to consider annual life cycles. *Global Change Biology*, *12*, 1627–1633. https://doi.org/10.1111/j.1365-2486.2006.01196.x

Adamík, P., Emmenegger, T., Briedis, M., Gustafsson, L., Henshaw, I., Krist, M., Laaksonen, T., Liechti, F., Procházka, P., Salewski, V., & Hahn, S. (2016). Barrier crossing in small avian migrants: individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy. *Scientific Reports*, *6*(January), 1–9. https://doi.org/10.1038/srep21560

Adams, W. M., Small, R. D. S., & Vickery, J. A. (2014). The impact of land use change on migrant birds in the Sahel. *Biodiversity*, *15*(2–3), 101–108. https://doi.org/10.1080/14888386.2014.931822

Ahola, M., Laaksonen, T., Sippola, K., Eeva, T., Rainio, K., & Lehikoinen, E. (2004). Variation in climate warming along the migration route uncouples arrival and breeding dates. *Global Change Biology*, *10*(9), 1610–1617. https://doi.org/10.1111/j.1365-2486.2004.00823.x

Åkesson, S., Klaassen, R. H. G., Holmgren, J., Fox, J. W., & Hedenström, A. (2012). Migration routes and strategies in a highly aerial migrant, the common swift *Apus apus*, revealed by light-level geolocators. *PLoS ONE*, *7*(7), 1–9. https://doi.org/10.1371/journal.pone.0041195

Alerstam, T. (1990). *Bird Migration*. Cambridge University Press.

Alerstam, T. (2011). Optimal bird migration revisited. *Journal of Ornithology*, *152*(Suppl 1), S5–S23. https://doi.org/10.1007/s10336-011-0694-1

Alerstam, T., Hedenström, A., & Åkesson, S. (2003). Long-distance migration: evolution and determinants. *Oikos*, *103*, 247–260. https://doi.org/10.1034/j.1600-0706.2003.12559.x

Allen, A. A., Ens, B. J., van de Pol, M., Van Der Jeugd, H., Frauendorf, M., Oosterbeek, K., & Jongejans, E. (2019). Seasonal survival and migratory connectivity of the Eurasian Oystercatcher revealed by citizen science. *The Auk*, *136*, 1–17. https://doi.org/10.1093/auk/uky001

Anders, A. D., Dearborn, D. C., Faaborg, J., & Thompson, F. R. (1997). Juvenile survival in a population of Neotropical migrant birds. *Conservation Biology*, *11*(3), 698–707. https://doi.org/10.1046/j.1523-1739.1997.95526.x

Arizaga, J., Barba, E., & Belda, E. J. (2008). Fuel management and stopover duration of Blackcaps *Sylvia atricapilla* stopping over in northern Spain during autumn migration period. *Bird Study*, *55*(1), 124–134. https://doi.org/10.1080/00063650809461513

Arlt, D., Olsson, P., Fox, J. W., Low, M., & Pärt, T. (2015). Prolonged stopover duration characterises migration strategy and constraints of a long-distance migrant songbird. *Animal Migration*, *2*, 47–62. https://doi.org/10.1515/ami-2015-0002

ASAB. (2020). Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour*, *159*, i–xi. https://doi.org/10.1016/j.anbehav.2019.11.002

Aymí, R., & Gargallo, G. (2021). Greater Whitethroat (*Curruca communis*), version 1.1. In J. del Hoyo, A. Elliott, J. Sargatal, D. Christie, & E. de Juana (Eds.), *Birds of the World*. Cornell Lab of Ornithology. https://doi.org/10.2173/bow.grewhi1.01.1

Bächler, E., Hahn, S., Schaub, M., Arlettaz, R., Jenni, L., Fox, J. W., Afanasyev, V., & Liechti, F. (2010). Year-round tracking of small trans-Saharan migrants using light-level geolocators. *PLoS ONE*, *5*(3), 3–6. https://doi.org/10.1371/journal.pone.0009566

Baillie, S. R., Marchant, J. H., Crick, H. Q. P., Noble, D. G., Balmer, D. E., Barimore, C., Coombes, R. H., Downie, I. S., Freeman, S. N., Joys, A. C., Leech, D. I., Raven, M. J., Robinson, R. A., & Thewlis, R. M. (2007). *Breeding Birds in the Wider Countryside: their conservation status 2007*. BTO Research Report No. 487.

Baillie, S. R., & Peach, W. J. (1992). Population limitation in Palaearctic-African migrant passerines. *Ibis*, *134*(Suppl 1), 120–132. https://doi.org/10.1111/j.1474-919X.1992.tb04742.x

Bairlein, F. (1988). How do migratory songbirds cross the Sahara? *Trends in Ecology and Evolution*, *3*(8), 191–194.

https://doi.org/10.1016/0169-5347(88)90005-5

Bairlein, F. (1992). Recent prospects on trans-Saharan migration of songbirds. *Ibis*, *134*(suppl. 1), 41–46. https://doi.org/10.1111/j.1474-919X.1992.tb04732.x

Bairlein, F. (2016). Migratory birds under threat. *Science*, *354*(6312), 547–548. https://doi.org/10.1126/science.aah6647

Barbet-Massin, M., Walther, B. A., Thuiller, W., Rahbek, C., & Jiguet, F. (2009). Potential impacts of climate change on the winter distribution of Afro-Palaearctic migrant passerines. *Biology Letters*, *5*(2), 248–251. https://doi.org/10.1098/rsbl.2008.0715

Barg, J. J., Jones, J., & Robertson, R. J. (2005). Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. *Journal of Animal Ecology*, *74*, 139–149. https://doi.org/10.1111/j.1365-2656.2004.00906.x

Barshep, Y., Ottosson, U., Waldenström, J., & Hulme, M. (2012). Non-breeding ecology of the Whinchat *Saxicola rubetra* in Nigeria. *Ornis Svecica*, *22*, 25–32. https://doi.org/10.34080/os.v22.22591

Barton, K. (2020). *MuMIn: Multi-Model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn*.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/doi:10.18637/jss.v067.i01

Belda, E. J., Barba, E., & Monrós, J. S. (2007). Resident and transient dynamics, site fidelity and survival in wintering Blackcaps *Sylvia atricapilla*: evidence from capture–recapture analyses. *Ibis*, *149*(2), 396–404. https://doi.org/10.1111/j.1474-919X.2007.00657.x

Bell, C. P. (2000). Process in the evolution of bird migration and pattern in avian ecogeography. *Journal of Avian Biology*, *31*, 258–265. https://doi.org/10.1034/j.1600-048X.2000.310218.x

Berthold, P. (1993). *Bird migration: a general survey*. Oxford University Press.

Berthold, P. (1996). *Control of bird migration* (1 edition). Chapman & Hall.

Berthold, P., Fiedler, W., Schlenker, R., & Querner, U. (1998). 25-year study of the population development of central European songbirds: A general decline, most evident in long-distance migrants. *Naturwissenschaften*, *85*(7), 350–353. https://doi.org/10.1007/s001140050514

Berthold, P., & Terrill, S. (1991). Recent advances in studies of bird migration. *Annual Review of Ecology and Systematics*, *22*, 357–378. https://doi.org/10.1146/annurev.es.22.110191.002041

Bibby, C., & Green, R. E. (1980). Foraging behaviour of migrant Pied flycatchers, *Ficedula hypoleuca*, on temporary territories. *Journal of Animal Ecology*, *49*(2), 507–521. https://doi.org/10.2307/4260

Biber, J., & Salathé, T. (1991). Threats to migratory birds. In T. Salathé (Ed.), *Conserving migratory birds. ICBP Technical Publication No. 12* (pp. 17–35). International Council for Bird Preservation.

Biebach, H., Biebach, I., Friedrich, W., Heine, G., Partecke, J., & Schmidl, D. (2000). Strategies of passerine migration across the Mediterranean Sea and the Sahara Desert: a radar study. *Ibis*, *142*(4), 623–634. https://doi.org/10.1111/j.1474-919x.2000.tb04462.x

BirdLife International. (2019). Sylvia communis *(ammended version of 2017 assessment). The IUCN Red List of Threatened Species 2019: e.T22716910A155623300*. https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T22716910A155623300.en

Blackburn, E., Burgess, M., Freeman, B., Risely, A., Izang, A., Ivande, S., Hewson, C., & Cresswell, W. (2016). An experimental evaluation of the effects of geolocator design and attachment method on between-year survival on whinchats *Saxicola rubetra*. *Journal of Avian Biology*, *47*, 530–539. https://doi.org/10.1111/jav.00871

Blackburn, E., Burgess, M., Freeman, B., Risely, A., Izang, A., Ivande, S., Hewson, C., & Cresswell, W. (2017). Low and annually variable migratory connectivity in a long-distance migrant: Whinchats *Saxicola rubetra* may show a bet-hedging strategy. *Ibis*, *159*, 902–918. https://doi.org/10.1111/ibi.12509

Blackburn, E., Burgess, M., Freeman, B., Risely, A., Izang, A., Ivande, S., Hewson, C., & Cresswell, W. (2019). Spring migration strategies of Whinchat *Saxicola rubetra* when successfully crossing potential barriers of the Sahara and the Mediterranean Sea. *Ibis*, *161*(1), 131–146. https://doi.org/10.1111/ibi.12610

Blackburn, E., & Cresswell, W. (2015). Fine-scale habitat use during the non-breeding season suggests that winter habitat does not limit breeding populations of a declining long-distance Palearctic migrant. *Journal of Avian Biology*, *46*(6), 622–633. https://doi.org/10.1111/jav.00738

Blackburn, E., & Cresswell, W. (2016a). High site fidelity in Northern Wheatears *Oenanthe oenanthe* wintering in

Africa revealed through colour marking. *Bird Study*, *63*(2), 284–288. https://doi.org/10.1080/00063657.2016.1180343

Blackburn, E., & Cresswell, W. (2016b). High winter site fidelity in a long-distance migrant: implications for wintering ecology and survival estimates. *Journal of Ornithology*, *157*(1), 93–108. https://doi.org/10.1007/s10336-015-1252-z

Blackburn, E., & Cresswell, W. (2016c). High within-winter and annual survival rates in a declining Afro-Palaearctic migratory bird suggest that wintering conditions do not limit populations. *Ibis*, *158*(1), 92–105. https://doi.org/10.1111/ibi.12319

Boano, G., Bonardi, A., & Silvano, F. (2004). Nightingale *Luscinia megarhynchos* survival rates in relation to Sahel rainfall. *Avocetta*, *28*, 77–85.

Boano, G., Pellegrino, I., Ferri, M., Cucco, M., Minelli, F., & Åkesson, S. (2020). Climate anomalies affect annual survival rates of swifts wintering in sub-Saharan Africa. *Ecology and Evolution*, *10*, 7916–7928. https://doi.org/10.1002/ece3.6525

Boddy, M. (1992). Timing of whitethroat *Sylvia communis* arrival, breeding and moult at a coastal site in Lincolnshire. *Ringing & Migration*, *13*(2), 65–72. https://doi.org/10.1080/03078698.1992.9674021

Boddy, M. (1993). Whitethroat *Sylvia communis* population studies during 1981–91 at a breeding site on the Lincolnshire coast. *Ringing & Migration Migration*, *14*(2), 73–83. https://doi.org/10.1080/03078698.1993.9674048

Boddy, M. (1994). Survival/return rates and juvenile dispersal in an increasing population of Lesser Whitethroats *Sylvia curruca*. *Ringing & Migration*, *15*(2), 65–78. https://doi.org/10.1080/03078698.1994.9674076

Both, C., Bijlsma, R. G., & Ouwehand, J. (2016). Repeatability in spring arrival dates in Pied Flycatchers varies among years and sexes. *Ardea*, *104*(1), 3–21. https://doi.org/10.5253/arde.v104i1.a1

Both, C., Bouwhuis, S., Lessells, C. M., & Visser, M. E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, *441*(1), 81–83. https://doi.org/10.1038/nature04539

Both, C., Sanz, J. J., Artemyev, A. V., Blaauw, B., Cowie, R. J., Dekhuizen, A. J., Enemar, A., Järvinen, A., Nyholm, N. E. I., Potti, J., Ravussin, P. A., Silverin, B., Slater, F. M., Sokolov, L. V., Visser, M. E., Winkel, W., Wright, J., & Zang, H. (2006). Pied flycatchers *Ficedula hypoleuca* travelling from Africa to breed in Europe: Differential effects of winter and migration conditions on breeding date. *Ardea*, *94*(3), 511–525.

Bridge, E. S., Kelly, J. F., Contina, A., Gabrielson, R. M., MacCurdy, R. B., & Winkler, D. W. (2013). Advances in tracking small migratory birds: a technical review of light-level geolocation. *Journal of Field Ornithology*, *84*(2), 121–137. https://doi.org/10.1111/jofo.12011

Bridge, E. S., Thorup, K., Bowlin, M. S., Chilson, P. B., Diehl, R. H., Fléron, R. W., Hartl, P., Kays, R., Kelly, J. F., Robinson, W. D., & Wikelski, M. (2011). Technology on the move: recent and forthcoming innovations for tracking migratory birds. *BioScience*, *61*(9), 689–698. https://doi.org/10.1525/bio.2011.61.9.7

Briedis, M., Bauer, S., Adamík, P., Alves, J. A., Costa, J. S., Emmenegger, T., Gustafsson, L., Koleček, J., Liechti, F., Meier, C. M., Procházka, P., & Hahn, S. (2019). A full annual perspective on sex-biased migration timing in long-distance migratory birds. *Proceedings of the Royal Society B: Biological Sciences*, *286*, 20182821. https://doi.org/10.1098/rspb.2018.2821

Briedis, M., Kurlavičius, P., Mackevičienė, R., Vaišvilienė, R., & Hahn, S. (2018). Loop migration, induced by seasonally different flyway use, in Northern European Barn Swallows. *Journal of Ornithology*, *159*, 885–891. https://doi.org/10.1007/s10336-018-1560-1

Brlík, V., Koleček, J., Burgess, M., Hahn, S., Humple, D., Krist, M., Ouwehand, J., Weiser, E. L., Adamík, P., Alves, J. A., Arlt, D., Barišić, S., Becker, D., Belda, E. J., Beran, V., Both, C., Bravo, S. P., Briedis, M., Chutný, B., … Procházka, P. (2020). Weak effects of geolocators on small birds: A meta-analysis controlled for phylogeny and publication bias. *Journal of Animal Ecology*, *89*(1), 207–220. https://doi.org/10.1111/1365-2656.12962

Brown, D. R., & Long, J. A. (2006). Experimental fruit removal does not affect territory structure of wintering Hermit Thrushes. *Journal of Field Ornithology*, *77*(4), 404–408. https://doi.org/10.1111/j.1557-9263.2006.00071.x

Brown, D. R., Stouffer, P. C., & Strong, C. M. (2000). Movement and territoriality of wintering Hermit thrushes in Southeastern Louisiana. *The Wilson Bulletin*, *112*(3), 347–353. https://doi.org/10.1676/0043-5643(2000)112[0347:MATOWH]2.0.CO;2

Brown, J. L. (1969). Territorial behavior and population regulation in birds: A review and re-Evaluation. *The Wilson Bulletin*, *81*(3), 293–329. https://doi.org/https://www.jstor.org/stable/4159863

Bruderer, B., & Boldt, A. (2001). Flight characteristics of birds: I. radar measurements of speeds. *Ibis*, *143*(2), 178–204. https://doi.org/10.1111/j.1474-919X.2001.tb04475.x

Bruderer, B., & Salewski, V. (2008). Evolution of bird migration in a biogeographical context. *Journal of Biogeography*, *35*, 1951–1959. https://doi.org/10.1111/j.1365-2699.2008.01992.x

Buechley, E. R., Oppel, S., Efrat, R., Phipps, W. L., Carbonell Alanís, I., Álvarez, E., Andreotti, A., Arkumarev, V., Berger-Tal, O., Bermejo Bermejo, A., Bounas, A., Ceccolini, G., Cenerini, A., Dobrev, V., Duriez, O., García, J., García-Ripollés, C., Galán, M., Gil, A., … Marra, P. P. (2021). Differential survival throughout the full annual cycle of a migratory bird presents a life-history trade-off. *Journal of Animal Ecology*, *90*(5), 1228–1238. https://doi.org/10.1111/1365-2656.13449

Bulluck, L., Ames, E., Bayly, N., Reese, J., Viverette, C., Wright, J., Caguazango, A., & Tonra, C. (2019). Habitat-dependent occupancy and movement in a migrant songbird highlights the importance of mangroves and forested lagoons in Panama and Colombia. *Ecology and Evolution*, *9*, 11064–11077. https://doi.org/10.1002/ece3.5610

Burgess, M. D., Finch, T., Border, J. A., Castello, J., Conway, G., Ketcher, M., Lawrence, M., Orsman, C. J., Mateos, J., Proud, A., Westerberg, S., Wiffen, T., & Henderson, I. G. (2020). Weak migratory connectivity, loop migration and multiple non-breeding site use in British breeding Whinchats *Saxicola rubetra*. *Ibis*, *162*(4), 1292–1302. https://doi.org/10.1111/ibi.12825

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, *24*(3), 346–352. https://doi.org/10.2307/1374834

Butler, S. J., Boccaccio, L., Gregory, R. D., Vorisek, P., & Norris, K. (2010). Quantifying the impact of land-use change to European farmland bird populations. *Agriculture, Ecosystems and Environment*, *137*, 348–357. https://doi.org/10.1016/j.agee.2010.03.005

Catry, P., Campos, A., Almada, V., & Cresswell, W. (2004). Winter segregation of migrant European Robins *Erithacus rubecula* in relation to sex, age and size. *Journal of Avian Biology*, *35*(3), 204–209. https://doi.org/https://www.jstor.org/stable/3677432

Catry, P., Catry, I., Catry, T., & Martins, T. (2003). Within and between-year winter-site fidelity of Chiffchaffs *Phylloscopus collybita*. *Ardea*, *91*(2), 213–220.

Catry, P., Encarnação, V., Araújo, A., Fearon, P., Fearon, A., Armelin, M., & Delaloye, P. (2004). Are long-distance migrant passerines faithful to their stopover sites? *Journal of Avian Biology*, *35*, 170–181. https://doi.org/https://www.jstor.org/stable/3677391

Catry, P., Phillips, R., & Croxall, J. (2005). Sexual segregation in birds: patterns, processes and implications for conservation. In K. Ruckstuhl & P. Neuhaus (Eds.), *Sexual segregation in vertebrates* (pp. 351–380). Cambridge University Press.

Chamberlain, D. E., Fuller, R. J., Bunce, R. G. H., Duckworth, J. C., & Shrubb, M. (2000). Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*, *37*(5), 771–788. https://doi.org/10.1046/j.1365-2664.2000.00548.x

Cheng, Y., Fiedler, W., Wikelski, M., & Flack, A. (2019). "Closer-to-home" strategy benefits juvenile survival in a long-distance migratory bird. *Ecology and Evolution*, *9*, 8945–8952. https://doi.org/10.1002/ece3.5395

Cohen, J. B., Maddock, S. B., Bimbi, M. K., Golder, W. W., Ledee, O. E., Cuthbert, F. J., Catlin, D. H., Fraser, J. D., & Gratto-Trevor, C. L. (2018). State uncertainty models and mark-resight models for understanding non-breeding site use by Piping Plovers. *Ibis*, *160*, 342–354. https://doi.org/10.1111/ibi.12546

Colles, A., Hsiang Liow, L., & Prinzing, A. (2009). Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. *Ecology Letters*, *12*, 849–863. https://doi.org/10.1111/j.1461-0248.2009.01336.x

Conklin, J. R., Battley, P. F., & Potter, M. A. (2013). Absolute consistency: Individual versus population variation in annual-cycle schedules of a long-distance migrant bird. *PLoS ONE*, *8*(1), e54535. https://doi.org/10.1371/journal.pone.0054535

Conway, C. J., Powell, G. V. N., & Nichols, J. D. (1995). Overwinter survival of Neotropical migratory birds in early-successional and mature tropical forests. *Conservation Biology*, *9*(4), 855–864. https://doi.org/https://www.jstor.org/stable/2386995

Cooper, N. W., Hallworth, M. T., & Marra, P. P. (2017). Light-level geolocation reveals wintering distribution, migration routes, and primary stopover locations of an endangered long-distance migratory songbird. *Journal of Avian Biology*, *48*(2), 209–219. https://doi.org/10.1111/jav.01096

Costantini, D., & Møller, A. P. (2013). A meta-analysis of the effects of geolocator application on birds. *Current Zoology*, *59*(6), 697–706. https://doi.org/10.1093/czoolo/59.6.697

Cotton, P. A. (2003). Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(21), 12219–12222. https://doi.org/10.1073/pnas.1930548100

Cowley, E., & Siriwardena, G. M. (2005). Long-term variation in survival rates of Sand Martins *Riparia riparia*: dependence on breeding and wintering ground weather, age and sex, and their population consequences. *Bird Study*, *52*(3), 237–251. https://doi.org/10.1080/00063650509461397

Cox, G. W. (1985). The evolution of avian migration systems between temperate and tropical regions of the new world. *American Society of Naturalists*, *126*(4), 451–474. https://doi.org/10.1086/284432

Cramp, S. (1992). *The birds of the Western Palearctic Vol VI*. Oxford University Press.

Cresswell, W. (2014). Migratory connectivity of Palaearctic-African migratory birds and their responses to environmental change: the serial residency hypothesis. *Ibis*, *156*(3), 493–510. https://doi.org/10.1111/ibi.12168

Cresswell, W., Boyd, M., & Stevens, M. (2009). Movements of Palearctic and Afrotropical bird species during the dry season (November – February) within Nigeria. In D. Harebottle, A. Craig, M. Anderson, H. Rakotomanana, & M. Muchai (Eds.), *Proceedings of the 12th Pan African Ornithological Congress, 2008* (pp. 18–28). Cape Town, Animal Demography Unit.

Cuadrado, M. (1992). Year to year recurrence and site-fidelity of blackcaps *Sylvia atricapilla* and robins *Erithacus rubecula* in a Mediterranean wintering area. *Ringing & Migration*, *13*(1), 36–42. https://doi.org/10.1080/03078698.1992.9674013

Cuadrado, M. (1995). Winter territoriality in migrant Black Redstarts *Phoenicurus ochrurus* in the Mediterranean area. *Bird Study*, *42*(3), 232–239. https://doi.org/10.1080/00063659509477172

Cuadrado, M. (1997). Why are migrant Robins (*Erithacus rubecula*) territorial in winter?: the importance of the anti-predatory behaviour. *Ethology, Ecology & Evolution*, *9*(1), 77–88. https://doi.org/10.1080/08927014.1997.9522904

da Prato, S., & da Prato, E. (1983). Movements of Whitethroats *Sylvia communis* ringed in the British Isles. *Ringing & Migration*, *4*(4), 193–210. https://doi.org//10.1080/03078698.1983.9673808

de la Hera, I., Pérez-Tris, J., & Tellería, J. L. (2010). Relationships among timing of moult, moult duration and feather mass in long-distance migratory passerines. *Journal of Avian Biology*, *41*, 609–614. https://doi.org/10.1111/j.1600-048X.2010.05075.x

Denac, K., & Kmecl, P. (2021). Land consolidation negatively affects farmland bird diversity and conservation value. *Journal for Nature Conservation*, *59*, 125934. https://doi.org/10.1016/j.jnc.2020.125934

Devictor, V., Julliard, R., & Jiguet, F. (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, *117*, 507–514. https://doi.org/10.1111/j.2008.0030-1299.16215.x

Diesselhorst, van G. (1968). Struktur einer Brutpopulation von *Sylvia communis* (Structure of a breeding population of *Sylvia communis*. *Bonn Zoological Bulletin*, *19*, 307–321.

Dokter, A. M., Farnsworth, A., Fink, D., Ruiz-Gutierrez, V., Hochachka, W. M., La Sorte, F. A., Robinson, O. J., Rosenberg, K. V, & Kelling, S. (2018). Seasonal abundance and survival of North America's migratory avifauna determined by weather radar. *Nature Ecology & Evolution*, *2*, 1603–1609. https://doi.org/10.1038/s41559-018-0666-4

Donald, P. F. (2007). Adult sex ratios in wild bird populations. *Ibis*, *149*(4), 671–692. https://doi.org/10.1111/j.1474-919X.2007.00724.x

Donald, P. F., Green, R. E., & Heath, M. F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1462), 25–29. https://doi.org/10.1098/rspb.2000.1325

Doswald, N., Willis, S. G., Collingham, Y. C., Pain, D. J., Green, R. E., & Huntley, B. (2009). Potential impacts of climatic change on the breeding and non-breeding ranges and migration distance of European *Sylvia* warblers. *Journal of Biogeography*, *36*(6), 1194–1208. https://doi.org/10.1111/j.1365-2699.2009.02086.x

Drake, A., Rock, C. A., Quinlan, S. P., Martin, M., & Green, D. J. (2014). Wind speed during migration influences the survival, timing of breeding, and productivity of a Neotropical migrant, *Setophaga petechia*. *PLoS ONE*, *9*(5), e97152. https://doi.org/10.1371/journal.pone.0097152

Drent, R., Both, C., Green, M., Madsen, J., & Piersma, T. (2003). Pay-offs and penalties of competing migratory schedules. *Oikos*, *103*(2), 274–292. https://doi.org/10.1034/j.1600-0706.2003.12274.x

Ekroos, J., Tiainen, J., Seimola, T., & Herzon, I. (2019). Weak effects of farming practices corresponding to agricultural greening measures on farmland bird diversity in boreal landscapes. *Landscape Ecology*, *34*(2), 389–402. https://doi.org/10.1007/s10980-019-00779-x

Elgood, J., Heigham, J., Moore, A., Nason, A., Sharland, R., & Skinner, N. (1994). *The birds of Nigeria* (2 edition). British Trust for Ornithology (BTO).

Ellegren, H., & Fransson, T. (1992). Fat loads and estimated flight-ranges in four *Sylvia* species analysed during autumn migration at Gotland, South-East Sweden. *Ringing and Migration*, *13*(1), 1–12. https://doi.org/10.1080/03078698.1992.9674009

Emmenegger, T., Hahn, S., & Bauer, S. (2014). Individual migration timing of common nightingales is tuned with vegetation and prey phenology at breeding sites. *BMC Ecology*, *14*(9), 1–8. https://doi.org/10.1186/1472-6785-14-9

Eraud, C., Rivière, M., Lormée, H., Fox, J. W., Ducamp, J. J., & Boutin, J. M. (2013). Migration routes and staging areas of Trans-Saharan Turtle Doves appraised from light-level geolocators. *PLoS ONE*, *8*(3), 1–10. https://doi.org/10.1371/journal.pone.0059396

Erni, B., Liechti, F., & Bruderer, B. (2005). The role of wind in passerine autumn migration between Europe and Africa. *Behavioral Ecology*, *16*(4), 732–740. https://doi.org/10.1093/beheco/ari046

Escandell, R., & García, Ó. (2011). Whitethroat *Sylvia communis*. In G. Gargallo, C. Barriocanal, J. Castany, O. Clarabuch, R. Escandell, G. López-Iborra, H. Rguibi-Idrissi, D. Robson, & M. Suárez (Eds.), *Spring migration in the western Mediterranean and NW Africa: the results of 16 years of the Piccole Isole project G.* (pp. 190–197). Monografies del Museu de Ciències Naturals 6.

European Environment Agency. (2019). *Report on progress and implementation (Article 12, Birds Directive). EIONET Central Data Repository*. https://www.eea.europa.eu/themes/biodiversity/state-of-nature-in-the-eu/article-12-national-summary-dashboards/breeding-population-and-distribution-trends

Faaborg, J., Holmes, R. T., Anders, A. D., Bildstein, K. L., Dugger, K. M., Gauthreaux, S. A., Heglund, P., Hobson, K. A., Jahn, A. E., Johnson, D. H., Latta, S. C., Levey, D. J., Marra, P. P., Merkord, C. L., Nol, E., Rothstein, S. I., Sherry, T. W., Sillett, T. S., Thompson, F. R., & Warnock, N. (2010). Conserving migratory land birds in the New World: Do we know enough? *Ecological Applications*, *20*(2), 398–418. https://doi.org/10.1890/09-0397.1

Farnsworth, G., Pollock, K., Nichols, J., Simons, T., Hines, J., & Sauer, J. (2002). A removal model for estimating detection probabilities from point-count surveys. *The Auk*, *119*(2), 414–425. https://doi.org/10.1093/auk/119.2.414

Fay, R., Schaub, M., Banik, M. V, Border, J. A., Henderson, I. G., Fahl, G., Feulner, J., Horch, P., Korner, F., Müller, M., Michel, V., Rebstock, H., Shitikov, D. A., Tome, D., Vögeli, M., & Grüebler, M. U. (2021). Whinchat survival estimates across Europe: can excessive adult mortality explain population declines? *Animal Conservation*, *24*(1), 15–25. https://doi.org/doi:10.1111/acv.12594

Finch, T., Butler, S. J., Franco, A. M. A., & Cresswell, W. (2017). Low migratory connectivity is common in long-distance migrant birds. *Journal of Animal Ecology*, *86*(3), 662–673. https://doi.org/10.1111/1365-2656.12635

Finlayson, C. (2011). *Avian survivors: the history and biogeography of Palearctic birds*. T. & A. D. Poyser.

Flegg, J. (2004). *Time to fly: exploring bird migration*. British Trust for Ornithology (BTO).

Fransson, T. (1995). Timing and speed of migration in North and West European populations of *Sylvia* warblers. *Journal of Avian Biology*, *26*(1), 39–48. https://doi.org/10.2307/3677211

Fraser, K. C., Stutchbury, B. J. M., Silverio, C., Kramer, P. M., Barrow, J., Newstead, D., Mickle, N., Cousens, B. F., Charlene Lee, J., Morrison, D. M., Shaheen, T., Mammenga, P., Applegate, K., & Tautin, J. (2012). Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 4901–4906. https://doi.org/10.1098/rspb.2012.2207

Fry, C. (1992). The Moreau ecological overview. *Ibis*, *134*(suppl. 1), 3–6. https://doi.org/10.1111/j.1474-919x.1992.tb04726.x

Fuller, R. J., Smith, K. W., Grice, P. V., Currie, F. A., & Quine, C. P. (2007). Habitat change and woodland birds in Britain: implications for management and future research. *Ibis*, *149*(suppl. 2), 261–268. https://doi.org/10.1111/j.1474-919X.2007.00775.x

Gardali, T., Barton, D. C., White, J. D., & Geupel, G. R. (2003). Juvenile and adult survival of Swainson's Thrush

(*Catharus ustulatus*) in coastal California: Annual estimates using capture-recapture analyses. *The Auk*, *120*(4), 1188–1194. https://doi.org/10.1093/auk/120.4.1188

Gilroy, J. J., Gill, J. A., Butchart, S. H. M., Jones, V. R., & Franco, A. M. A. (2016). Migratory diversity predicts population declines in birds. *Ecology Letters*, *19*, 308–317. https://doi.org/10.1111/ele.12569

Graham, M. H. (2003). Confronting multicollinearity in ecological multiple regression. *Ecology*, *84*(11), 2809–2815. https://doi.org/10.1890/02-3114

Greenberg, R. (1986). Competition in migrant birds in the nonbreeding season. In R. F. Johnston (Ed.), *Current Ornithology* (Vol. 3, pp. 281–307). Plenum Press.

Greenwood, P. J., & Harvey, P. H. (1982). The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, *13*, 1–21. https://doi.org/10.1146/annurev.es.13.110182.000245

Gregory, R. D., Vorisek, P., Van Strien, A., Gmelig Meyling, A. W., Jiguet, F., Fornasari, L., Reif, J., Chylarecki, P., & Burfield, I. J. (2007). Population trends of widespread woodland birds in Europe. *Ibis*, *149*(suppl. 2), 78–97. https://doi.org/10.1111/j.1474-919X.2007.00698.x

Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology*, *24*, 699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Grüebler, M. U., Korner-Nievergelt, F., & Naef-Daenzer, B. (2014). Equal nonbreeding period survival in adults and juveniles of a long-distant migrant bird. *Ecology and Evolution*, *4*(6), 756–765. https://doi.org/10.1002/ece3.984

Haas, C. (1998). Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. *The Auk*, *115*(4), 929–936. https://doi.org/10.2307/4089511

Hahn, S., Amrhein, V., Zehtindijev, P., & Liechti, F. (2013). Strong migratory connectivity and seasonally shifting isotopic niches in geographically separated populations of a long-distance migrating songbird. *Oecologia*, *173*, 1217–1225. https://doi.org/10.1007/s00442-013-2726-4

Hahn, S., Bauer, S., & Liechti, F. (2009). The natural link between Europe and Africa - 2.1 billion birds on migration. *Oikos*, *118*(4), 624–626. https://doi.org/10.1111/j.1600-0706.2008.17309.x

Hallworth, M. T., Sillett, T. S., Van Wilgenburg, S. L., Hobson, K. A., & Marra, P. P. (2015). Migratory connectivity of a Neotropical migratory songbird revealed by archival light-level geolocators. *Ecological Applications*, *25*(2), 336–347. https://doi.org/10.1890/14-0195.1

Halupka, K., Borowiec, M., Karczewska, A., Kunka, A., & Pietrowiak, J. (2002). Habitat requirements of Whitethroats *Sylvia communis* breeding in an alluvial plain. *Bird Study*, *49*, 297–299. https://doi.org/10.1080/00063650209461278

Halupka, L., Wierucka, K., Sztwiertnia, H., & Klimczuk, E. (2017). Conditions at autumn stopover sites affect survival of a migratory passerine. *Journal of Ornithology*, *158*(4), 979–988. https://doi.org/10.1007/s10336-017-1472-5

Hammond, P. (2018). Mark-Recapture. In B. Wursig, J. G. . Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of Marine Mammals* (3 edition, pp. 580–584). Academic Press. https://doi.org/10.1016/B978-0-12-804327-1.00168-0

Harestad, A., & Bunnell, F. (1979). Home range and body weight--A reevaluation. *Ecology*, *60*(2), 389–402. https://doi.org/10.2307/1937667

Heckscher, C. M., Taylor, S. M., Fox, J. W., & Afanasyev, V. (2011). Veery (*Catharus fuscescens*) wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology. *The Auk*, *128*(3), 531–542. https://doi.org/10.1525/auk.2011.10280

Hedenström, A., & Alerstam, T. (1997). Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. *Journal of Theoretical Biology*, *189*(3), 227–234. https://doi.org/10.1006/jtbi.1997.0505

Hedenström, A., Bensch, S., Hasselquist, D., Lockwood, M., & Ottosson, U. (1993). Migration, stopover and moult of the Great Reed Warbler *Acrocephalus arundinaceus* in Ghana, West Africa. *Ibis*, *135*(2), 177–180. https://doi.org/10.1111/j.1474-919X.1993.tb02829.x

Heldbjerg, H., & Fox, T. (2008). Long-term population declines in Danish trans-Saharan migrant birds. *Bird Study*, *55*(3), 267–279. https://doi.org/10.1080/00063650809461532

Herremans, M. (2003). The study of bird migration across the Western Sahara; a contribution with sound luring. In *Report of field research in Mauritania during spring and autumn 2003 in association with the Sahara project of the Swiss Ornithological Institute (Vogelwarte Sempach)*.

Herrera, C. M., & Rodriguez, M. (1979). Year-to-year site constancy among three passerine species wintering at a Southern Spanish locality. *Ringing & Migration*, *2*(3), 160. https://doi.org/10.1080/03078698.1979.9673751

Hewson, C. M., & Noble, D. G. (2009). Population trends of breeding birds in British woodlands over a 32-year period: relationships with food, habitat use and migratory behaviour. *Ibis*, *151*(3), 464–486. https://doi.org/10.1111/j.1474-919X.2009.00937.x

Hewson, C. M., Thorup, K., Pearce-Higgins, J. W., & Atkinson, P. W. (2016). Population decline is linked to migration route in the Common Cuckoo. *Nature Communications*, *7*, 1–8. https://doi.org/10.1038/ncomms12296

Hiemer, D., Salewski, V., Fiedler, W., Hahn, S., & Lisovski, S. (2018). First tracks of individual Blackcaps suggest a complex migration pattern. *Journal of Ornithology*, *159*(1), 205–210. https://doi.org/10.1007/s10336-017-1490-3

Hijmans, R. J. (2019). *geosphere: Spherical Trigonometry. R package version 1.5-10. https://CRAN.R-project.org/package=geosphere*.

Hines, J. E., Kendall, W. L., & Nichols, J. D. (2003). On the use of the robust design with transient capture-recapture models. *The Auk*, *120*(4), 1151–1158. https://doi.org/10.1093/auk/120.4.1151

Hjort, C., & Lindholm, C.-G. (1978). Annual bird ringing totals and population fluctuations. *Oikos*, *30*(2), 387–392. https://doi.org/10.2307/3543487

Holmes, R. T. (2007). Understanding population change in migratory songbirds: long-term and experimental studies of Neotropical migrants in breeding and wintering areas. *Ibis*, *149*(suppl. 2), 2–13. https://doi.org/10.1111/j.1474-919X.2007.00685.x

Holmes, R. T., Sherry, T. W., & Reitsma, L. (1989). Population structure, territoriality and overwinter survival of two migrant warbler species in Jamaica. *The Condor*, *91*, 545–561. https://doi.org/10.2307/1368105

Horns, J. J., Buechley, E., Chynoweth, M., Aktay, L., Çoban, E., Kırpık, M. A., Herman, J. M., Şaşmaz, Y., & Şekercioğlu, Ç. H. (2016). Geolocator tracking of Great Reed-Warblers (*Acrocephalus arundinaceus*) identifies key regions for migratory wetland specialists in the Middle East and sub-Saharan East Africa. *The Condor*, *118*(4), 835–849. https://doi.org/10.1650/condor-16-63.1

Hötker, H. (2002). Arrival of Pied Avocets *Recurvirostra avosetta* at the breeding site: Effects of winter quarters and consequences for reproductive success. *Ardea*, *90*, 379–387.

Hulme, M., & Cresswell, W. (2012). Density and behaviour of Whinchats *Saxicola rubetra* on African farmland suggest that winter habitat conditions do not limit European breeding populations. *Ibis*, *154*(4), 680–692. https://doi.org/10.1111/j.1474-919X.2012.01258.x

Hutto, R. (1980). Winter habitat distribution of migratory land birds in western Mexico, with special reference to small, foliage-gleaning insectivores. In A. Keast & E. Morton (Eds.), *Migrant birds in the Neo-tropics: ecology, behavior, distribution, and conservation* (pp. 181–203). Smithsonian Institution Press.

IPCC. (2014). *Climate Change 2014: Synthesis Report. Contribution of working groups I, II and III to the Fifth Assessment Report of the Intergovernamental Panel on Climate Change*.

IPCC. (2021). *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (V. Masson-Delmotte, P. Zhai, A. Pirani, S. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. Matthews, T. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (eds.)). Cambridge University Press.

Ivande, S. T., & Cresswell, W. (2016). Temperate migrants and resident bird species in Afro-tropical savannahs show similar levels of ecological generalism. *Ibis*, *158*, 496–505. https://doi.org/10.1111/ibi.12371

Iwajomo, S. B., Ottosson, U., & Thorup, K. (2017). Spatial behaviour and food choice of the Garden Warbler *Sylvia borin* during the non-breeding season. *Ostrich*, *88*(1), 19–25. https://doi.org/10.2989/00306525.2016.1221477

Jacobsen, L. B., Jensen, N. O., Willemoes, M., Hansen, L., Desholm, M., Fox, A. D., Tøttrup, A. P., & Thorup, K. (2017). Annual spatiotemporal migration schedules in three larger insectivorous birds: European nightjar, common swift and common cuckoo. *Animal Biotelemetry*, *5*(4). https://doi.org/10.1186/s40317-017-0119-x

Jenni-Eiermann, S., Almasi, B., Maggini, I., Salewski, V., Bruderer, B., Liechti, F., & Jenni, L. (2011). Numbers, foraging and refuelling of passerine migrants at a stopover site in the western Sahara: diverse strategies to cross a desert. *Journal of Ornithology*, *152*(Suppl 1), S113–S128. https://doi.org/10.1007/s10336-010-0572-2

Johnston, A., Newson, S. E., Risely, K., Musgrove, A. J., Massimino, D., Baillie, S. R., & Pearce-Higgins, J. W. (2014). Species traits explain variation in detectability of UK birds. *Bird Study*, *61*(3), 340–350.

https://doi.org/10.1080/00063657.2014.941787

Johnston, A., Robinson, R. A., Gargallo, G., Julliard, R., Van Der Jeugd, H., & Baillie, S. R. (2016). Survival of Afro-Palaearctic passerine migrants in western Europe and the impacts of seasonal weather variables. *Ibis*, *158*(3), 465–480. https://doi.org/10.1111/ibi.12366

Jones, P. (1995). Migration strategies of palearctic passerines in Africa. *Israel Journal of Zoology*, *41*(3), 393–406. https://doi.org/10.1080/00212210.1995.10688809

Jones, P., Vickery, J. A., Holt, S., & Cresswell, W. (1996). A preliminary assessment of some factors influencing the density and distribution of palearctic passerine migrants wintering in the Sahel zone of West Africa. *Bird Study*, *43*(1), 73–84. https://doi.org/10.1080/00063659609460997

Julliard, R., Clavel, J., Devictor, V., Jiguet, F., & Couvet, D. (2006). Spatial segregation of specialists and generalists in bird communities. *Ecology Letters*, *9*(11), 1237–1244. https://doi.org/10.1111/j.1461-0248.2006.00977.x

Kamp, J., Frank, C., Trautmann, S., Busch, M., Dröschmeister, R., Flade, M., Gerlach, B., Karthäuser, J., Kunz, F., Mitschke, A., Schwarz, J., & Sudfeldt, C. (2021). Population trends of common breeding birds in Germany 1990–2018. *Journal of Ornithology*, *162*(1), 1–15. https://doi.org/10.1007/s10336-020-01830-4

Karlsson, H., Nilsson, C., Bäckman, J., & Alerstam, T. (2012). Nocturnal passerine migrants fly faster in spring than in autumn: a test of the time minimization hypothesis. *Animal Behaviour*, *83*(1), 87–93. https://doi.org/10.1016/j.anbehav.2011.10.009

Kassen, R. (2002). The experimental evolution of specialists, generalist, and the maintenance of diversity. *Journal of Evolutionary Biology*, *15*, 173–190. https://doi.org/10.1046/j.1420-9101.2002.00377.x

Kelsey, M. G. (1989). A comparison of the song and territorial behaviour of a long-distance migrant, the Marsh Warbler *Acrocephalus palustris*, in summer and winter. *Ibis*, *131*, 403–414.

Kelsey, M. G. (1992). Conservation of migrants on their wintering grounds: an overview. *Ibis*, *134*(suppl. 1), 109–112. https://doi.org/10.1111/j.1474-919X.1992.tb04740.x

Kenward, R. (2001). *A manual for wildlife radio tagging*. Academic Press.

King, J. M. B., & Hutchinson, J. M. C. (2001). Site fidelity and recurrence of some migrant bird species in The Gambia. *Ringing & Migration*, *20*(4), 292–302. https://doi.org/10.1080/03078698.2001.9674255

Kirby, J. S., Stattersfield, A. J., Butchart, S. H. M., Evans, M. I., Grimmett, R. F. A., Jones, V. R., O'Sullivan, J., Tucker, G. M., & Newton, I. (2008). Key conservation issues for migratory land- and waterbird species on the world's major flyways. *Bird Conservation International*, *18*, S49–S73. https://doi.org/10.1017/S0959270908000439

Kiss, C., Molnár, P., Karcza, Z., Lukács, K. O., Winkler, D., & Gyurácz, J. (2020). Study of apparent survival and capture probabilities of some passerines in Hungary. *North-Western Journal of Zoology*, *16*(1), 78–83.

Klaassen, M. (1996). Metabolic constraints on long-distance migration in birds. *Journal of Experimental Biology*, *199*(1), 57–64. https://doi.org/10.1242/jeb.199.1.57

Klaassen, R. H. G., Hake, M., Strandberg, R., Koks, B. J., Trierweiler, C., Exo, K. M., Bairlein, F., & Alerstam, T. (2014). When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology*, *83*(1), 176–184. https://doi.org/10.1111/1365-2656.12135

Klaassen, R. H. G., Strandberg, R., Hake, M., Olofsson, P., Tøttrup, A. P., & Alerstam, T. (2010). Loop migration in adult marsh harriers *Circus aeruginosus*, as revealed by satellite telemetry. *Journal of Avian Biology*, *41*(2), 200–207. https://doi.org/10.1111/j.1600-048X.2010.05058.x

Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology*, *68*, 940–950. https://doi.org/10.1046/j.1365-2656.1999.00343.x

Kokko, H., Gunnarsson, T. G., Morrell, L. J., & Gill, J. A. (2006). Why do female migratory birds arrive later than males? *Journal of Animal Ecology*, *75*(6), 1293–1303. https://doi.org/10.1111/j.1365-2656.2006.01151.x

Koleček, J., Procházka, P., El-Arabany, N., Tarka, M., Ilieva, M., Hahn, S., Honza, M., de la Puente, J., Bermejo, A., Gürsoy, A., Bensch, S., Zehtindjiev, P., Hasselquist, D., & Hansson, B. (2016). Cross-continental migratory connectivity and spatiotemporal migratory patterns in the great reed warbler. *Journal of Avian Biology*, *47*(6), 756–767. https://doi.org/10.1111/jav.00929

Koronkiewicz, T. J., Sogge, M. K., Van Riper, C., & Paxton, E. H. (2006). Territoriality, site fidelity, and survivorship of Willow flycatchers wintering in Costa Rica. *The Condor*, *108*, 558–570. https://doi.org/10.1650/0010-5422(2006)108[558:TSFASO]2.0.CO;2

Kristensen, M. W., Tøttrup, A. P., & Thorup, K. (2013). Migration of the Common Redstart (*Phoenicurus phoenicurus*): a Eurasian songbird wintering in highly seasonal conditions in the West African Sahel. *The Auk*, *130*(2), 258–264. https://doi.org/10.1525/auk.2013.13001

La Sorte, F. A., & Fink, D. (2017). Migration distance, ecological barriers and en-route variation in the migratory behaviour of terrestrial bird populations. *Global Ecology and Biogeography*, *26*, 216–227. https://doi.org/10.1111/geb.12534

Laaksonen, T., & Lehikoinen, A. (2013). Population trends in boreal birds: Continuing declines in agricultural, northern, and long-distance migrant species. *Biological Conservation*, *168*, 99–107. https://doi.org/10.1016/j.biocon.2013.09.007

Latta, S. C., & Faaborg, J. (2001). Winter site fidelity of Prairie warblers in the Dominican Republic. *The Condor*, *103*, 455–468. https://doi.org/10.1093/condor/103.3.455

Lebreton, J. D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, *62*(1), 67–118. https://doi.org/10.2307/2937171

Lemke, H. W., Tarka, M., Klaassen, R. H. G., Åkesson, M., Bensch, S., Hasselquist, D., & Hansson, B. (2013). Annual cycle and migration strategies of a Trans-Saharan migratory songbird: A geolocator study in the Great Reed Warbler. *PLoS ONE*, *8*(10), 1–10. https://doi.org/10.1371/journal.pone.0079209

Lemoine, N., & Böhning-Gaese, K. (2003). Potential impact of global climate change on species richness of long-distance migrants. *Conservation Biology*, *17*(2), 577–586. https://doi.org/10.1046/j.1523-1739.2003.01389.x

Lerche-Jørgensen, M., Mallord, J. W., Willemoes, M., Orsman, C. J., Roberts, J. T., Skeen, R. Q., Eskildsen, D. P., Salewski, V., Tøttrup, A. P., & Thorup, K. (2019). Spatial behavior and habitat use in widely separated breeding and wintering distributions across three species of long-distance migrant *Phylloscopus* warblers. *Ecology and Evolution*, *9*(11), 6492–6500. https://doi.org/10.1002/ece3.5226

Lerche-Jørgensen, M., Willemoes, M., Tøttrup, A. P., Snell, K. R. S., & Thorup, K. (2017). No apparent gain from continuing migration for more than 3000 kilometres: willow warblers breeding in Denmark winter across the entire northern Savannah as revealed by geolocators. *Movement Ecology*, *5*(17), 1–7. https://doi.org/10.1186/s40462-017-0109-x

Lettink, M., & Armstrong, D. P. (2003). Mark-recapture analysis for monitoring threatened species. *Department of Conservation Technical Series*, *28A*, 5–32, Department of Conservation, Wellington, New. http://canuck.dnr.cornell.edu/HyperNews/get/marked/marked.html

Liechti, F., Scandolara, C., Rubolini, D., Ambrosini, R., Korner-Nievergelt, F., Hahn, S., Lardelli, R., Romano, M., Caprioli, M., Romano, A., Sicurella, B., & Saino, N. (2015). Timing of migration and residence areas during the non-breeding period of barn swallows *Hirundo rustica* in relation to sex and population. *Journal of Avian Biology*, *46*(3), 254–265. https://doi.org/10.1111/jav.00485

Lind, J., & Cresswell, W. (2006). Anti-predation behaviour during bird migration; the benefit of studying multiple behavioural dimensions. *Journal of Field Ornithology*, *147*, 310–316. https://doi.org/10.1007/s10336-005-0051-3

Lisovski, S., & Hahn, S. (2012). GeoLight– processing and analysing light-based geolocator data in R. *Methods in Ecology and Evolution*, *3*(6), 1055–1059. https://doi.org/10.1111/j.2041-210X.2012.00248.x

Lisovski, S., Hewson, C. M., Klaassen, R. H. G., Korner-Nievergelt, F., Kristensen, M. W., & Hahn, S. (2012). Geolocation by light: accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution*, *3*, 603–612. https://doi.org/10.1111/j.2041-210X.2012.00185.x

Lok, T., Overdijk, O., & Piersma, T. (2015). The cost of migration: spoonbills suffer higher mortality during trans-Saharan spring migrations only. *Biology Letters*, *11*, 20140944. https://doi.org/http://dx.doi.org/10.1098/rsbl.2014.0944

López-Ornat, A., & Greenberg, R. (1990). Sexual segregation by habitat in migratory warblers in Quintana Roo, Mexico. *The Auk*, *107*(3), 539–543. https://doi.org/10.1093/auk/107.3.539

MacArthur, R. H., & MacArthur, A. T. (1974). On the use of mist nets for population studies of birds. *Proceedings of the National Academy of Sciences of the United States of America*, *71*(8), 3230–3233. https://doi.org/10.1073/pnas.71.8.3230

Maggini, I., & Bairlein, F. (2011). Body condition and stopover of trans-Saharan spring migrant passerines caught at a site in southern Morocco. *Ringing and Migration*, *26*(1), 31–37. https://doi.org/10.1080/03078698.2011.586591

Maggini, I., Cardinale, M., Favaretto, A., Voříšek, P., Spina, F., Maoret, F., Ferri, A., Riello, S., & Fusani, L. (2021). Comparing population trend estimates of migratory birds from breeding censuses and capture data at a spring migration bottleneck. *Ecology and Evolution*, *11*(2), 967–977. https://doi.org/10.1002/ece3.7110

Mallord, J. W., Orsman, C. J., Roberts, J. T., Skeen, R., Sheehan, D. K., & Vickery, J. A. (2016). Habitat use and tree selection of a declining Afro-Palaearctic migrant at sub-Saharan staging and wintering sites. *Bird Study*, *63*(4), 459–469. https://doi.org/10.1080/00063657.2016.1214813

Mallord, J. W., Smith, K. W., Bellamy, P. E., Charman, E. C., & Gregory, R. D. (2016). Are changes in breeding habitat responsible for recent population changes of long-distance migrant birds? *Bird Study*, *63*(2), 250–261. https://doi.org/10.1080/00063657.2016.1182467

Marques, T., Ramos Pereira, M. J., Marques, T. A., Santos, C. D., Santana, J., Beja, P., & Palmeirim, J. M. (2013). Optimizing sampling design to deal with mist-net avoidance in Amazonian birds and bats. *PLoS ONE*, *8*(9), e74505. https://doi.org/10.1371/journal.pone.0074505

Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E., & Tonra, C. M. (2015). A call for full annual cycle research in animal ecology. *Biology Letters*, *11*(20150552). https://doi.org/http://dx.doi.org/10.1098/rsbl.2015.0552

Marra, P. P., Hobson, K. A., & Holmes, R. T. (1998). Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science*, *282*(5395), 1884–1886. https://doi.org/10.1126/science.282.5395.1884

Marra, P. P., & Holmes, R. T. (2001). Consequences of dominance-mediated habitat segregation in American Redstarts during the Nonbreeding season. *The Auk*, *18*(1), 92–104. https://doi.org/10.1093/auk/118.1.92

Marra, P. P., Studds, C. E., Wilson, S., Scott Sillett, T., Sherry, T. W., & Holmes, R. T. (2015). Non-breeding season habitat quality mediates the strength of density-dependence for a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1811), 20150624. https://doi.org/10.1098/rspb.2015.0624

Marshall, M. R., Wilson, R. R., & Cooper, R. J. (2000). Estimating survival of Neotropical-Nearctic migratory birds: are they dead or just dispersed? *Proceedings of the 3rd Partners in Flight Workshop*, 195–199.

Martin, T. E., Clobert, J., & Anderson, D. R. (1995). Return rates in studies of life history evolution: Are biases large? *Journal of Applied Statistics*, *22*(5–6), 863–876. https://doi.org/10.1080/02664769524676

Martin, T. G., Chadès, I., Arcese, P., Marra, P. P., Possingham, H. P., & Norris, D. R. (2007). Optimal conservation of migratory species. *PLoS ONE*, *2*(8), 3–7. https://doi.org/10.1371/journal.pone.0000751

Mason, C. F. (1976). Breeding biology of the *Sylvia* warblers. *Bird Study*, *23*(3), 213–232. https://doi.org/10.1080/00063657609476506

Mason, C. F. (1995). Long-term trends in the arrival dates of spring migrants. *Bird Study*, *42*, 182–189. https://doi.org/10.1080/00063659509477167

Matantseva, M. V, & Simonov, S. A. (2012). Specific features of the territorial behavior of *Sylvia* warblers at the northern periphery of their ranges (southern Karelia). *Russian Journal of Ecology*, *43*(3), 225–230. https://doi.org/10.1134/S1067413612030095

Mayor, S. J., Guralnick, R. P., Tingley, M. W., Otegui, J., Withey, C., Elmendorf, S. C., Andrew, M. E., Leyk, S., Pearse, I. S., & Schneider, D. (2017). Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Scientific Reports*, *1*, 1902. https://doi.org/10.1038/s41598-017-02045-z

Mazerolle, D. F., & Hobson, K. A. (2004). Territory size and overlap in male Ovenbirds: contrasting a fragmented and contiguous boreal forest. *Canadian Journal of Zoology*, *82*(11), 1774–1781. https://doi.org/10.1139/z04-175

McCulloch, M. N., Tucker, G. M., & Baillie, S. R. (1992). The hunting of migratory birds in Europe: a ringing recovery analysis. *Ibis*, *134*(suppl. 1), 55–65. https://doi.org/10.1111/j.1474-919X.1992.tb04734.x

McKim-Louder, M. I., Hoover, J. P., Benson, T. J., & Schelsky, W. M. (2013). Juvenile survival in a Neotropical migratory songbird is lower than expected. *PLoS ONE*, *8*(2), e56059. https://doi.org/10.1371/journal.pone.0056059

McKinnon, E. A., Fraser, K. C., Stanley, C. Q., & Stutchbury, B. J. M. (2014). Tracking from the tropics reveals behaviour of juvenile songbirds on their first spring migration. *PLoS ONE*, *9*(8), e105605. https://doi.org/10.1371/journal.pone.0105605

McKinnon, E. A., Fraser, K. C., & Stutchbury, B. J. M. (2013). New discoveries in landbird migration using geolocators, and a flight plan for the future. *The Auk*, *130*(2), 211–222. https://doi.org/10.1525/auk.2013.12226

McKinnon, E. A., & Love, O. P. (2018). Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging. *The Auk*, *135*(4), 834–856. https://doi.org/10.1642/auk-17-202.1

McKinnon, E. A., Stanley, C. Q., Fraser, K. C., MacPherson, M. M., Casbourn, G., Marra, P. P., Studds, C. E., Diggs, N., & Stutchbury, B. J. M. (2013). Estimating geolocator accuracy for a migratory songbird using live ground-truthing in tropical forest. *Animal Migration*, *1*, 31–38. https://doi.org/10.2478/ami-2013-0001

McNamara, J. M., Welham, R. K., & Houston, A. I. (1998). The timing of migration within the context of an annual routine. *Journal of Avian Biology*, *29*(4), 416–423. https://doi.org/10.2307/3677160

Meichtry-Stier, K. S., Korner-Nievergelt, F., Kormann, U., Spiess, M., Mosimann-Kampe, P., Strebel, S., Zollinger, J.-L., & Spaar, R. (2013). Habitat selection of the Common Whitethroat *Sylvia communis* in the western part of Switzerland: implications for species conservation. *Der Ornithologische Beobachter*, *110*, 1–15.

Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aaasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F. M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., … Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, *12*(10), 1969–1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x

Møller, A. P., Rubolini, D., & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(42), 16195–16200. https://doi.org/10.1073/pnas.0803825105

Mönkkönen, M. (1992). Life history traits of Palaearctic and Nearctic migrant passerines. *Ornis Fennica*, *69*(4), 161–172.

Moreau, R. (1952). The place of Africa in the Palaearctic migration system. *Journal of Animal Ecology*, *21*(2), 250–271. https://doi.org/10.2307/1961

Moreau, R. (1969). The recurrence in winter quarters (Ortstreue) of trans-Saharan migrants. *Bird Study*, *16*(2), 108–110. https://doi.org/10.1080/00063656909476227

Moreau, R. (1972). *The Palaearctic-African bird migration systems*. Academic Press.

Morel, G. (1973). The Sahel zone as an environment for Palearctic migrants. *Ibis*, *115*, 413–417. https://doi.org/10.1111/j.1474-919X.1973.tb01979.x

Morel, G., & Morel, M. Y. (1992). Habitat use by Palaearctic migrant passerine birds in West Africa. *Ibis*, *134*(suppl. 1), 83–88. https://doi.org/10.1111/j.1474-919X.1992.tb04737.x

Morrison, C. A., Robinson, R. A., Clark, J. A., Risely, K., & Gill, J. A. (2013). Recent population declines in Afro-Palaearctic migratory birds: The influence of breeding and non-breeding seasons. *Diversity and Distributions*, *19*(8), 1051–1058. https://doi.org/10.1111/ddi.12084

Newton, I. (1995). Relationship between breeding and wintering ranges in Palaearctic-African migrants. *Ibis*, *137*(2), 241–249. https://doi.org/https://doi.org/10.1111/j.1474-919X.1995.tb03246.x

Newton, I. (2004). Population limitation in migrants. *Ibis*, *146*(2), 197–226. https://doi.org/10.1111/j.1474-919X.2004.00293.x

Newton, I. (2008). *The migration ecology of birds*. Academic Press.

Newton, I. (2010). *Bird Migration*. HarperCollins Publisher.

Nolan, V., & Ketterson, E. D. (1990). Timing of autumn migration and its relation to winter distribution in Dark-Eyed Juncos. *Ecology*, *71*(4), 1267–1278. https://doi.org/10.2307/1938264

Norris, D. R., Marra, P. P., Kyser, T. K., Sherry, T. W., & Ratcliffe, L. M. (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1534), 59–64. https://doi.org/10.1098/rspb.2003.2569

Nwaogu, C. J., & Cresswell, W. (2016). Body reserves in intra-African migrants. *Journal of Ornithology*, *157*(1), 125–135. https://doi.org/10.1007/s10336-015-1259-5

Ockendon, N., Hewson, C. M., Johnston, A., & Atkinson, P. W. (2012). Declines in British-breeding populations of Afro-Palaearctic migrant birds are linked to bioclimatic wintering zone in Africa, possibly via constraints on arrival time advancement. *Bird Study*, *59*(2), 111–125. https://doi.org/10.1080/00063657.2011.645798

Ockendon, N., Johnston, A., & Baillie, S. R. (2014). Rainfall on wintering grounds affects population change in many species of Afro-Palaearctic migrants. *Journal of Ornithology*, *155*, 905–917. https://doi.org/10.1007/s10336-014-1073-5

Ockendon, N., Leech, D., & Pearce-Higgins, J. W. (2013). Climatic effects on breeding grounds are more important drivers of breeding phenology in migrant birds than carryover effects from wintering grounds. *Biology Letters*, *9*(6). https://doi.org/10.1098/rsbl.2013.0669

Ottosson, U., Bairlein, F., & Hjort, C. (2002). Migration patterns of Palaearctic *Acrocephalus* and *Sylvia* warblers in north-eastern Nigeria. *Die Vogelwarte*, *41*(4), 249–262.

Ottosson, U., Barshep, Y., Boyi, M. G., Hulme, M., Waldenström, J., & Ottvall, R. (n.d.). *The ecology of the Whitethroat* Sylvia communis *at Jos Plateau, Nigeria during the non-breeding season*.

Ottosson, U., Rumsey, S., & Hjort, C. (2001). Migration of four *Sylvia* warblers through northern Senegal. *Ringing* *and Migration*, *20*(4), 344–351. https://doi.org/10.1080/03078698.2001.9674261

Ottosson, U., Waldenström, J., Hjort, C., & McGregor, R. (2005). Garden Warbler *Sylvia borin* migration in sub-Saharan West Africa: phenology and body mass changes. *Ibis*, *147*(4), 750–757. https://doi.org/10.1111/j.1474-919X.2005.00460.x

Ouwehand, J., Ahola, M. P., Ausems, A. N. M. A., Bridge, E. S., Burgess, M., Hahn, S., Hewson, C. M., Klaassen, R. H. G., Laaksonen, T., Lampe, H. M., Velmala, W., & Both, C. (2016). Light-level geolocators reveal migratory connectivity in European populations of pied flycatchers *Ficedula hypoleuca*. *Journal of Avian Biology*, *47*(1), 69–83. https://doi.org/10.1111/jav.00721

Ouwehand, J., & Both, C. (2017). African departure rather than migration speed determines variation in spring arrival in pied flycatchers. *Journal of Animal Ecology*, *86*, 88–97. https://doi.org/10.1111/1365-2656.12599

Paxton, E. H., Durst, S. L., Sogge, M. K., Koronkiewicz, T. J., & Paxton, K. L. (2017). Survivorship across the annual cycle of a migratory passerine, the willow flycatcher. *Journal of Avian Biology*, *48*, 1126–1131. https://doi.org/10.1111/jav.01371

Peach, W. J., Baillie, S. R., & Underhill, L. (1991). Survival of British Sedge Warblers *Acrocephalus schoenobaenus* in relation to west African rainfall. *Ibis*, *133*(3), 300–305. https://doi.org/https://doi.org/10.1111/j.1474-919X.1991.tb04573.x

Peach, W. J., Hanmer, D., & Oatley, T. (2001). Do southern African songbirds live longer than their European counterparts? *Oikos*, *93*, 235–249. https://doi.org/https://www.jstor.org/stable/3547302

Pearson, D. J., & Lack, P. C. (1992). Migration patterns and habitat use by passerine and near-passerine migrant birds in eastern Africa. *Ibis*, *134*(Suppl 1), 89–98. https://doi.org/10.1111/j.1474-919X.1992.tb04738.x

Pérez-Tris, J., & Tellería, J. L. (2002). Migratory and sedentary Blackcaps in sympatric non-breeding grounds: Implications for the evolution of avian migration. *Journal of Animal Ecology*, *71*(2), 211–224. https://doi.org/10.1046/j.1365-2656.2002.00590.x

Persson, B. (1971). Habitat selection and nesting of a south Swedish Whitethroat *Sylvia communis* Lath. Population. *Ornis Scandinavica (Scandinavian Journal of Ornithology)*, *2*(2), 119–126.

Piersma, T., & Van de Sant, S. (1992). Pattern and predictability of potential wind assistance for waders and geese migrating from West Africa and the Wadden Sea to Siberia. *Ornis Svecica*, *2*(2), 55–66. https://doi.org/10.34080/os.v2.21614

Piper, W. H. (2011). Making habitat selection more “familiar”: a review. *Behavioral Ecology*, *65*, 1329–1351. https://doi.org/10.1007/s00265-011-1195-1

Pradel, R., Hines, J. E., Lebreton, J., & Nichols, J. D. (1997). Capture-recapture survival models taking account of transients. *Biometrics*, *53*(1), 60–72. https://doi.org/10.2307/2533097

Pulido, F. (2007). Phenotypic changes in spring arrival: evolution, phenotypic plasticity, effects of weather and condition. *Climate Research*, *35*(1), 5–23. https://doi.org/10.3354/cr00711

R Core Team. (2020). *R: A language and environment for statistical computing.* (3.6.3). R Foundation for Statistical Computing. https://www.r-project.org/

Rappole, J. H., & Jones, P. (2002). Evolution of old and new world migration systems. *Ardea*, *90*(3), 525–538.

Rappole, J. H., & Tipton, A. R. (1991). New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology*, *62*(3), 335–337. https://doi.org/https://sora.unm.edu/node/51662

Redfern, C., & Clark, J. A. (2001). *Ringer’s Manual*. British Trust for Ornithology (BTO).

Remsen, J. V, & Good, D. A. (1996). Misuse of data from mist-net captures to assess relative abundance in bird populations. *The Auk*, *113*(2), 381–398. https://doi.org/10.2307/4088905

Richardson, W. J. (1990). Timing of bird migration in relation to weather: updated review. In E. Gwinner (Ed.), *Bird Migration*. Springer Berlin Heidelberg.

Ringnér, M. (2008). What is principal component analysis? *Nature Biotechnology*, *26*(3), 303–304. https://doi.org/10.1038/nbt0308-303

Risely, A., Blackburn, E., & Cresswell, W. (2015). Patterns in departure phenology and mass gain on African non-breeding territories prior to the Sahara crossing in a long-distance migrant. *Ibis*, *157*(4), 808–822. https://doi.org/10.1111/ibi.12288

Robinson, R. A., Balmer, D. E., & Marchant, J. H. (2008). Survival rates of hirundines in relation to British and African rainfall. *Ringing & Migration*, *24*, 1–6. https://doi.org/10.1080/03078698.2008.9674375

Rockwell, S. M., Wunderle, J. M., Sillett, T. S., Bocetti, C. I., Ewert, D. N., Currie, D., White, J. D., & Marra, P. P. (2017). Seasonal survival estimation for a long-distance migratory bird and the influence of winter precipitation. *Oecologia*, *183*(3), 715–726. https://doi.org/10.1007/s00442-016-3788-x

Rolando, A. (2002). On the ecology of home range in birds. *Revue d'Ecologie (La Terre et La Vie)*, *57*, 53–73.

Röseler, D., Schmaljohann, H., & Bairlein, F. (2017). Timing of migration, routes and wintering grounds of a short-distance diurnal migrant revealed by geolocation: a case study of Linnets *Carduelis cannabina*. *Journal of Ornithology*, *158*(3), 875–880. https://doi.org/10.1007/s10336-017-1450-y

Rotics, S., Turjeman, S., Kaatz, M., Resheff, Y. S., Zurell, D., Sapir, N., Eggers, U., Fiedler, W., Flack, A., Jeltsch, F., Wikelski, M., & Nathan, R. (2017). Wintering in Europe instead of Africa enhances juvenile survival in a long-distance migrant. *Animal Behaviour*, *126*, 79–88. https://doi.org/10.1016/j.anbehav.2017.01.016

Ruiz-Gutierrez, V., Kendall, W. L., Saracco, J. F., & White, G. C. (2016). Overwintering strategies of migratory birds: a novel approach for estimating seasonal movement patterns of residents and transients. *Journal of Applied Ecology*, *53*, 1035–1045. https://doi.org/10.1111/1365-2664.12655

Safriel, U. N. (1995). The evolution of Palearctic migration – the case for southern ancestry. *Israel Journal of Zoology*, *41*(3), 417–431. https://doi.org/10.1080/00212210.1995.10688811

Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Hüppop, K., Hüppop, O., Lehikoinen, A., Lehikoinen, E., Rainio, K., Romano, M., & Sokolov, L. (2010). Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1707). https://doi.org/10.1098/rspb.2010.1778

Salewski, V., Almasi, B., Heuman, A., Thoma, M., & Schlageter, A. (2007). Agonistic behaviour of Palaearctic passerine migrants at a stopover site suggests interference competition. *Ostrich*, *78*(2), 349–355. https://doi.org/10.2989/OSTRICH.2007.78.2.37.117

Salewski, V., Altwegg, R., Erni, B., Falk, K., Bairlein, F., & Leisler, B. (2004). Moult of three Palaearctic migrants in their West African winter quarters. *Journal of Ornithology*, *145*, 109–116. https://doi.org/10.1007/s10336-004-0020-2

Salewski, V., Bairlein, F., & Leisler, B. (2000). Recurrence of some palaearctic migrant passerine species in West Africa. *Ringing & Migration*, *20*(1), 29–30. https://doi.org/10.1080/03078698.2000.9674224

Salewski, V., Bairlein, F., & Leisler, B. (2002). Different wintering strategies of two Palearctic migrants in West Africa - a consequence of foraging strategies? *Ibis*, *144*, 85–93. https://doi.org/10.1046/j.0019-1019.2001.00007.x

Salewski, V., & Bruderer, B. (2007). The evolution of bird migration — a synthesis. *Naturwissenschaften*, *94*, 268–279. https://doi.org/10.1007/s00114-006-0186-y

Salewski, V., & Jones, P. (2006). Palearctic passerines in Afrotropical environments: a review. *Journal of Ornithology*, *147*, 192–201. https://doi.org/10.1007/s10336-006-0057-5

Salewski, V., Schmaljohann, H., & Liechti, F. (2010). Spring passerine migrants stopping over in the Sahara are not fall-outs. *Journal of Ornithology*, *151*(2), 371–378. https://doi.org/10.1007/s10336-009-0464-5

Sandercock, B. K., & Jaramillo, A. (2002). Annual survival rates of wintering sparrows: Assessing demographic consequences of migration. *The Auk*, *119*(1), 149–165. https://doi.org/10.1093/auk/119.1.149

Sanderson, F. J., Donald, P. F., Pain, D. J., Burfield, I. J., & van Bommel, F. P. J. (2006). Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation*, *131*(1), 93–105. https://doi.org/10.1016/j.biocon.2006.02.008

Schaub, M., & Jenni, L. (2000). Body mass of six long-distance migrant passerine species along the autumn migration route. *Journal of Ornithology*, *141*, 441–460. https://doi.org/10.1007/BF01651574

Schaub, M., & Royle, J. A. (2014). Estimating true instead of apparent survival using spatial Cormack–Jolly–Seber models. *Methods in Ecology and Evolution*, *5*(12), 1316–1326. https://doi.org/10.1111/2041-210X.12134

Schaub, M., & Von Hirschheydt, J. (2009). Effect of current reproduction on apparent survival, breeding dispersal, and future reproduction in barn swallows assessed by multistate capture–recapture models. *Journal of Animal Ecology*, *78*, 625–635. https://doi.org/10.1111/j.1365-2656.2008.01508.x

Schmaljohann, H., Buchmann, M., Fox, J. W., & Bairlein, F. (2012). Tracking migration routes and the annual cycle of a trans-Sahara songbird migrant. *Behavioral Ecology and Sociobiology*, *66*, 915–922. https://doi.org/10.1007/s00265-012-1340-5

Schmaljohann, H., Liechti, F., & Bruderer, B. (2007). Songbird migration across the Sahara: the non-stop hypothesis rejected! *Proceedings of the Royal Society B: Biological Sciences*, *274*, 735–739. https://doi.org/10.1098/rspb.2006.0011

Schmaljohann, H., Müller, F., Klinner, T., & Eikenaar, C. (2018). Potential age differences in the migratory behaviour of a nocturnal songbird migrant during autumn and spring. *Journal of Avian Biology*, *49*(7), 1–16. https://doi.org/10.1111/jav.01815

Seavy, N. E., Humple, D. L., Cormier, R. L., & Gardali, T. (2012). Establishing the breeding provenance of a temperate-wintering North American passerine, the golden-crowned sparrow, using light-level geolocation. *PLoS ONE*, *7*(4), 4–9. https://doi.org/10.1371/journal.pone.0034886

Seber, G. (1982). *The estimation of animal abundance and related parameters* (2 edition). Macmillan.

Senar, J. C., & Borras, A. (2004). Sobrevivir al invierno: estrategias de las aves invernantes en la Península Ibérica [Surviving to winter: strategies of wintering birds in the Iberian Peninsula]. *Ardeola*, *51*(1), 133–168.

Sergio, F., Tavecchia, G., Tanferna, A., Blas, J., Blanco, G., & Hiraldo, F. (2019). When and where mortality occurs throughout the annual cycle changes with age in a migratory bird: individual vs population implications. *Scientific Reports*, *9*(17352), 1–8. https://doi.org/10.1038/s41598-019-54026-z

Sheehan, D. K., & Sanderson, F. J. (2012). Seeing the bigger picture: how anthropogenic landscape modification in Africa affects declining migratory birds and the need for trans-continental research and conservation. *Ibis*, *154*, 659–662. https://doi.org/10.1111/j.1474-919X.2012.01275.x

Sherry, T. W., & Holmes, R. T. (1996). Winter habitat quality, population imitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology*, *77*(1), 36–48. https://doi.org/10.2307/2265652

Shirihai, H., Gargallo, G., & Helbig, A. J. (2001). *Sylvia warblers* (G. M. Kirwan & L. Svensoon (eds.)). Princeton University Press.

Shitikov, D. A., Morozova, M. M., Yurchenko, Y. A., & Anna, D. (2013). Apparent survival rates of two *Sylvia* warbler species in northwestern Russia. *Ringing & Migration*, *28*(1), 16–20. https://doi.org/10.1080/03078698.2013.810858

Sillett, T. S., & Holmes, R. T. (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology*, *71*(2), 296–308. https://doi.org/10.1046/j.1365-2656.2002.00599.x

Siriwardena, G. M., Baillie, S. R., & Wilson, J. D. (1998). Variation in the survival rates of some British passerines with respect to their population trends on farmland. *Bird Study*, *45*(3), 276–292. https://doi.org/10.1080/00063659809461099

Sliwinski, M., Powell, L., Koper, N., Giovanni, M., & Schacht, W. (2016). Research design considerations to ensure detection of all species in an avian community. *Methods in Ecology and Evolution*, *7*, 456–462. https://doi.org/10.1111/2041-210X.12506

Somershoe, S. G., Brown, C. R. D., & Poole, R. T. (2009). Winter site fidelity and over-winter site persistence of passerines in Florida. *The Wilson Journal of Ornithology*, *121*(1), 119–125. https://doi.org/10.1676/07-142.1

Soykan, C. U., Sauer, J., Schuetz, J. G., LeBaron, G. S., Dale, K., & Langham, G. M. (2016). Population trends for North American winter birds based on hierarchical models. *Ecosphere*, *7*(5), 1–16. https://doi.org/10.1002/ecs2.1351

Stach, R., Jakobsson, S., Kullberg, C., & Fransson, T. (2012). Geolocators reveal three consecutive wintering areas in the thrush nightingale. *Animal Migration*, *1*, 1–7. https://doi.org/10.2478/ami-2012-0001

Stach, R., Kullberg, C., Jakobsson, S., Ström, K., & Fransson, T. (2016). Migration routes and timing in a bird wintering in South Asia, the Common Rosefinch *Carpodacus erythrinus*. *Journal of Ornithology*, *157*(3), 671–679. https://doi.org/10.1007/s10336-016-1329-3

Stanley, C. Q., MacPherson, M., Fraser, K. C., McKinnon, E. A., & Stutchbury, B. J. M. (2012). Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. *PLoS ONE*, *7*(7), 5–10. https://doi.org/10.1371/journal.pone.0040688

Stoate, C., & Moreby, S. J. (1995). Premigratory diet of trans-Saharan migrant passerines in the western Sahel. *Bird Study*, *42*(2), 101–106. https://doi.org/10.1080/00063659509477156

Stoate, C., Morris, R. M., & Wilson, J. D. (2001). Cultural ecology of Whitethroat (*Sylvia communis*) habitat management by farmers: winter in farmland trees and shrubs in Senegambia. *Journal of Environmental Management*, *62*, 343–356. https://doi.org/10.1006/jema.2001.0457

Stoate, C., & Szczur, J. (2001). Whitethroat *Sylvia communis* and Yellowhammer *Emberiza citrinella* nesting success and breeding distribution in relation to field boundary vegetation. *Bird Study*, *48*(2), 229–235. https://doi.org/10.1080/00063650109461222

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *8*(11), 1639–1644. https://doi.org/10.1111/2041-210X.12797

Strandberg, R., Klaassen, R. H. G., Hake, M., & Alerstam, T. (2010). How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors. *Biology Letters*, *6*(3), 297–300. https://doi.org/doi:10.1098/rsbl.2009.0785

Stutchbury, B. J. M., Siddiqui, R., Applegate, K., Hvenegaard, G. T., Mammenga, P., Mickle, N., Pearman, M., Ray, J. D., Savage, A., Shaheen, T., & Fraser, K. C. (2016). Ecological causes and consequences of Intratropical migration in temperate-breeding migratory birds. *The American Naturalist*, *188*(suppl. 1), S28–S40. https://doi.org/10.1086/687531

Stutchbury, B. J. M., Tarof, S. A., Done, T., Gow, E., Kramer, P. M., Tautin, J., Fox, J. W., & Afanasyev, V. (2009). Tracking long-distance songbird migration by using geolocators. *Science*, *323*(5916), 896. https://doi.org/10.1126/science.1166664

Svensson, L. (1992). *Identification guide to European Passerines* (4 edition).

Szép, Ti. (1995). Relationship between west African rainfall and the survival of central European Sand Martins *Riparia riparia*. *Ibis*, *137*(2), 162–168. https://doi.org/10.1111/j.1474-919X.1995.tb03235.x

Szymański, P., & Antczak, M. (2013). Structural heterogeneity of linear habitats positively affects Barred Warbler *Sylvia nisoria*, Common Whitethroat *Sylvia communis* and Lesser Whitethroat *Sylvia curruca* in farmland of Western Poland. *Bird Study*, *60*(4), 484–490. https://doi.org/10.1080/00063657.2013.840555

Thaxter, C. B., Joys, A. C., Gregory, R. D., Baillie, S. R., & Noble, D. G. (2010). Hypotheses to explain patterns of population change among breeding bird species in England. *Biological Conservation*, *143*(9), 2006–2019. https://doi.org/10.1016/j.biocon.2010.05.004

Thorup, K., Alerstam, T., Hake, M., & Kjellén, N. (2003). Bird orientation: compensation for wind drift in migrating raptors is age dependent. *Proceedings of the Royal Society B: Biological Sciences*, *270*(suppl. 1), 8–11. https://doi.org/10.1098/rsbl.2003.0014

Thorup, K., Sørensen, I. H., Willemoes, M., Lerche-Jørgensen, M., Fjeldså, J., Tøttrup, A. P., Jacobsen, E. M., Reeve, A. H., Oteng-Appau, R., Asamoah, A., & Lehmberg, T. (2019). Winter site use by Afro-Palearctic migrants in Ghana: site persistence and densities of Willow Warbler, Pied Flycatcher, Melodious Warbler and Common Redstart. *Ostrich*, *90*(2), 173–177. https://doi.org/10.2989/00306525.2019.1616229

Tøttrup, A. P., Klaassen, R. H. G., Strandberg, R., Thorup, K., Kristensen, M. W., Jorgensen, P. S., Fox, J., Afanasyev, V., Rahbek, C., & Alerstam, T. (2012). The annual cycle of a trans-equatorial Eurasian-African passerine migrant: Different spatio-temporal strategies for autumn and spring migration. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 1008–1016. https://doi.org/10.1098/rspb.2011.1323

Tøttrup, A. P., Thorup, K., Rainio, K., Yosef, R., Lehikoinen, E., & Rahbek, C. (2008). Avian migrants adjust migration in response to environmental conditions *en route*. *Biology Letters*, *4*, 685–688. https://doi.org/10.1098/rsbl.2008.0290

Tsiakiris, R., Stara, K., Pantis, J., & Sgardelis, S. (2009). Microhabitat selection by three common bird species of montane farmlands in northern Greece. *Environmental Management*, *44*, 874–887. https://doi.org/10.1007/s00267-009-9359-8

Urban, E., Fry, C., & Keith, S. (1997). *The Birds of Africa, Volume V*. San Diego: Academic Press.

van Wijk, R. E., Souchay, G., Jenni-Eiermann, S., Bauer, S., & Schaub, M. (2016). No detectable effects of lightweight geolocators on a Palaearctic-African long-distance migrant. *Journal of Ornithology*, *157*(1), 255–264. https://doi.org/10.1007/s10336-015-1274-6

Venables, W. N., & Ripley, B. D. (2002). *Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0*.

Vickery, J. A., Bradbury, R. B., Henderson, I. G., Eaton, M. A., & Grice, P. V. (2004). The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. *Biological Conservation*, *119*(1), 19–39. https://doi.org/10.1016/j.biocon.2003.06.004

Vickery, J. A., Ewing, S. R., Smith, K. W., Pain, D. J., Bairlein, F., Škorpilová, J., & Gregory, R. D. (2014). The decline of Afro-Palaearctic migrants and an assessment of potential causes. *Ibis*, *156*(1), 1–22. https://doi.org/10.1111/ibi.12118

Vickery, J. A., Rowcliffe, M., Cresswell, W., Jones, P., & Holt, S. (1999). Habitat selection by Whitethroats *Sylvia communis* during spring passage in the sahel zone of northern Nigeria. *Bird Study*, *46*(3), 348–355. https://doi.org/10.1080/00063659909461149

Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 2561–2569.

https://doi.org/10.1098/rspb.2005.3356

Visser, M. E., Holleman, L. J. M., & Gienapp, P. (2006). Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia*, *147*(1), 164–172. https://doi.org/10.1007/s00442-005-0299-6

Waldenström, J., & Ottosson, U. (2000). The accuracy of field sex determination in the Common Whitethroat *Sylvia c. communis*. *Ornis Svecica*, *10*, 67–70. https://doi.org/10.34080/os.v10.20574

Waldenström, J., & Ottosson, U. (2002). Moult strategies in the Common Whitethroat *Sylvia c. communis* in northern Nigeria. *Ibis*, *144*, E11–E18. https://doi.org/10.1046/j.0019-1019.2001.00030.x

Walther, B. A. (2016). A review of recent ecological changes in the Sahel, with particular reference to land-use change, plants, birds and mammals. *African Journal of Ecology*, *54*(3), 268–280. https://doi.org/10.1111/aje.12350

Walther, B. A., & Pirsig, L. H. (2017). Determining conservation priority areas for Palearctic passerine migrant birds in sub-Saharan Africa. *Avian Conservation and Ecology*, *12*(1), 2. https://doi.org/10.5751/ace-00934-120102

Walther, B. A., & Rahbek, C. (2002). Where do palearctics overwinter in Africa? *Dansk Ornitologisk Forenings Tidsskrift*, *96*, 4–8.

Walther, B. A., Van Niekerk, A., Thuiller, W., Baumann, S., Dean, W. R. J., de Bruijn, B., Gutteridge, K., Jones, P., Nikolaus, G., Pearson, D. J., Robinson, S. P., Salewski, V., Schäffer, N., Taylor, P. B., Tushabe, H., Williams, P. H., & Rahbek, C. (2010). A database of Western Palearctic birds migrating within Africa to guide conservation decisions. In D. Harebottle, A. Craig, M. Anderson, H. Rakotomanana, & M. Muchai (Eds.), *Proceedings of the 12th Pan-African Ornithological Congress, 2008* (pp. 50–104). Cape Town, Animal Demography Unit.

Wangai, P., Burkhard, B., & Müller, F. (2016). A review of studies on ecosystem services in Africa. *International Journal of Sustainable Built Environment*, *5*, 225–245.

Warkentin, I. G., & Hernández, D. (1996). The conservation implications of site fidelity: A case study involving Nearctic-Neotropical migrant songbirds wintering in a Costa Rican mangrove. *Biological Conservation*, *3207*(95), 143–150. https://doi.org/10.1080/00222216.1999.11949868

Webster, M. S., & Marra, P. P. (2005). The importance of understanding migratory connectivity and seasonal interactions. In R. Greenberg & P. P. Marra (Eds.), *Birds of Two Worlds: The Ecology and Evolution of Migration* (pp. 199–209). Johns Hopkins University Press.

Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S., & Holmes, R. T. (2002). Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution*, *17*(2), 76–83. https://doi.org/10.1016/S0169-5347(01)02380-1

White, G. C., & Burnham, K. P. (2009). Program MARK: survival estimation from populations of marked animals. *Bird Study*, *46*(sup1), S120–S139. https://doi.org/10.1080/00063659909477239

White, G. C., & Garrott, R. (1990). *Analysis of wildlife radio-tracking data*. Academic Press.

Wilcove, D. S., & Wikelski, M. (2008). Going, going, gone: Is animal migration disappearing? *PLoS Biology*, *6*(7), 1361–1364. https://doi.org/10.1371/journal.pbio.0060188

Willemoes, M., Strandberg, R., Klaassen, R. H. G., Tøttrup, A. P., Vardanis, Y., Howey, P. W., Thorup, K., Wikelski, M., & Alerstam, T. (2014). Narrow-front loop migration in a population of the common cuckoo *Cuculus canorus*, as revealed by satellite telemetry. *PLoS ONE*, *9*(1), e83515. https://doi.org/10.1371/journal.pone.0083515

Willemoes, M., Tøttrup, A. P., Lerche-Jørgensen, M., Jacobsen, E. M., Reeve, A. H., & Thorup, K. (2017). Spatial behaviour and density of three species of long-distance migrants wintering in a disturbed and non-disturbed woodland in northern Ghana. *Bird Conservation International*, 1–14. https://doi.org/10.1017/S0959270917000132

Williams, H. M., Willemoes, M., Klaassen, R. H. G., Strandberg, R., & Thorup, K. (2016). Common Cuckoo home ranges are larger in the breeding season than in the non-breeding season and in regions of sparse forest cover. *Journal of Ornithology*, *157*(2), 461–469. https://doi.org/10.1007/s10336-015-1308-0

Wilson, J. M., & Cresswell, W. (2006). How robust are Palearctic migrants to habitat loss and degradation in the Sahel? *Ibis*, *148*, 789–800. https://doi.org/10.1111/j.1474-919X.2006.00581.x

Wilson, J. M., & Cresswell, W. (2010). Densities of Palearctic warblers and Afrotropical species within the same guild in Sahelian West Africa. *Ostrich*, *81*(3), 225–232. https://doi.org/10.2989/00306525.2010.519899

Winkler, H., & Leisler, B. (1992). On the ecomorphology of migrants. *Ibis*, *134*(suppl. 1), 21–28. https://doi.org/10.1111/j.1474-919X.1992.tb04729.x

Winstanley, D., Spencer, R., & Williamson, K. (1974). Where have all the whitethroats gone? *Bird Study*, *21*(1), 1–14. https://doi.org/10.1080/00063657409476397

Woodward, I., Massimino, D., Hammond, M., Barber, L., Barimore, C., Harris, S., Leech, D. I., Noble, D. G., Walker, R. H., Baillie, S. R., & Robinson, R. A. (2020). *BirdTrends 2020: trends in numbers, breeding success and survival for UK breeding birds*. Research Report 732. BTO, Thetford.

Wunderle, J. M., & Latta, S. C. (2000). Winter site fidelity of Nearctic migrants in shade coffee plantations of different sizes in the Dominican Republic. *The Auk*, *117*(3), 596–614. https://doi.org/10.1093/auk/117.3.596

Xenophontos, M., Blackburn, E., & Cresswell, W. (2017). Cyprus wheatears *Oenanthe cypriaca* likely reach sub-Saharan African wintering grounds in a single migratory flight. *Journal of Avian Biology*, *48*, 529–535. https://doi.org/10.1111/jav.01119

Xenophontos, M., & Cresswell, W. (2016). Survival and dispersal of the Cyprus wheatear *Oenanthe cypriaca*, an endemic migrant. *Journal of Ornithology*, *157*(3), 707–719. https://doi.org/10.1007/s10336-015-1315-1

Yohannes, E., Biebach, H., Nikolaus, G., & Pearson, D. J. (2009). Migration speeds among eleven species of long-distance migrating passerines across Europe, the desert and eastern Africa. *Journal of Avian Biology*, *40*(2), 126–134. https://doi.org/10.1111/j.1600-048X.2008.04403.x

Zabel, C. J., Mckelvey, K., & Ward, J. P. (1995). Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (*Strix occidentalis caurina*). *Canadian Journal of Zoology*, *73*, 433–439.

Zúñiga, D., Gager, Y., Kokko, H., Fudickar, A. M., Schmidt, A., Naef-Daenzer, B., Wikelski, M., & Partecke, J. (2017). Migration confers winter survival benefits in a partially migratory songbird. *ELife*, *6*(e28123), 1–12. https://doi.org/10.7554/eLife.28123

Zwarts, L., & Bijlsma, R. G. (2015). Detection probabilities and absolute densities of birds in trees. *Ardea*, *103*, 99–122. https://doi.org/10.5253/arde.v103i2.a1

Zwarts, L., Bijlsma, R. G., van der Kamp, J., & Wymenga, E. (2009). *Living on the edge: wetland and birds in a changing Sahel*. KNNV Publishing.

Appendix 1. Home Office Reports.

Home office reports stating all ethical concerns. The first report was submitted on 25/09/2019, and an updated report was submitted on 20/10/2020.

University of St Andrews

NON-LICENCE REVIEW FORM

Date: 25/09/19

Title of Project: The non-breeding ecology of the Common Whitethroat in central Nigeria

Supervisor: Prof. Will Cresswell

PLEASE SEE APPENDED MORE DETAILED TECHNICAL REPORT FOR A FULLER EVALUATION, ALTHOUGH THIS IS WORK IN PROGESS.

1. For the programme of work you have carried out;

a. Is the work now complete?

No the work is ongoing.

We can evaluate the effects of mist-netting and colour-ringing: nothing to report with respect to any observable harm, and nothing occurred that was different from standard mist-netting and colour-ringing carried out elsewhere.

We can evaluate the effects of radio-tracking: no observable or measurable harm.

We cannot evaluate the effects of geolocators until the birds return this winter and we can see whether there is any differential survival relative to the control colour-ringed only birds. Nevertheless, after fitting of geolocators last winter, 33% of individuals were observed opportunistically up to six weeks afterwards, before they all left on migration (but many birds were tagged immediately before migration and so would not be expected to be resighted), behaving in the same way in the same location as before fitting with tags.

b. Please briefly outline the outcomes and impact of the animal work conducted.

The results of the study so far are:

Measures of site fidelity and over winter survival of the common Whitethroat to determine if the winter period has higher or lower mortality than other stages in the annual cycle. We have found high site fidelity, but individuals may have several over wintering sites on a large spatial scale.

Within winter apparent survival is high but over winter apparent survival is low indicating both low site fidelity, and detection probabilities as well as mortality occurring in other parts of the annual cycle.

Territory size is small and habitat choice is not very specific (any bush will do) suggesting that energy costs are low on the wintering ground, food is easily available.

Density varies between years: this helps to confirm the serial residency hypothesis which predicts stochastic recruitment spatially between years. The importance of this is that it indicates habitats are not saturated ad density dependent effects are likely to less important.

Overall, and importantly, the results suggest that the overwintering stage is not likely to be the limiting part of the annual cycle in terms of population dynamics in common Whitethroat – we need to concentrate on the migratory or breeding stages.

- publications that resulted from this work.

None as yet – the third field season's data will make our conclusions much more robust and so we are waiting to complete the study before publication. Papers that will be written are:

Territory size and habitat use in the Common Whitethroat indicate that density dependent habitat limitation is unlikely during the non-breeding season.

Overwinter and between winter survival in the common Whitethroat

Migration pathways and timing of common Whitethroats wintering in central Africa.

2. Please complete the following on your programme of work:

Species used	Number of animals	Comments regarding harms
Common Whitethroat	326 colour-ringed	No observable or measurable harm. Habitat use and occurrence

		of ringed and unringed birds was very similar.
Common Whitethroat	11 fitted with radio tags	No observable or measurable harm: time budgets of tagged and untagged birds were very similar.
Common Whitethroat	60 fitted with geolocators	No observable or measurable harm post fitting (20/60 birds observed afterwards directly before migration) but we await results from return rates after migration

a. **Describe any reason for harms in excess of those expected.**

No harm expected because methods have been proven on many other similar species and contexts. No harm observed.

3. Can any lessons be learned from your work that may contribute to the implementation of the principles of replacement, reduction and refinement?

a. Have any alternatives been developed since the application that could replace some or all of the animal work?

No. Tags get smaller, lighter and with longer battery life so reducing their impact and we adopt these as and when they become commercially available. But the principle and justification of tagging and marking animals remains the same and is unlikely to change. We cannot understand animal population dynamics without following individuals' behaviour and fates.

b. For each aspect of the research performed were the predicted numbers of animals used? Explain any changes to animal numbers.

On 22 November 2017, the School of Biology Ethics Committee of the University of St. Andrews approved (1) the use of mist nets and spring traps to capture up to 100 individuals of six species of small migratory birds (*i.e*. Yellow Wagtails, Tree Pipits, Pied Flycatchers, Whinchats, Nightingales, and Common Whitethroats), (2) the use of standard colour rings, and (3) the use of radio tags on up to 25 individuals per species.

However, during the first fieldwork season it became clear that working with all six species would not be plausible and we decided to focus strictly on the Common Whitethroats. On 28 October 2018, the same committee approved (1) the increase in Common Whitethroats to be captured, ringed, processed and followed to up to 700 individuals during the totality of the study, and (2) the use of radio tags and geolocators on up to 100 individuals per year.

Although a mixed species study would have been preferable to make general conclusions about migrants, focussing on one of the species that was the most logistically easy, allows more questions to be asked in more detail.

c. Describe any refinements you have been able to carry out.

During November and December 2018, 11 Common Whitethroats were fitted with "Life TagsTM", a 0.45 gr-solar powered and battery-free radio transmitter sold by Cellular Tracking Techonologies. Once individuals were fitted with radio tags, they were sought out at least twice a week for over a month. But there were some technical issues. We felt that the signals we were receiving were not as strong as we thought they would be making birds detectable only at very short distances (a few metres). We think that a combination of harsh harmattans (cool dry winds that come from the Sahara Desert that create dense clouds of dust) and the fact that Common Whitethroats tend to hide inside dense bushes, were the reason tags were not getting as much solar energy as they should in order to work ideally. The latter, combined with the extra work we had to carry out for this project, led us to take the decision of stopping the use of these radio tags. Nevertheless, even though these tags were used for a short amount of time, we obtained valuable information that allowed us to confirm visual detection probabilities and territory and habitat use for a few birds.

4. Did your project deviate from your application? If so how?

As above in shift of focus from a multi-species study to a single species study.

5. Are there any other matters related to your project that should be brought to the attention of the School Ethics Committee?

No

University of St Andrews

NON-LICENCE REVIEW FORM

Date: 20/10/2020
Title of Project: The non-breeding ecology of the Common Whitethroat in central Nigeria
Supervisor: Prof. Will Cresswell

1. **For the programme of work you have carried out**;
    a. Is the work now complete?

All data collection finished in March 2020. The thesis is currently being written and is aimed to be submitted by June 2021.

Here, we evaluated the effects of:

- Mist-netting and colour-ringing:
    - nothing to report with respect to any observable harm, and nothing occurred that was different from standard mist-netting and colour-ringing carried out elsewhere.
- Radio-tracking:
    - Data obtained from 3 radio-tagged individuals and 6 control individuals (individuals that were colour-ringed during the same period but were not deployed with a radio tag), revealed that the average proportion of time distributed to different activities such as vocalizing, moving, foraging, resting, and flying is similar between tagged and untagged individuals.
    - The time that an individual remained in the study site, since it was ringed until the last time it was seen or heard, did not vary between 11 radio-tagged individuals and 11 randomly selected control birds ($F_{(1,20)} = 0.05$, $p = 0.82$).
    - 2 out of 11 individuals that were carrying a radio tag returned the following year (18%). Of the same 11 randomly selected birds, 3 returned the following year (27%). ($\chi^2 = 0.3$, df = 1, $p = 0.60$)

  - Overall, our evidence does not suggest that tagging had a negative effect on the behaviour or survival of this species. These return rates were not statistically different from each other ($\chi^2 = 0.3$, df = 1, $p = 0.60$).
- Geolocators:
  - After fitting birds with geolocators, 33% of individuals were observed opportunistically up to six weeks afterwards, before they all left on migration (but many birds were tagged immediately before migration and so would not be expected to be resighted), behaving in the same way in the same location as before fitting with tags.
  - 7 out of 60 individuals that were carrying a geolocator returned the following year (11.7%), while 9 out of 60 control birds (individuals that were colour-ringed during the same period but were not deployed with geolocators) returned the following year (15%). These return rates were not statistically significant ($\chi^2 = 0.3$, df = 1, $p = 0.60$).
  - The mean weight of recovered geolocated birds was similar to non-geolocated birds that were captured during the same period (geolocated = 14.05 g, non-geolocated = 14.4 g; two sample *t*-test: t = 0.8, df = 9.5, $p = 0.43$).
  - All individuals survived at least until their departure on spring migration once the geolocator was retrieved.
  - Except for a small patch of dry skin seen in the back of one individual, no visual harm was detected on birds while retrieving geolocators. Bird weighed and behaved similar to other individuals.
  - Overall, our evidence does not suggest that tagging had a strong negative effect on the survival of this species.

b. Please briefly outline the outcomes and impact of the animal work conducted.

The results of the study so far are:

- Common Whitethroats wintering in Nigeria breed across Eastern Europe on average 5,151 km from our study site, covering an area of 425,000 km^2. This reflects a somewhat high migratory spread defined by a north-eastern flight pattern.
- Spring migration does not differ significantly from autumn migration.

- There is clear evidence to show that Whitethroats have a first non-breeding site in the Sahel region prior to arriving at our study site.
- Between 16 and 20% return to the same site the following year.
- During the stationary wintering period in Nigeria, we found that only a small proportion of individuals remain throughout the non-breeding period, but many establish small temporary territories. Habitat choice is not very specific (any bush will do) suggesting that energy costs are low on the wintering ground. Food is easily available and birds can adjust their diet according to what resource is more abundant.
- Individuals show high site fidelity; many individuals return to the same territory they had established the previous year.
- Density varies between years: this helps to confirm the serial residency hypothesis which predicts stochastic recruitment spatially between years. The importance of this is that it indicates habitats are not saturated and density dependent effects are likely to less important.
- With a detection probability of 0.33, we estimate that within winter apparent survival is high (>80% of birds survive between November and March).
- Apparent annual survival seems to be <40%.
- Our study location seems is an important stopover and stationary site for the species.
- The generalist traits of the Common Whitethroats observed during our study, their use of a wide variety of resources throughout the year and their flexibility to use different migratory strategies, suggest that the non-breeding period is unlikely to be the limiting stage of the annual cycle affecting population dynamics of the species – we need to concentrate on the migratory or breeding stages.
- The effect global changes will have on the species will depend on their degree and at what spatial scale they are working at. Thus it is of crucial importance to conserve suitable habitat for Common Whitethroats over a very large area in both the breeding and non-breeding grounds.

No publications have resulted from this work yet.

The papers that will be written are:

- Migration pathways and timing of Common Whitethroats wintering in central Africa.

- Territory size, residency patterns and habitat use in the Common Whitethroat indicate that density dependent habitat limitation is unlikely during the non-breeding season.
- Within- and between-winter survival rates of the Common Whitethroat.

2. Please complete the following on your programme of work:

Species used	Number of animals	Comments regarding harms
Common Whitethroat	338 colour-ringed	No observable or measurable harm. Habitat use and occurrence of ringed and unringed birds was very similar.
Common Whitethroat	11 fitted with radio tags	No observable or measurable harm. Time budgets of tagged and untagged birds were very similar. Return rates from one year to the next was similar between tagged and untagged individuals.
Common Whitethroat	60 fitted with geolocators	No observable or measurable harm right after fitting (20/60 birds observed afterwards directly before migration). Observed a small patch of dry skin seen in the back of one individual when retrieving geolocator. This did not seem to have any obvious negative effect on the bird. Return rates from one year to the next was similar between geolocated and control individuals.

b. **Describe any reason for harms in excess of those expected.**

We did not expect, neither did we find, evident harm on individuals throughout the 3 years that the study was carried out for.

3. Can any lessons be learned from your work that may contribute to the implementation of the principles of replacement, reduction and refinement?

a. Have any alternatives been developed since the application that could replace some or all of the animal work?

No. We used the smallest and lightest radio tag and geolocator commercially available. The principle and justification of tagging and marking animals remains the same and is unlikely to change. We cannot understand animal population dynamics without following individuals' behaviour and return rates.

b. For each aspect of the research performed were the predicted numbers of animals used? Explain any changes to animal numbers.

On 22 November 2017, the School of Biology Ethics Committee of the University of St. Andrews approved: (1) the use of mist nets and spring traps to capture up to 100 individuals of six species of small migratory birds (*i.e*. Yellow Wagtails, Tree Pipits, Pied Flycatchers, Whinchats, Nightingales, and Common Whitethroats), (2) the use of standard colour rings, and (3) the use of radio tags on up to 25 individuals per species.

However, during the first fieldwork season it became clear that working with all six species would not be plausible and we decided to focus strictly on the Common Whitethroat. On 28 October 2018, the same committee approved (1) the increase in Common Whitethroats to be captured, ringed, processed and followed to up to 700 individuals during the totality of the study, and (2) the use of radio tags and geolocators on up to 100 individuals per year.

Although a mixed species study would have been preferable to make general conclusions about migrants, focussing on one of the species that was the most logistically easy, allows more questions to be answered in more detail.

c. Describe any refinements you have been able to carry out.

During November and December 2018, 11 Common Whitethroats were fitted with "Life Tags^{TM}", a 0.45 gr-solar powered and battery-free radio transmitter sold by Cellular Tracking Techonologies. Once individuals were fitted with radio tags, they were sought out at least twice a week for over a month. But there were some technical issues. We felt that the signals we were receiving were not as strong as we thought they would be making birds detectable only at very short distances (a few metres). We think that a combination of harsh harmattans (cool dry winds that come from the Sahara Desert that create dense clouds of dust) and the fact that Common Whitethroats tend to hide inside dense bushes, were the reason tags were not getting as much solar energy as they should in order to work ideally. The latter, combined with the extra work we had to carry out for this project, led us to take the decision of stopping the use of these radio tags. Nevertheless, even though these tags were used for a short amount of time, we obtained valuable information that allowed us to confirm visual detection probabilities and territory and habitat use for a few birds.

4. Did your project deviate from your application? If so how?

As mentioned above, we shifted from a multi-species study to a single species study and as a result added the number of individuals to be ringed and fitted with radio tags and geolocators.

5. Are there any other matters related to your project that should be brought to the attention of the School Ethics Committee?

No