

UNIVERSITÀ DEGLI STUDI DI PADOVA

DIPARTIMENTO DI BIOLOGIA

Corso di Laurea Magistrale in Biologia Evoluzionistica

**Site fidelity at stopover sites in the common cuckoo
(*Cuculus canorus*), a trans-Saharan nocturnal migrant**

Relatore: MATTEO GRIGGIO

Dipartimento di Biologia

Correlatore: KASPER THORUP

University of Copenhagen, Zoological Museum

Laureanda: CARLOTTA BONALDI

ANNO ACCADEMICO 2017/2018

CONTENTS

RIASSUNTO	1
1. INTRODUCTION	6
1.1 Migration	6
1.1.1 Methods to study migration	6
1.1.2 Physiological mechanisms underlying the migratory behaviour.....	7
1.1.3 Evolution of migratory behaviour	10
1.2 Site fidelity	11
1.2.1 Migration time and route repeatability.....	12
1.2.2 The importance of stopover sites	13
2. METHODS	15
2.1 The study species.....	15
2.1.1 Ecology and breeding behaviour of the study species	15
2.1.2 Conservation status	18
2.2 Aim of the study	20
2.2.1 Tracking data.....	20
2.2.2 Staging sites throughout the annual cycle.....	21
2.2.3 Degree of site fidelity.....	23
2.2.4 Statistical analyses	23
3. RESULTS	25
4. DISCUSSION	29
4.1 Migratory routes and timing in cuckoos.....	29
4.2 The effect of stopover duration	31
4.3 The effect of staging sites	32
4.4 Individual effect.....	33
5. CONCLUSIONS	35
6. REFERENCES	37
7. APPENDIX 1	41
8. APPENDIX 2	46
9. ACKNOWLEDGEMENTS	49

RIASSUNTO

Alla fine di ogni estate, miliardi di uccelli lasciano i loro territori riproduttivi per trascorrere l'inverno in zone con condizioni più favorevoli e migrare nuovamente nelle zone riproduttive in primavera (Gwinner, 1990). La migrazione degli uccelli ha da sempre affascinato l'uomo, che sin dai tempi di Aristotele cerca di trovare una spiegazione alla sparizione di numerose specie al termine dell'estate (Davies, 2015). Molte teorie hanno cercato di rispondere a questo quesito, ma le prime evidenze arrivarono alla fine dell'Ottocento, quando il danese Mortensen fabbricò per primo degli anelli di metallo con i quali identificare univocamente gli uccelli che vedeva nel suo giardino e che ogni anno, con l'inizio dell'autunno, scomparivano (Lopez-Lopez, 2016). Fu quindi lui il pioniere dell'inanellamento e il primo a dimostrare che singoli individui facevano ritorno ogni anno negli stessi territori riproduttivi. Lo studio delle migrazioni si è successivamente evoluto parallelamente al progredire della tecnologia: lo sviluppo di geolocalizzatori e di trasmettitori satellitari ha permesso di scoprire aspetti dell'ecologia degli uccelli che prima erano del tutto sconosciuti, dalle aree di foraggiamento fino all'identificazione di intere rotte migratorie. Grazie ai trasmettitori satellitari, in particolare, è possibile ora seguire da remoto gli spostamenti di un individuo e scoprire così diversi aspetti della sua migrazione (Newton, 2014). Come lo stesso Darwin aveva osservato, quasi tutti gli uccelli migratori fanno ritorno ogni anno agli stessi siti riproduttivi (Darwin, 1861): un'alta fedeltà a questi siti permette infatti agli individui di favorire della familiarità sia con i siti di foraggiamento sia con le zone migliori in cui costruire i nidi e deporre le uova; la conoscenza dei territori e dei predatori, insieme ad eventuali adattamenti alle condizioni di particolari regioni, potrebbero essere le forze selettive alla base dell'evoluzione di questo comportamento. Tuttavia, la *site fidelity* può rivelarsi svantaggiosa in quanto aumenta la probabilità di riprodursi con individui appartenenti allo stesso nucleo familiare (*inbreeding*) e potrebbe richiedere maggiori capacità cognitive per localizzare una zona geografica precisa (Vardanis, 2016); inoltre, la fedeltà ai siti potrebbe ridurre la sopravvivenza e/o il risultato dello sforzo riproduttivo in caso di improvvisi cambiamenti climatici o ambientali, che potrebbero determinare la scarsità di risorse alimentari o il

sovrapopolamento e rendere quindi l'area meno favorevole (Newton, 2008). Grazie agli avanzamenti tecnologici, sappiamo che quasi tutte le specie di uccelli migratori non volano ininterrottamente dai siti riproduttivi a quelli di svernamento, ma si servono di aree di sosta (*stopovers*) per accumulare energie e riguadagnare quelle perse durante il volo (Merom et al., 2000), oltre che per evitare condizioni meteorologiche svantaggiose come forti piogge e venti (Calvert et al., 2009). Queste soste possono durare da qualche giorno fino ad alcuni mesi e sono di fondamentale importanza per la sopravvivenza degli individui: è stato infatti dimostrato che sostare in un'area non favorevole può essere energeticamente più svantaggioso rispetto a continuare la migrazione (Wikelski et al., 2003) e che le condizioni trovate agli *stopovers* influiscono direttamente sulla mortalità degli individui e potrebbero essere una delle cause del declino di alcune popolazioni (Hewson et al., 2016). Inoltre è stato dimostrato che gli individui tendono a stare solo un giorno in *stopovers* dall'habitat sfavorevole, mentre trascorrono più tempo in aree di buona qualità (Ktitorov et al., 2010): la durata di uno *stopover* può quindi essere indice della qualità dell'habitat. È stato dimostrato che, mentre i passeriformi presentano un'alta fedeltà solo ai siti riproduttivi e a quelli di svernamento, molte specie di uccelli acquatici tendono a fare uso ogni anno anche degli stessi *stopovers* (Catry et al., 2004). La fedeltà ai siti di sosta presenta vantaggi e svantaggi simili a quella ai siti riproduttivi, ma ha cominciato ad essere studiata solo di recente, grazie alle nuove tecnologie che permettono di monitorare gli individui lungo tutto il loro ciclo annuale (Newton, 2008).

Il cuculo (*Cuculus canorus*) è un uccello appartenente alla famiglia dei Cuculidi, che si riproduce in Europa e in Asia Settentrionale e sverna nelle foreste tropicali del Centrafrica e dell'Asia Meridionale, cibandosi di larve di lepidotteri e coleotteri; è lungo 32-34 cm e con una caratteristica coda lunga fino a 15 cm (Cramp et al., 1985). È un parassita di covata e ogni femmina depone un uovo in diversi nidi della specie ospite: l'uovo di cuculo si schiude solitamente prima delle uova degli ospiti e appena nato il pullo, grazie ad un'incavatura sul dorso, spinge fuori dal nido le altre uova e alle volte perfino gli altri pulli già nati. L'evidente costo, in termini di fitness, che rappresenta il venire parassitati da un cuculo per i genitori ospiti è alla base di una corsa evolutiva tuttora in atto: nonostante il

cuculo parassiti più di cento specie di passeriformi, ogni femmina si specializza solo su una di queste; si definiscono quindi diverse *gentes*, caratterizzate da uova con colore e macchiatura diverse per favorirne il mimetismo. Le specie ospiti, invece, continuano ad evolvere segni sempre più particolari nelle loro uova, in modo da poterle distinguere da quelle di cuculo (Cramp et al., 1985; Davies, 2015). Nelle ultime decadi, il cuculo ha subito un forte declino, soprattutto per quanto riguarda alcune popolazioni europee, tra cui quelle del Regno Unito. I fattori sottostanti a questo declino sono stati ricercati: nell'intensificazione dell'agricoltura, con conseguente diminuzione delle risorse alimentari (BirdLife International, 2016); nell'anticipo dell'arrivo delle specie ospiti ai territori riproduttivi, in seguito all'anticipo della stagione primaverile, che causa un *mismatch* tra il periodo riproduttivo degli ospiti e quello del cuculo, che non ha avanzato il suo arrivo quanto quello degli ospiti che migrano a brevi distanze (Møller et al., 2008; Saino et al., 2009); nelle diverse rotte migratorie intraprese da popolazioni differenti, che presentano diversi tassi di mortalità a seconda delle condizioni delle diverse zone di sosta (Hewson et al., 2016).

Vista l'importanza di diverse rotte migratorie e della qualità degli *stopovers* sulla dinamica di popolazione degli uccelli migratori (Wikelski et al., 2003; Chevallier et al., 2011; Hewson et al., 2016), questo studio si propone di investigare se esista una relazione tra la durata di uno *stopover* e la probabilità che un individuo faccia ritorno nella stessa zona l'anno successivo; inoltre, se questa relazione abbia la stessa intensità in tutte le regioni utilizzate come *staging sites*. In questo studio sono stati analizzati dei dati provenienti da trasmettitori satellitari che hanno permesso di tracciare rotte migratorie ripetute, da due fino a quattro anni, di tredici cuculi maschi adulti, provenienti da tre diverse popolazioni, con territorio riproduttivo rispettivamente in Danimarca, Regno Unito e Svezia. Grazie ai trasmettitori satellitari, è stato scoperto che i cuculi utilizzano diverse aree di sosta durante il loro viaggio in senso orario dalle zone riproduttive a quelle di svernamento e viceversa (Willemoes et al., 2014). Ogni *stopover* è stato definito come una sosta di almeno tre giorni e posizioni entro un raggio di 25 km sono state considerate come uno stesso *stopover*. Gli *stopovers* sono stati poi raggruppati in regioni di sosta, corrispondenti a sei diverse aree utilizzate dagli

individui nel loro ciclo annuale: il territorio riproduttivo, in cui i cuculi, a differenza di altre specie, trascorrono solo poco più di un mese e mezzo, un'area di sosta in Europa, in cui si fermano durante la migrazione autunnale, seguita da un'altra sosta nella regione del Sahel prima di arrivare nella zona di svernamento, nelle foreste pluviali del Centrafrica; al termine della stagione invernale e all'inizio della stagione secca, i cuculi ricominciano il loro viaggio, fermandosi prima nell'Africa Occidentale e poi in Nord Africa o in Europa Meridionale, per ritornare, a maggio, nelle zone riproduttive. Abbiamo considerato la distanza alla quale un individuo si trovava in un anno rispetto all'anno precedente come misura di *site fidelity* e abbiamo indagato se questo valore fosse correlato all'esperienza che l'individuo aveva di quella zona. Abbiamo considerato la durata di ogni *stopover* come indice di esperienza e abbiamo inoltre indagato se diversi siti di sosta presentassero diversi pattern, considerando nelle analisi statistiche solo tre delle sei aree di sosta: l'area in Europa durante la migrazione in autunno, l'area del Sahel e l'area di svernamento.

Analizzando diversi modelli lineari e confrontandoli con *linear mixed models*, abbiamo potuto concludere che la fedeltà ai siti è maggiore quanto più un individuo ha confidenza con quel sito: più tempo un individuo trascorre in una zona, più è probabile che l'anno successivo si fermi in un luogo a bassa distanza da questo. Questo risultato è coerente con l'importanza della familiarità con i luoghi soprattutto negli *stopovers* e con l'impatto della qualità degli habitat di questi sulla sopravvivenza degli individui (Calvert et al., 2009; Chevallier et al., 2011; Hewson et al., 2016). Questo pattern è risultato molto evidente nell'area di sosta europea, mentre è meno marcato nelle zone di svernamento e presenta una tendenza intermedia nella regione del Sahel. Un'ipotesi per spiegare questa differenza risiede nel fatto che l'area di sosta europea è di fondamentale importanza, perché rappresenta l'ultima tappa prima dell'attraversamento del mar Mediterraneo e del Sahara, la barriera ecologica più pericolosa durante la migrazione (Chevallier et al., 2011). Gli individui hanno quindi bisogno di foraggiarsi in luoghi che sanno essere di buona qualità, per non rischiare di trovarsi a dover affrontare zone sconosciute. Nella regione del Sahel, invece, sono presenti molte zone con habitat e condizione climatica simile (Willemoes et al.,

2014) e questa omogeneità potrebbe risultare in una minore rilevanza nel ritrovare un'area esatta con cui l'individuo è già familiare. Il periodo invernale è caratterizzato nel cuculo da un comportamento itinerante, in cui gli individui seguono l'andamento delle piogge, e di conseguenza della disponibilità di insetti (Cramp et al., 1985; Thorup et al., 2017). In questa zona la fedeltà ai siti è risultata essere generalmente più alta rispetto alle altre due aree, ma comunque più bassa di quanto ci si aspettasse: in molte specie di passeriformi, la fedeltà ai siti di svernamento equivale quella ai siti riproduttivi (Catry et al., 2004). Il comportamento itinerante del cuculo potrebbe aver reso più vantaggioso tornare ogni anno nella stessa ampia zona, in cui trascorrere la stagione invernale spostandosi da un luogo all'altro, invece di localizzare l'esatta posizione occupata in precedenza. È infine emerso dalle nostre analisi che individui diversi presentano una tendenza diversa: questo risultato deriva tuttavia dal fatto che uno dei tredici individui, Whortle, ha seguito due rotte completamente diverse da un anno all'altro, a differenza degli altri individui. Questo ha aggiunto una variabilità al nostro campione che non c'è quando non si considera questo individuo: le analisi statistiche effettuate non considerando Whortle, infatti, mostrano che non è necessario includere il fattore individuale per spiegare i nostri dati. Abbiamo tuttavia deciso di considerare questo individuo poiché potrebbe riflettere una variabilità a livello di popolazione o di specie. Sono necessari ulteriori studi e un campione più ampio per stabilire se sia corretto tenere in considerazione anche questo comportamento eccezionale o se questo sia un risultato dovuto al piccolo campione a nostra disposizione.

Altri studi come il presente saranno necessari in futuro per investigare ulteriormente la *site fidelity* agli *stopovers*, aspetto ancora poco noto nell'ecologia del cuculo, così come in quella di altre specie. Ulteriori studi saranno richiesti soprattutto alla luce dell'impatto della migrazione sulla sopravvivenza degli uccelli (Chevallier et al., 2011), dei cambiamenti ambientali in atto e di come questi influiscano sulla dinamica di popolazione (Møller et al., 2008; Saino et al., 2009), in particolare in un'ottica di conservazione di popolazioni o specie in declino (Tottrup et al., 2012; Hewson et al., 2016).

1. INTRODUCTION

1.1 Migration

The migrating behaviour is typical of many different taxa, from insects to fishes, from birds to mammals, and it includes movements in different areas of the world and in different periods of the year, although most of them take place during spring and autumn (Newton, 2008), with organisms leaving their breeding grounds every autumn in order to spend the rest of the year in areas with seasonally more favourable conditions (Gwinner, 1990). Animal movement, and particularly bird movement, has caught the interest and curiosity of scientists since Aristotle (Lopez-Lopez, 2016): the Greek philosopher tried to explain the disappearing of redstarts (*Phoenicurus phoenicurus*) and garden warblers (*Sylvia borin*) at the end of summer in his book *Historia animalium*, writing that these species were transforming each autumn respectively into robins (*Erithacus rubecula*) and blackcaps (*Sylvia atricapilla*), whereas he thought that swallows (*Hirundo rustica*) were spending their winters hibernating under the ground (Davies, 2015). These explanations lasted until very recently.

1.1.1 Methods to study migration

Although bird movement has always caught the interest and curiosity of scientists, almost every aspect of this topic was unknown until naturalists started to come up with methods that could enable them to uniquely identify birds. Only in 1899 Hans Christian Cornelius Mortensen, a Danish schoolmaster, produced his first metal rings to uniquely identify birds like common starlings (*Sturnus vulgaris*) he caught in nestboxes in his home area, introducing a whole new method to study bird biology: since then, bird ringing became more and more popular and it has been used to study many aspects of this subject, from population monitoring and dynamics to orientation and navigation mechanisms (Lopez-Lopez, 2016). In the 1960s radio transmitters were developed: these new devices allow to discover the movements of individuals in a small area, helping to understand movements in breeding and foraging territories. Radio tags are however limited by the fact that they require an observer to detect the signal with an antenna and that they can be used only for distances up to a few kilometres (Newton, 2014). Technology is getting more and more useful to discover the

secret life of migratory birds, allowing us to follow them during their journey though continents: during the 1980s, birds started to be tracked all over their routes thanks to satellite transmitters (Newton, 2014). Signals are sent from the tags to ARGOS satellites, which transmit the locations to ground stations. This method provides almost real-time information on migration routes and timing, together with stopover locations and durations, flight speed, wind effect and orientation abilities. The first transmitters (Platform Transmitter Terminals, PTTs) weighed more than 100 g, due to the heavy battery, and could be used only on large birds. Now, PTTs are alimented by solar power and they are lighter than before (5 g), allowing the use on juveniles and small species and even smaller tags are predicted for the future. Some tags also combine satellite with Global Positioning System (GPS) technology and allow more precise location estimates (Newton, 2014).

1.1.2 Physiological mechanisms underlying the migratory behaviour

In the 1940s, the German ornithologist Gustav Kramer noticed that migratory birds kept in cages showed a higher level of locomotor activity, flapping their wings and hopping, at the time when they would have been migrating in the wild: Kramer called this behaviour *Zugunruhe*, or migratory restlessness, and started studying the mechanisms underlying this behaviour (Kishkinev, 2011). He hypothesized that birds use a “map and compass” model, since they need to know both where they are located, like when reading a map, and the direction where they need to go, as if they were using a compass (Birkhead, 2012). Since Kramers’s cages were too complex and heavy, a new prototype was proposed in the 1960s by Steve Emlen: the device, called Emlen funnel, is still used nowadays in orientation studies and consists in a blotting paper funnel with an ink pad at the bottom and a screen on top, through which birds can see the sky (Kishkinev, 2011; Birkhead, 2012). Hopping, the bird’s feet leave traces of ink on the blotting paper, providing an index of both the direction and the intensity of the migration (Birkhead, 2012). Thanks to these methods, three types of compass have been identified so far: a Sun compass, used by birds that migrate during the day, a star compass, used by nocturnal migrants, and a magnetic compass.

More than ten bird species, like mallards (*Anas platyrhynchos*), European starlings (*Sturnus vulgaris*) and meadow pipits (*Anthus pratensis*), have been demonstrated to use a Sun compass, which is not inherited and thanks to which they are able to orientate during their diurnal migration (Kishkinev, 2011). Nocturnal songbird migrants like blackcaps (*Sylvia atricapilla*) and European redstarts (*Phoenicurus phoenicurus*) were instead shown to use a star compass, which is dependent on individual experience: if nestlings are artificially not exposed to a rotating starry sky before their first migration, they won't be able to use the stars as a cue to orientate during the following migration periods (Kishkinev, 2011).

Experiments with European robins (*Erithacus rubecula*), which migrate during the night, kept in cages, revealed that they don't base their orientation only on stars and that they can find their way even in complete darkness; when the magnetic field around the cage was experimentally altered, the birds started hopping in the wrong direction, as if they were following the altered magnetic field (Birkhead, 2012). After other studies, in the 1980s it became generally agreed that birds have a magnetic compass and cells containing aggregates of magnetite nanocrystals were found in the nasal cavity of the upper beak of homing pigeons (Birkhead, 2012). Thanks to an experiment on European robins, it was found that the putative magnetosensitive organ in the upper beak is innervated by the ophthalmic branch of the trigeminal nerve (Kishkinev, 2011).

Other experiments with robins (Wiltschko et al., 2002) revealed that when a bird's right eye was covered with a patch, so that it could not receive light, the bird could not detect the Earth's magnetic field; the bird could instead orientate normally when the left eye was covered and the right eye was receiving light. This huge difference between left and right eye was linked to a strong lateralization of birds' brain, but was later refuted by another experiment, in which robins were found to be able to orientate also with the right eye covered (Kishkinev, 2011). Moreover, in the latter study it was underlined that there is not a strong lateralization in the avian brain, but only a modest preference on one side of the brain over the other (Kishkinev, 2011). It was found that the molecules responsible for the detection of the magnetic field in the eyes are cryptochromes,

flavoprotein photoreceptors forming radical pair intermediates when excited by light: they play a key role in circadian rhythm in both plants and animals and contain light photoreceptive cofactors that allow them to absorb photons (Kishkinev, 2011). The cryptochromes related to magnetoreception are expressed in both eyes, so this could be another confirmation to the studies of Wiltschko and his colleagues (Kishkinev, 2011). Nocturnal migrants were also found to process information coming from the visually mediated magnetic compass in a region of the forebrain called Cluster N, specialized in processing light: a bird with a lesion at Cluster N is not able to orientate (Kishkinev, 2011). The use of the magnetic compass is not restricted to the migratory season, but is also applied to everyday movements, like foraging and exploratory movements. Cryptochromes (Cry1, Cry2) involved in circadian tasks were found to be expressed following circadian rhythms, whereas Cry4 is expressed at a constant level during the day and may therefore be considered as a candidate as a magnetoreceptor of the light-dependent magnetic compass (Pinzon-Rodriguez et al., 2018).

The chemical mechanisms operating in the eye have been identified by some scientists as the “compass” which detects the direction of the magnetic field, whereas the “map” might be provided by the magnetite receptors that are located in the beak and detect the strength of the magnetic field (Birkhead, 2012).

Adult birds can travel not only using the “map and compass” method, but also integrating it with their previous experience, as demonstrated by displacement experiments, in which adult birds showed true navigation abilities (Thorup et al., 2007). But what about unexperienced juveniles? In many non-passerine species, like cranes, geese, storks and birds of prey, juvenile birds travel together with adults, so they can easily follow them while learning which path to follow during the following migration. Nocturnal solitary migrants, like passerines, cannot rely on adults to find their way during their first migration and are thought to use an innate mechanism of *clock-and-compass*. Thanks to this behavioural programme, also called *vector navigation* strategy, juveniles know which direction to choose and how long they should fly to reach their species-specific wintering grounds, while also integrating this information with the photoperiodic, nutritional and energetic situation, together with external cues

associated with species-specific regions they find along the route (Kishkinev, 2011). Whereas adults can correct for an artificial displacement and fly in the direction of their wintering grounds, there are evidences that juveniles fly towards their innate direction, not showing the ability to correct for a displacement (Thorup et al., 2007).

1.1.3 Evolution of migratory behaviour

Thanks to different new technologies, we now know that many birds fly for very long distances to reach their wintering grounds and then back to their breeding areas: for example, bar-tailed godwits (*Limosa lapponica*) breeding in Alaska migrate to New Zealand in autumn, covering a distance of 11000 km during one single flight (Birkhead, 2012). Long travels, including the crossing of ecological barriers such as deserts and large bodies of water like seas or even oceans, are very costly for birds: during migration, they can encounter bad weather conditions and rain and strong winds can be directly or indirectly dreadful for them. Moreover, in order to face the energetic costs of migration, birds need to gain weight and strengthen their muscular mass before the flight, sometimes even doubling their weight (Newton, 2008). Given all the risks and costs that a bird needs to face to migrate, one could ask how the migratory behaviour evolved and what are its benefits.

Many studies tried to answer to this question, but there is still not one clear explanation. A study considered seven bird families from the South American tropics, that include both short- and long-distance migrants: the study showed that the dependence on seasonally variable resources, such as fruit and nectar, determined the evolution of seasonal movements within the tropics that might have predisposed birds to migrate outside the tropics (Levey and Stiles, 1992). More recently, another study was conducted about *Catharus* thrushes, a genus containing 12 species, 7 of which are resident in an area between Mexico and South America, whereas the other five breed in North America and travel back South in autumn (Outlaw et al., 2003). A phylogenetic approach to the study of this genus showed that migratory species do not form a monophyletic group and that the migratory behaviour has evolved and has been lost several times (Outlaw et al., 2003). Another study about the phylogeny of warblers, belonging to the

family Parulidae, showed that the ancestral species was migrant and the evolutionary tree indicates that the migratory behaviour has been lost repeatedly during the warblers radiation: it has been therefore hypothesized that sedentary species might derive from migratory ones, emphasizing the fact that having tropical sedentary species as relatives does not imply that this is the ancestral condition (Winger et al., 2012). However, the first ancestral migrant bird from this family might have evolved from a sedentary tropical species and the hypothesis that the migratory behaviour evolved from non-migratory birds may therefore still be true (Alcock, 2013).

The opportunity to find big amounts of food, particularly protein-rich insects, along with the longer days typical of northern areas during the summer, could be two ecological conditions that contribute to balance the costs of migration (Alcock, 2013). Changes in weather conditions, especially regarding rainy and dry season in areas near the Equator, might have been another selective force behind the evolution of the migratory behaviour (Alcock 2013): some birds, like red-backed shrikes (*Lanius collurio*), common cuckoos (*Cuculus canorus*) and nightingales (*Luscinia megarhynchos*), were found to track vegetation greenness during their movements, following the rain season along their migration route (Thorup et al., 2017). Studying the NDVI (Normalized Difference Vegetation Index), a clear pattern emerged, with birds moving from different staging areas to match the variation in food availability given by variations in rainfall and sun radiation (Thorup et al., 2017).

1.2 Site fidelity

“It may be here remarked that most animals and plants keep to their proper homes, and do not needlessly wander about; we see this even with migratory birds, which almost always return to the same spot” (Darwin, 1861).

Although many mysteries remain about the subject of bird migration, it is well known that most species return to the same breeding site, as Darwin pointed out in *The Origin of Species*. Many studies based on ringing recoveries verified Darwin’s observation, showing that most migrating birds breed in the same area every year (Newton 2008). In almost all bird species that have been studied, individuals move much greater distance between natal site and breeding site than

between breeding sites among different years (Newton 2008). Site-fidelity and dispersal have been studied primarily with the help of ringing and the first problem arose by this type of studies is the fact that study areas are usually smaller than the natal dispersal distance, resulting in an underestimation of the site fidelity, since individuals breeding outside the study area may be overlooked (Newton, 2008). However, bird ringing allows the analysis of large-scale and long-term data, therefore representing a valid instrument to study bird biology, particularly when combined with newer methods (Newton, 2014). Fidelity at breeding sites has been largely studied and is usually very high in migrants, with long-distance migrant passerines showing a high fidelity to wintering sites as well (Newton, 2008; Catry et al., 2004).

By returning to the same site, birds can benefit from local knowledge, which can give them an advantage in competitive interactions with other individuals in defending feeding and/or breeding sites. Some species may also present different adaptations to the conditions of one particular region and this aspect, together with local experience, could be the main selective force underlying the evolution of site-fidelity in birds. However, site-fidelity presents some costs as well, like the higher probability of inbreeding and a reduced survival and reproductive prospects when facing changing conditions: birds could not be able to avoid a decline of the habitat in terms of feeding resources or overpopulation and site fidelity might therefore result in a disadvantageous attitude (Newton, 2008). Another potential cost of site fidelity might be the increased cognitive capacities necessary to locate previously visited sites (Vardanis, 2016).

1.2.1 Migration time and route repeatability

Thanks to ringing recoveries, it was revealed that birds arriving early in one year are recaptured early in the same season in the following year, showing individual consistency in migration timing (Vardanis et al., 2011; Thorup et al., 2013). Moreover, birds arriving earlier in spring usually leave later in autumn: an explanation to this pattern might be given from the fact that an early arrival allows individuals to start their breeding season earlier and this might lead to an extended breeding period, with the possibility of laying more than one clutch (Thorup et al., 2013). Time repeatability is stronger than repeatability in space: this might be due

to the fact that timing of migration is controlled by endogenous mechanisms, whereas route flexibility is influenced by environmental conditions, such as habitat quality and weather (Vardanis et al., 2011). It was also found that migration during spring is faster and more straight-forward than the autumnal one, in which individuals use more stopover sites during their trip (Alerstam et al., 2006). This might be due to the fact that migration timing in spring is restricted by environmental conditions and that the opportunities to forage vary between the two periods (Alerstam et al., 2006). Moreover, birds need to arrive earlier than conspecifics at the breeding sites in order to assess the best territories, resources and mates. This is not necessary in the non-breeding (wintering) areas, where birds need to find a good area to forage, but an early arrival does not have a direct impact on their fitness. Understanding the behaviour of birds during migration and their tendency to use the same routes every year is of fundamental importance, since migration is known to be a bottleneck during the annual cycle of many bird species (Chevallier et al., 2011).

1.2.2 The importance of stopover sites

It was once thought that migrating small Palearctic passerines would fly to their winter quarters in Africa and back without stopping along the route (Merom et al., 2000). Thanks to the new technologies available, it was instead revealed that many passerines use various stopovers during their flight and that these stays can have different duration (Merom et al., 2000).

Successful migration for passerine birds depends largely on the quality of stopover habitats: an experimental study about reed warblers (*Acrocephalus scirpaceus*) demonstrated that birds spend more days at optimal stopovers, whereas they tend to leave sooner from sub-optimal stopovers (Ktitorov et al., 2010). Like many other passerines, reed warblers migrate during the night, stop at dawn and spend the day foraging before starting again the migration the following night. It is therefore very important for them to stop in a good place, since they need to stay there until the next night and a bad quality stopover could lead them to the risk of losing energies (Wikelski et al., 2003). When birds were left at a suboptimal site, they would leave it the following day, in order to find a better foraging site; if they were staying in a good quality site, they would spend there

more than one day (Ktitorov et al., 2010). A stopover represents for a migrant an opportunity both to rest and store energy and to wait until flight conditions become favourable, particularly before the crossing of geographical barriers, to avoid bad weather and strong wind. It is therefore reasonable to consider the duration of a stopover as a measure of habitat quality and to assume that a bird is more likely to spend a longer time in a favourable place, particularly in terms of food availability. Despite the benefits, stopping the migration has some costs in terms of time and energy loss as well (Wikelski et al., 2003), since birds at stopovers can have a higher risk of mortality and misorientation, especially if they have never been to that stopover before and if the weather conditions are dangerous (Calvert et al., 2009): bad conditions during flight can indeed force birds to stop even if they are in an unsuitable area and this could lead to the loss of energy and fat reserves, which might eventually lead them to death (Biebach, 1990). A study revealed that black storks (*Ciconia nigra*) tend to use more stopovers in years with low abundance of food at breeding or wintering grounds, whereas they are able to fly without stopping if they fatten up enough during those stays (Chevallier et al., 2011). Stopping the migration could therefore be a consequence not only of the conditions found along the route, like rain or strong headwinds, but also of the food abundance found at the crucial areas used during the breeding and wintering periods. Stopovers should both offer access to water and food and ensure protection, so that birds can restore the energy expended during the previous flight while also storing energy for the subsequent part of the trip (Chevallier et al., 2011).

Thanks to studies based on ringing recoveries we know that birds like waders and waterfowl show a high fidelity not only to breeding and wintering areas, but also to stopover sites: this might be a result of the fact that these birds migrate in flocks and can therefore learn about the best stopovers from their older conspecifics. Moreover, waterfowl and waders are more selective in relation to the habitat, whereas terrestrial birds are more flexible in their habitat selection and therefore show less site fidelity (Catry et al., 2004).

2. METHODS

2.1 The study species

The common cuckoo (*Cuculus canorus*), hereafter cuckoo, is a member of the avian Order of Cuculiformes, which includes only the family Cuculidae. Its size is similar to that of the Collared Dove (*Streptopelia decaocto*), with 32-34 cm length and a wing-span of 55-60 cm, but with a longer and characteristic tail (13-15 cm). It is well recognizable during flight, because wings are not raised above horizontal. The plumage is similar to that of the Eurasian sparrowhawk (*Accipiter nisus*), with a grey plumage except for black bars forming a pattern of lines over the white chest, in both males and females. Some females present a different morph, called rufous, with a more brownish colour. Juveniles present two types of plumage: a grey one and a rufous one, the latter being more common than in females. They have many white fringes on feathers of upperparts and white spots on tail from which they can be distinguished from adults (Cramp et al., 1985) (**Figure 1**).



Figure 1: From left to right: grey female (which has a plumage very similar to that of males), rufous female, juvenile (Trnka et al., 2015).

2.1.1 Ecology and breeding behaviour of the study species

The cuckoo is an obligate brood parasite, breeding in Europe and Northern Asia and wintering in Central African and South Asian rainforests. It parasitizes different passerine species, including reed warblers (*Acrocephalus scirpaceus*) in reed beds, dunnocks (*Prunella modularis*) in bushy areas and meadow pipits

(*Anthus pratensis*) in grasslands and more than one hundred species have been recorded as hosts (Cramp et al., 1985). The female cuckoo eats one of the host's eggs and substitutes it laying her own egg in the host's nest (**Figure 2**). The cuckoo chick hatches before the hosts and starts ejecting the other eggs outside the nest, thanks to a hollow between the shoulders, that disappears after 4-5 days from hatching, together with the ejecting behaviour (Cramp et al., 1985); if the cuckoo egg is laid late, the cuckoo chick might hatch after the other chicks and it will evict the chicks out of the nest as well, until there is no competitor left in the nest (Cramp et al., 1985; Davies, 2015). The chick is then raised by the foster parents, that are tricked by its strong food-calls and orange-red gape, which serve as feeding stimuli (Cramp et al., 1985). Being parasitized by a cuckoo represents an enormous fitness cost for the host parents: therefore, there is a strong selection for them to recognize and eject the cuckoo egg before it hatches. This means that there is a strong selection for cuckoos to evolve mimic eggs, to avoid rejection: this results in a coevolutionary arms race between hosts and parasite which is still ongoing, with hosts evolving specific colour or marks on their eggs (Davies, 2015). On the other hand, cuckoos evolved several host-specific races, called *gentes*, with females perfectly mimicking the host eggs, in order to minimize the probability of rejection (Davies and Brooke, 1989; Fossøy et al., 2011). The mechanism underlying the evolution and the maintenance of different *gentes* without the occurrence of speciation is assumed to be linked to the fact that females are the heterogametic sex in birds: the sexual chromosomes in birds are Z and W, the W-chromosome being present only in females and therefore thought to carry the eggshell-related genes; on the contrary, males are known to mate with females from different *gentes* and this behaviour might be crucial in maintaining the genetic flow necessary to avoid speciation (Gibbs et al., 2000; Davies, 2015). However, the W-chromosome is very small and some argued that it is unlikely for it to carry all the information needed for the different aspects of the egg phenotype, which could be controlled by autosomal loci instead (Fossøy et al., 2011); this would imply that females and males mate assortatively, in order to maintain the host races, but the issue still needs to be further investigated. It has also been proposed that the absence of a clear explanation to the coexistence of

different cuckoo races might be due to the fact that cuckoo mating behaviour varies between populations (Davies, 2015).



Figure 2: Reed warbler nest parasitized by common cuckoo. The pink chick is a cuckoo chick, whereas the darker chicks and the egg are reed warblers (picture taken by me).

On their breeding grounds, female cuckoos need not only an adequate food supply –which consists in mostly caterpillars (Lepidoptera) and beetles (Coleoptera)- and a population of hosts, but also some strategical spots, like treetops, fences or rocks, for communicating with conspecifics and monitoring hosts breeding stages. (Cramp, 1985). Due to their parasitic habits, cuckoos fitness depends on their familiarity with the host species density and distribution: it is therefore of great importance for them to have a good knowledge of their breeding areas, in order to maximize their reproductive effort. As for many other species, cuckoos have been intensively studied at their breeding areas, but, until recently, less was known about their behaviour and distribution outside the breeding grounds. It is known that cuckoos return every year to the same breeding sites (Vardanis, 2016), but site-fidelity at wintering and stopover sites started to be investigated only with the recent developing of new study methods, such as satellite tracking.

Since cuckoos are raised from host parents and migrate solitarily at night, it is evident that they cannot relate on conspecifics to find their way during

migration, but they need to rely on an innate mechanism at least for their first autumnal migration. However, only one study was conducted so far about juvenile cuckoos, in which 13 juveniles have been fitted with satellite trackers, but only four of them transmitted for 46 days and only one individual transmitted for the whole autumn migration. The study compared juveniles movements with the movements of 20 adults and showed that young cuckoos were leaving breeding grounds later than adults and started their migration flying in a different direction than adults. The only juvenile surviving successfully reached the same wintering grounds as the adult birds, guided only by its innate migration programme (Vega et al., 2016). Thanks to the improving technology, we will hopefully soon be able to further investigate the migratory behaviour of young cuckoos, both with the study of their routes and with experimental approaches involving displacement in space and time (Willemoes et al., 2014).

An experimental approach has already been used with adult cuckoos, that were displaced from their breeding sites to unfamiliar areas (Willemoes et al., 2015): this study revealed a first general tendency for the birds to fly back to their usual breeding area after the displacement. After this attempt, the cuckoos showed flexibility in the routes used to reach the Sahel area and the wintering grounds. This variability could have been due to differences in the birds personalities or in the areas where they were displaced, but may also be traced back to their physiological conditions or their experience from previous years of migration (Willemoes et al., 2015). After the wintering season, almost all the displaced birds used the same routes as the control, non-displaced, cuckoos, to return to their usual breeding sites. Overall, this experimental approach revealed that cuckoos, like other bird species, don't need familiar cues to find their way and to navigate back to their normal migration route, even if the mechanisms underlying this ability are still unclear.

2.1.2 Conservation status

The species is listed as Least Concern (LC) from the IUCN Red List, even if some populations of cuckoos are declining, particularly the ones in Britain, with a decline of 61% since 1985 (Douglas et al., 2010): the species has a very large range and a large population size and the decreasing population trend which has

been ongoing is not rapid enough to reach the threshold which would make the species classified as Vulnerable (BirdLife International, 2016). Many reasons might stand behind this decline: intensification of agriculture, resulting in less availability of food and hosts, climate change causing an advancement of hosts arrival at breeding grounds and consequential reproductive mismatch between the cuckoo and its hosts (Davies, 2015; BirdLife International, 2016). Another factor that was found to explain cuckoos decline is their migratory route: a study considering routes of individuals from different populations breeding in the UK found out that they use two different routes to reach the same wintering grounds, with different stopovers before crossing the biggest ecological barrier of their migration, the Sahara desert. Some of the birds stop in Spain, whereas others fuel up in Italy. The researchers discovered that the mortality was higher for birds using the former path and hypothesised that this pattern might be due to the conditions at the European stopover: Spain had faced a reduction in rainfall a few years before the study, leading to severe droughts which were eventually associated with wildfires (Hewson et al., 2016). Other hypotheses to explain why only one of the two populations is declining are habitat change and increased predation pressure both at breeding grounds and at the Spanish stopover (Hewson et al., 2016). In general, this study clearly revealed that conditions faced during migration affect population dynamics and survival of long-distance migrants; it is therefore particularly important to study the conditions along migration routes together with those at breeding sites, in order to maximize the conservation efforts directed towards declining populations.

Climate change is causing phenological changes in many species, from plants to animals: the increase in spring temperatures is resulting in an advance of annual cycle in many plants and insects, including optimal timing of reproduction (Møller et al., 2008). This is resulting in a mistiming in the reproduction of predators and consumers of plants and insects in relation to the peak of food availability. This mismatch is exacerbated in migrating species and it has been demonstrated that species which are not advancing their arrival at breeding grounds are declining, whereas species which advanced their arrival time have been stable or even increasing during the last decades (Møller et al., 2008). Short-

distance migrants have advanced their arrival at breeding grounds more than long-distance migrants (Saino et al., 2009): this result is very important, considering that common cuckoos are parasitizing different host species, some of which are short-distance and others long-distance migrants. It has been shown that the mismatch between cuckoos' and hosts' arrival may contribute to the decline of cuckoo populations and that the mismatch is stronger with short-distance migrants, which winter in North Africa or southern Europe, and/or residents as hosts, e.g. dunnocks (*Prunella modularis*), meadow pipits (*Anthus pratensis*), white wagtails (*Motacilla alba*) (Saino et al., 2009). On the other hand, it was demonstrated that the decline of cuckoo populations in UK is not related to a decline in host populations (Douglas et al., 2010).

2.2 Aim of the study

Given the impact of migration costs and stopover habitat quality on the population dynamics of migratory birds (Wikelski et al., 2003; Chevallier et al., 2011; Hewson et al., 2016), the aim of our study was to investigate if there is a relationship between site fidelity at stopover sites and previous experience in cuckoos, also in the light of the decline of some populations (BirdLife International, 2016). Since birds tend to stay longer in a good quality stopover (Ktitorov et al., 2010), we considered the stopping in a site as a way for the bird to gain experience about that area and the duration of each stay as a measure of habitat quality. We also wanted to understand if the pattern is similar for the different staging sites used by the birds or if there is a discrepancy between regions.

2.2.1 Tracking data

We analysed satellite-tracking data from 13 adult male common cuckoos, that were tracked during two, three or four successive years, from June 2010 to February 2015 (**Table 1**). Three individuals were coming from a population breeding in Denmark (55.61-56.09°N, 12.12-12.59°E), nine in Great Britain (50.49-57.39°N, -5.82-1.97°E) and one in northern Sweden (68.44°N, 18.29°E). Geographical positions of the transmitters were obtained from ARGOS/CLS Service Argos. A location quality class is assigned to each position estimate from

ARGOS (3, 2, 1, 0, A, B or Z, where 3 has the highest and Z the lowest accuracy): we excluded all positions of class Z. Each transmitter was programmed to operate on a duty cycle of 10 hours on and 48 hours off, aiming to optimize the balance between data resolution and time span with battery charge via the solar panel. For this analysis we selected the location with the highest quality position from each 10h transmission period.

Individual	Breeding area	Monitored period
36331	Denmark	06/2010-03/2013
36328	Denmark	06/2010-07/2012
36487	Denmark	06/2010-05/2013
BB	UK (Scotland)	05/2012-11/2014
Chance	UK (Scotland)	05/2012-12/2013
Chris	UK (England)	06/2011-02/2015
David	UK (Wales)	05/2012-01/2015
Derek	UK (England)	06/2013-02/2015
Livingstone	UK (Scotland)	05/2013-01/2015
Skinner	UK (England)	06/2013-11/2014
Waller	UK (Scotland)	05/2013-10/2014
Whortle	UK (England)	05/2013-01/2015
75	Sweden	06/2011-06/2013

Table 1: Summary of individuals used for this study.

2.2.2 Staging sites throughout the annual cycle

The cuckoos completed an annual loop migration between breeding and wintering areas, using different staging sites throughout their annual cycle (**Figure 3**). We defined staging periods as when a bird interrupted migration for a minimum of 3 days and we grouped all the positions (latitude, longitude) in stopovers, considering positions within a 25 km radius as part of the same stopover. We subsequently grouped the stopovers in bigger areas to identify staging sites, corresponding to six different regions or phases of the cuckoo annual cycle: (1) breeding area (50.49-68.48°N, -5.82-18.80°E), (2) staging site in Europe during autumn migration (39.71-67.42°N, -3.38-30.41°E), (3) staging site in the Sahel region during autumn migration (-1.22-19.45°N, -0.24-27.09°E), (4)

wintering region in central Africa (-10.24-8.19°N, 2.75-21.75°E), (5) staging site in West-Africa during spring migration (6.21-11.32°N, -12.12-5.27°E), (6) staging site in Europe during spring migration (33.16-49.12°N, -6.86-14.65°E).

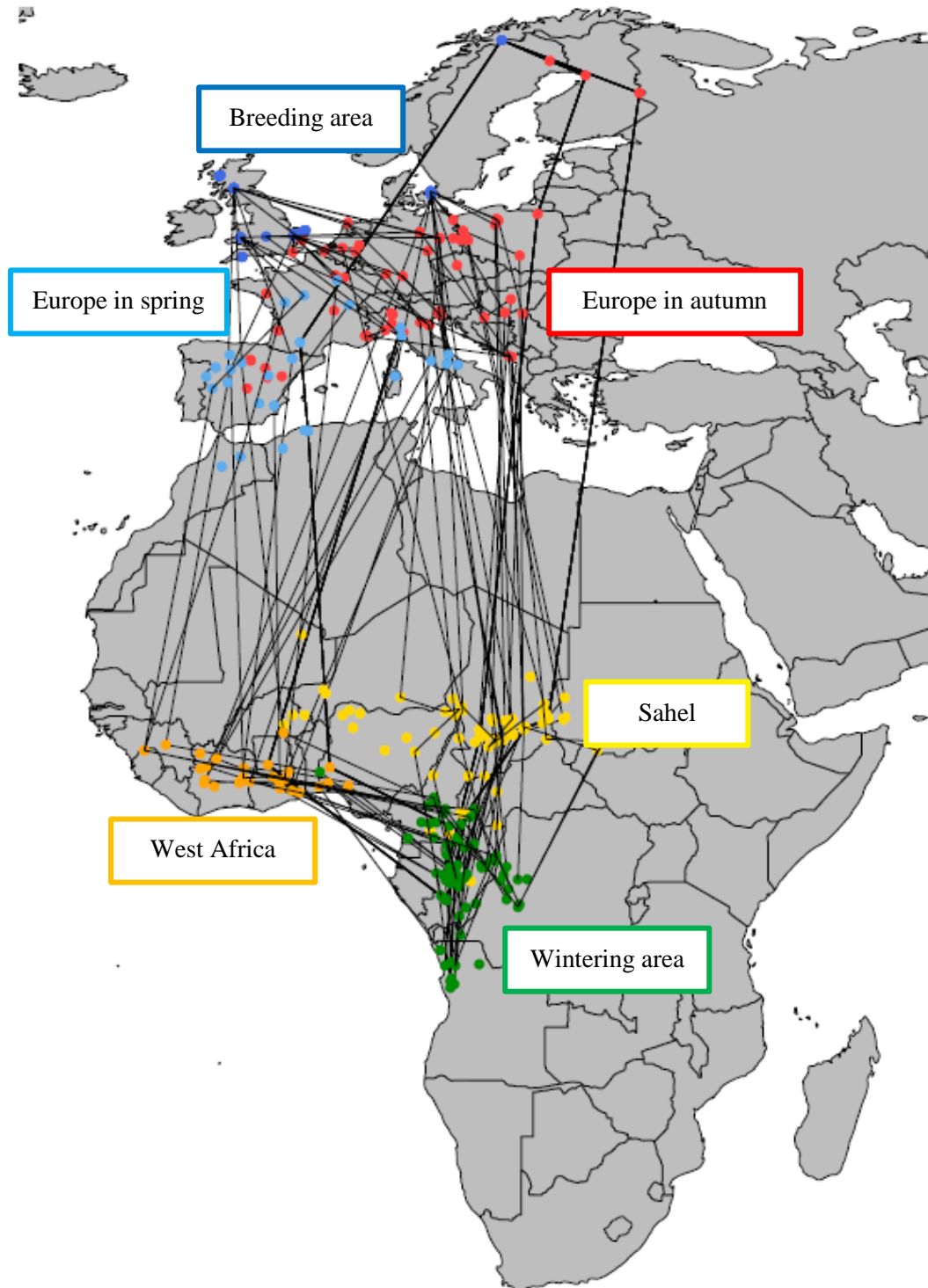


Figure 3: Routes of the thirteen individuals. Staging areas are indicated with different colours: blue – breeding area, red – European autumn stopover, yellow- Sahel region, green – wintering site, orange – West Africa, light blue – European spring stopover.

2.2.3 Degree of site fidelity

A previous study about annual cycle site fidelity in cuckoos (Vardanis, 2016) considered two locations differing by less than 50 km between two years as the same site and calculated site fidelity as the number of observed revisits of one site divided by the number of possible revisits: this corresponded with the average probability for an individual to revisit a given site. Using a 50 km threshold, a site was considered as revisited even if there was no spatial overlap between the distributions of the locations, overestimating the site fidelity. To avoid this overestimation, in our study we compared all the positions from one year with the ones from the previous year: in this way, we found the minimum distance between the position occupied from a bird and the stopover it was using during the same period in the previous year. We then calculated the average minimum distance for each stopover and considered this a measure of site fidelity, since a small distance means that the bird didn't stop far away from the site it visited the year before.

We finally calculated the duration of each stay, measured in days, and we used this as a measure of previous experience.

2.2.4 Statistical analyses

Data from the West-African and the European spring stopover were too scarce in comparison with the other stopovers, so we performed the analyses only considering data from the other three regions.

We tested different models to assess whether site fidelity (considered as distance between stopovers in consecutive years and measured in km) can be predicted by the duration of the stopover (measured in days) and if this relationship differs between different staging sites. We first ran some linear mixed models, considering the logarithm of the average minimum distance between stopovers in consecutive years ($\ln\text{AvgMinDist}$) as the dependent variable. In one model we considered only the duration of the stopover (Days) as the fixed effect, whereas in another model we considered also the staging site (Region) as a fixed effect. In both models, individual (ID) was considered a random effect. We tested the effect of stopover duration and staging site, together and separately, using linear models in which the individual was considered as fixed effect or was not

considered at all. We then tested another linear mixed model, in which we considered also the interaction between staging site and stopover duration. We finally compared these models with linear models, in which individual was also considered as a fixed effect or was not considered. All the comparisons between models have been done comparing the AIC (Akaike Information Criterion) scores to assess which model fitted best our data.

Statistical analyses were performed using R version 3.4.3 (R Core Team, 2017).

3. RESULTS

A preliminary analysis of all five staging sites revealed an overall higher degree of site fidelity at the wintering grounds, in the West African staging site and in the European stopover in autumn. The Sahel region showed a lower degree of site fidelity and the European staging site in spring showed an average tendency for the birds to have a lower fidelity to stopover sites in this region (**Figure 4**). The average site fidelity in the three staging sites we considered for the statistical analyses are shown in **Figure 5**. The average, minimum and maximum values regarding the distance from previous year position in each staging site are shown in **Table 2**. The full dataset is shown in **Appendix 1**.

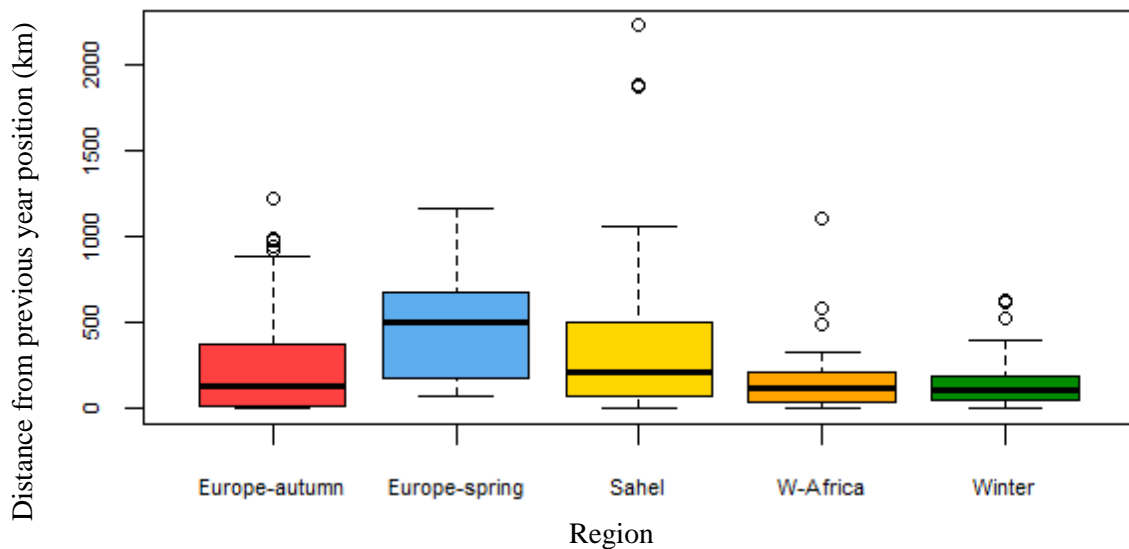


Figure 4: Boxplot showing the average distance from previous year position (km) in all the staging sites.

Staging site	Distance from previous year position (km)		
	Average value	Minimum value	Maximum value
Europe in autumn	287.84	1.57	1222.49
Sahel	363.04	0.76	2222.30
Winter	141.96	0.30	627.77
West Africa	213.56	1.14	1098.92
Europe in spring	510.41	72.69	1162.09

Table 2: Average, minimum and maximum values regarding the distance from previous year position in each staging site.

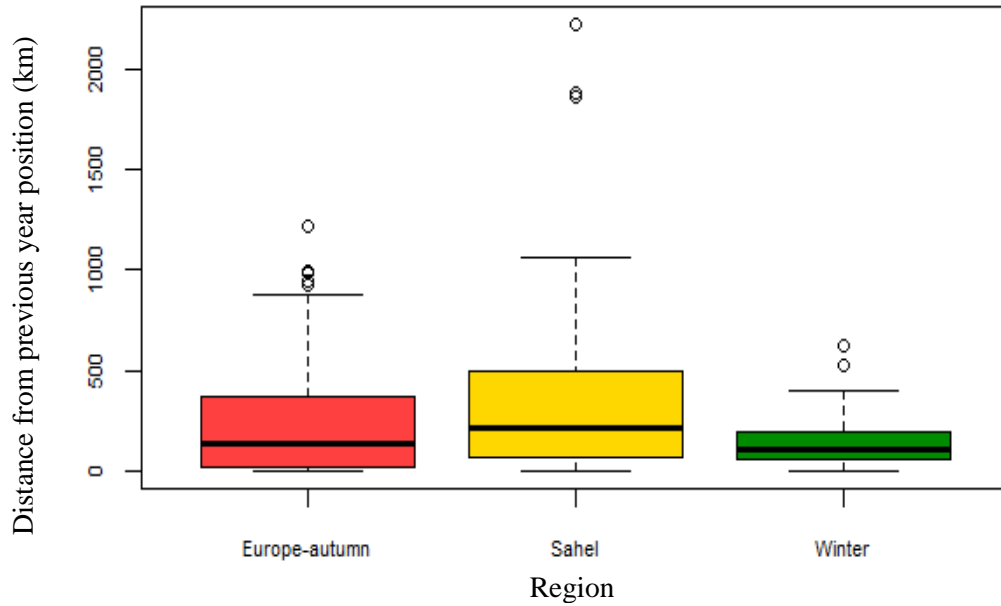


Figure 5: Boxplot showing the average distance from previous year position (km) in the staging sites used for our analyses (European stopover in autumn, Sahel region, wintering area).

The full linear model with individual as a fixed effect and considering the interaction of staging site and stopover duration had an AIC score of 642.79, which was lower than both the linear mixed model considering individual as a random effect (AIC= 647.61) and the linear model which was not considering individual (AIC= 651.14). The AIC score of the full model was also lower than the models not considering the interaction between staging site and duration of the stopover: the linear model considering only staging site, stopover duration and individual had an AIC score of 651.76, while the linear mixed model with individual as a random effect had an AIC score of 657.87 and the linear model considering only staging site and stopover duration but not individual had an AIC score of 664.15. Models not considering the effect of the staging site also had a higher AIC score than the best model: the linear model considering stopover duration and individual had an AIC score of 656.05; the linear mixed model with individual as a random effect had an AIC score of 660.97. The model considering only the stopover duration, but neither the effect of staging site nor the one of individual had the highest AIC score (AIC= 665.81). The model selection, considering as response variable the logarithm of the average minimum distance of each position from the positions occupied in the previous year, is summarized in **Table 3**.

Model	AIC
lnAvgMinDist ~ Days	665.81
lnAvgMinDist ~ Days + (1 ID)	660.97
lnAvgMinDist ~ Days + ID	656.05
lnAvgMinDist ~ Region + Days	664.15
lnAvgMinDist ~ Region + Days + (1 ID)	657.87
lnAvgMinDist ~ Region + Days + ID	651.76
lnAvgMinDist ~ Region + Days + Region * Days	651.14
lnAvgMinDist ~ Region + Days + Region * Days + (1 ID)	647.61
lnAvgMinDist ~ Region + Days + Region * Days + ID	642.79

Table 3: Summary of AIC values from the different models tested.

The best model, selected on the base of the lower AIC score, was the linear model considering the effect of both staging site, stopover duration and the interaction between the two, and individual. The summary is shown in **Table 4**.

Covariate	Estimate	Std. Error	t value	p-value
Intercept (Europe autumn)	5.70459	0.52412	10.884	0 (***)
Sahel	-0.08874	0.44967	-0.197	0.84
Winter	-0.89712	0.43307	-2.072	0.04 (*)
Days	-0.09399	0.01969	-4.772	0 (***)
ID36331	-0.29090	0.50630	-0.575	0.57
ID36487	-0.08080	0.54026	-0.150	0.88
ID75	0.87315	0.56321	1.550	0.12
IDBB	-0.69414	0.60987	-1.138	0.26
IDChance	-0.20501	0.63640	-0.322	0.75
IDChris	0.37267	0.48537	0.768	0.44
IDDavid	0.29500	0.50870	0.580	0.56
IDDerek	-0.15516	0.57708	-0.269	0.79
IDLivingstone	-0.81303	0.58853	-1.381	0.17
IDSkinner	0.34207	0.53399	0.641	0.52
IDWaller	-0.17275	0.57283	-0.302	0.76
IDWhortle	1.56363	0.56720	2.757	0.01 (**)
RegionSahel:Days	0.05361	0.02235	2.399	0.02 (*)
RegionWinter:Days	0.07112	0.02098	3.390	0 (***)

Table 4: Summary of the best model ($\ln \text{AvgMinDist} \sim \text{Region} + \text{Days} + \text{Region} * \text{Days} + \text{ID}$).

The relationship between duration of stopover and average minimum distance from previous year position is shown in **Figure 6**, with different staging sites shown in different colours. The distribution is best represented with an exponential curve, that shows a steeper relationship at the European staging site, intermediate at the Sahel region and a weak relationship at the wintering grounds. The extremely high distance values visible at the Sahel region are all from one individual, that undertook two completely different migration routes during consecutive years. Considerations about the effect of this individual on the best model selection are shown in the fourth paragraph of **Discussion**. Statistical analyses and graphs not considering this individual, as well as its migration routes, are shown in **Appendix 2**.

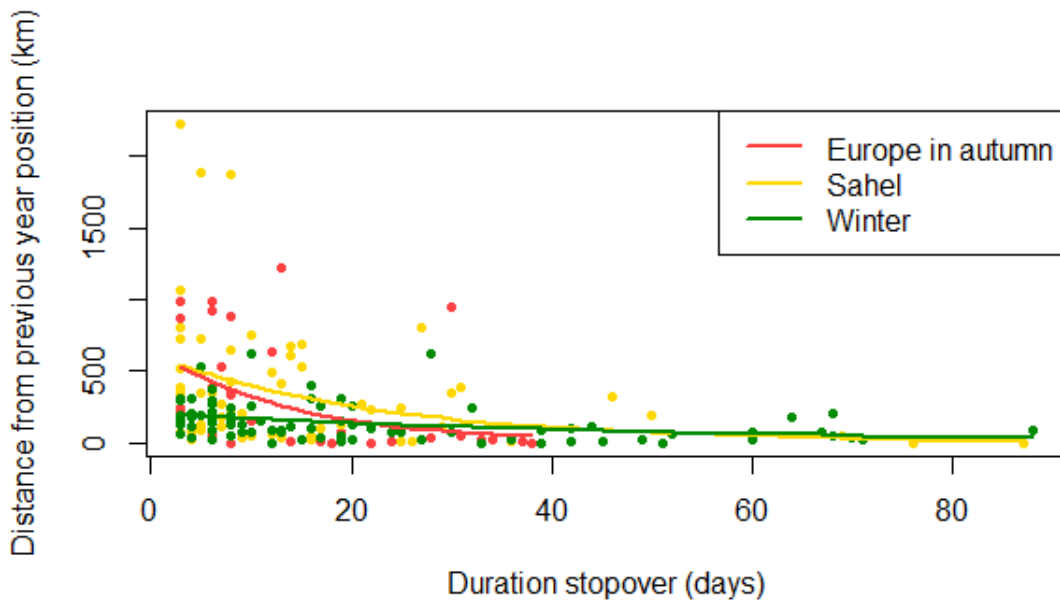


Figure 6: Relationship between stopover duration (days) and the average minimum distance from the sites visited in the previous year (km) in the three stopover regions.

4. DISCUSSION

Our analysis of satellite tracking data from thirteen adult male common cuckoos revealed that there is a significant relationship between the time spent at a stopover from an individual and the probability for it to return to that stopover in the next year. This relationship is stronger in the European stopover in autumn, whereas it is weaker in the wintering area and intermediate in the Sahel region. All individuals in our study were faithful to their previous tracks among the years, except for one individual, that used two completely different routes during the first and the second migration from the breeding area to the wintering grounds in Central Africa.

4.1 Migratory routes and timing in cuckoos

The cuckoos in our study belonged to three different populations, breeding respectively in Denmark, United Kingdom and Sweden. Due to their parasitic habit, the breeding period is relatively short for cuckoos (Davies, 2015): the individuals in our study spent from a minimum of five weeks to a maximum of two months at their reproductive sites. Around the second half of June or July, birds left the breeding sites and stopped for around one month in different sites in Europe, some remaining for a whole month in one site and some others spending a few weeks in Northern Europe (particularly Netherlands, Germany and Poland) and the remaining weeks in Southern Europe, where many of them stopped in Delta del Po World Heritage Site, an area of wetlands in North-Eastern Italy, and others stayed in Spain or the Balkans, fattening up before their trip over the Mediterranean Sea and the Sahara Desert: cuckoos cross these two ecological barriers during one non-stop flight of 3000-4000 km without refueling (Davies, 2015). Even though cuckoos migrate almost exclusively at night, the crossing of the Sahara Desert usually happens during one flight of about 60 hours, when birds fly both during day and night (Davies, 2015). Flying during the day can be very expensive not only in terms of energy but also of water loss, particularly when the air temperature is high. For this reason, when birds fly during the day above the desert, they are thought to fly at high altitudes, around 3000 metres, where the air temperature is around 10°C, an optimal temperature to avoid water loss. Air temperature lowers during the night, allowing birds to fly at 1000 metres without

losing too much body water. Another important aspect during migration is the effect of wind: favourable winds are usually under 3000 metres above the ground, whereas over 3000 metres birds could encounter headwinds that would result in huge losses of energies (Biebach, 1990). Therefore, balancing their water budget flying at lower or higher altitudes and correcting for hard winds, birds are able to cross the Sahara Desert in one non-stop flight. After this effort, birds need to stop again in the Sahel region and the individuals in our study stopped in this area for a minimum of three weeks and up to four months, flying from one site to another, between Sudan, South Sudan, Chad, Niger and Nigeria, to refuel before leaving again to reach the wintering grounds. Some of the cuckoos in our study arrived in the wintering areas around October, whereas others, which spent more time in the Sahel region, arrived in December. Cuckoos spend their winter solitarily in rainforests and they move in response to rainy seasons and fluctuating food supplies (Cramp et al., 1985). Since they don't need to defend a territory while they are not breeding, cuckoos show an itinerant behaviour inside the wintering area, associated with changes in resource availability (Vardanis, 2016). Indeed, the birds in our study did not spend the entire winter in one site, but they travelled between different regions belonging to a bigger area: during one winter, cuckoos stayed in Congo, Angola, Gabon, Cameroon, Centrafrican Republic, Democratic Republic of Congo, often spending a few weeks in some or all of these regions, showing an itinerant behaviour that might be due to the change in rainfall and therefore insects availability. The majority of our cuckoos stayed in Centrafrican tropical forests until the beginning of March, when they started their travel back.

Migration in spring is usually faster than in autumn and it includes less and shorter stopovers, since timing is very important before the breeding season (Nilsson et al., 2013): although birds in our study spent from a few days to more than one month in West Africa preparing for their long flight over the desert, spring migration was overall much faster than the autumnal one. After the stopover in West Africa, where birds stayed between Ghana, Ivory Coast, Nigeria, Burkina Faso, Guinea, Sierra Leone and Togo, the cuckoos briefly stopped again in Northern Africa or Southern Europe: here, they recovered for a minimum of a few days to a maximum of three weeks in Morocco, Algeria, Spain, France or

Italy, before returning to the breeding sites around May. The timing of arrival at breeding sites depends also on the conditions that a bird needs to face during migration: the crossing of the Sahara and the subsequent stopping in Europe during spring can be delayed if conditions are particularly advantageous in the wintering areas or along the route (Tøttrup et al., 2008). The late departure from wintering grounds due to good conditions forces birds to speed up their migration in order to take advantage of the climate-induced earlier spring (Tøttrup et al., 2008): this might also explain why spring migration is usually faster and stopovers in Europe are shorter in spring than in autumn.

The three individuals from the Danish population followed tracks that were very close to each other, indicating that birds may navigate through specific *en route* goal areas, flying through a narrow front with no significant variation between individuals to reach the wintering grounds (Willemoes et al., 2014). On the contrary, the British individuals followed very different migration routes, confirming a pattern already found (Hewson et al., 2016). We could not identify a pattern for the Swedish population, since only one individual was considered in our study. Considering populations breeding in different European regions, it is evident that changes in the breeding range result in different routes being optimal and therefore in different populations using different migration routes and stopovers, even if they share the same winter range. Migration routes and stopover areas are likely an adaptation to fit the optimal route in relation to habitat, available resources, safe barrier crossing and dominating wind systems (Willemoes et al., 2014).

4.2 The effect of stopover duration

The results of this study clearly show that cuckoos are more prone to return to a stopover if they already visited it for a long time in the previous year. This pattern might be explained by the fact that given the high risk of mortality during migration, it is very important for a bird to optimize the process of fattening up and avoid bad weather conditions, by choosing the best stopovers along the route. While stopping during the migration could be useful to regain the energy lost during the flight, it could be even more harmful than continuing migrating: stopping in an unfamiliar place might determine a higher risk of

predation or a lower probability to find food resources, resulting in the stopping being more costly than continuing migrating (Wikelski et al., 2003).

Birds usually leave a stopover within one day from their arrival if its quality is suboptimal (Ktitorov et al., 2010), showing that the duration of a stopover can be considered as a measure of the quality of the area. Stopover duration in cuckoos can go from of a minimum of a few days to several weeks, or even months: this variation in the duration of the stay might therefore reflect the importance of each stationary period and of the stopover site (Vardanis, 2016). It might be better for birds to stop in areas they already visited for a long time, in order to take advantage from the familiarity with the site, minimizing the energy costs deriving from stopping in an unfamiliar site (Wikelski et al., 2003) and this might be the reason behind the fact that cuckoos are more prone to use a stopover if they already visited it for a long time in the previous year.

4.3 The effect of staging sites

Our results show that the relationship between stopover duration and site fidelity is present at a different degree at different staging sites: the European staging site shows a stronger relationship, whereas this is weaker at wintering grounds and intermediate at the Sahel region.

Local knowledge given by previous experience might be of greater importance before the crossing of an important geographical barrier, such as the Mediterranean Sea and the Sahara Desert, when birds particularly need to accumulate energy (Chevallier et al., 2011): this could explain the pattern we found in our study, indicating that previous experience was more important at the European staging site, even if the degree of fidelity was overall low in this region. Whereas migration in spring is time selected, autumn migration strategies might be more depending on the energy availability, in terms of food, at stopover sites (Nillson et al., 2013): the crucial need for a good quality habitat during this part of migration could partly explain why site fidelity is more strictly related to previous experience at European sites during the autumn migration. This might determine a higher vulnerability of birds to the effects of environmental changes, as shown for

British populations, and might therefore be a factor contributing to the decline of some of the cuckoos populations (Hewson et al., 2016).

The weaker relationship found in the Sahel region might be traced back to the fact that the region presents comparable habitats with similar seasonal timing (Willemoes et al., 2014). This might result in a lower need to find the same sites among different years, since different regions present similar conditions. Species that migrate using routes that cover unlimited potential stopover sites, like many long-distance migrant passerines, are indeed more likely to show weak fidelity to these sites (Catry et al., 2004; Newton, 2008). Given the high number of potential stopover sites, cuckoos are less likely to show a high fidelity to the Sahel region (Vardanis, 2016) and this was confirmed by our data; this might also determine previous experience to be less relevant than in an area with a higher spatial variability, like the European region.

Since cuckoos spend their winter moving in response to rainy seasons and to the distribution of food (Cramp et al., 1985), it might be more important for them to find the same large area in subsequent years than to locate the exact position that they occupied in the previous years (Vardanis, 2016). The degree of site fidelity at the wintering grounds was higher than at the other staging sites, but it was overall very low, compared to the high levels of philopatry shown at wintering sites by many species of long-distance migrant passerines (Catry et al., 2004). This could be explained by the itinerant behaviour of cuckoos at wintering areas: the ability to go back to a general area might be more adaptive than locating the exact site occupied in the previous year, determining a weaker relationship between stopover duration and site fidelity. Variation in rainfall and therefore in insects availability might be the selective forces maintaining the itinerant behaviour, whereas spending the whole period in one region might not be the best strategy in order to take advantage of the food resources.

4.4 Individual effect

The results of our analyses showed that the model that better explained our data was the one considering individual as a fixed effect. However, all the individuals in our study were faithful to their previous tracks among the years,

following a common pattern, except for one British individual (Whortle), which used two completely different routes during the first and second migration from the breeding area to the wintering grounds. When we ran all the analyses not considering Whortle, the results changed, showing that the individual effect was resulting only from the exceptional behaviour of this particular individual. Without taking into account Whortle, it was possible to show that different individuals behave similarly in regard to site fidelity and that the variability was given only by that particular individual. Indeed, the best model without considering Whortle was the one which did not take into account the effect of individual (see **Appendix 2**), showing that there was a general pattern of site fidelity followed by all the other individuals. We decided to show the results considering all individuals, because the variability given by Whortle may reflect a general pattern in the species, with some individuals showing a different tendency in migratory route repeatability. However, a bigger sample size is needed to determine if this variability is present at a species or population level or if it is only an artifact due to the small sample size used in this study. However, also when not considering Whortle, we found a significant effect of both stopover duration, staging site and their interaction on site fidelity.

5. CONCLUSIONS

The common cuckoos are sometimes also called “European cuckoos” (IUCN, 2016): since Aristotle, we are used to see them at their breeding grounds in Europe, which they were once thought to leave only briefly to spend their winter elsewhere: what satellite trackers revealed is that the common cuckoos should actually be considered as African birds spending very little of their time breeding in Europe. Indeed, they spend almost half of their year in Central African rainforests, whereas they spend only 15% of their annual cycle at breeding grounds (Davies, 2015; British Trust for Ornithology, 2016). The main consequence of this discovery is that studying these birds at their breeding grounds is not enough to have a full understanding of their population dynamics and whether a conservation effort is needed in some of the other areas of interest of the species: annual survival of migratory birds depends on survival on both breeding and wintering season and also during migration (Chevallier et al., 2011).

Due to their parasitic habit, cuckoos return every year to the breeding site they already used, in order to take advantage of the local knowledge in terms of feeding sites and hosts distribution and behaviour (Cramp et al., 1985). Their behaviour is different outside the breeding sites, with cuckoos conducting a solitary life both while migrating and while feeding at the wintering grounds (Cramp et al., 1985). Even though the ecology outside the breeding territory has not been widely studied yet, we know that cuckoos do not show territoriality at non-breeding areas and one could therefore assume that site fidelity is less crucial at these sites (Vardanis, 2016). However, since the decline of some cuckoo populations was linked to the different migration routes and stopovers used by the individuals (Hewson et al., 2016), it is evident that understanding site fidelity outside the breeding grounds can be relevant also in the light of the decreasing population trend observed during the last decades (BirdLife International, 2016).

Our study showed that previous experience at stopover sites, in terms of stopover duration, is a predictor of site fidelity. Given the impact on mortality of the migration period and in particular of conditions found at stopovers (Hewson et al., 2016), it is clear that conservation efforts need to focus not only on breeding grounds, but particularly on staging sites used by individuals during their

migration. The recent development of new tracking technologies is helping us shedding light on the lives of individuals outside the breeding area, where we usually see them. These technologies are fundamental in order to understand not only migration, but population dynamics as well, since they allow us to determine how decisions during migration affect the survival of individuals. It is therefore of great importance to use these methods to understand in which direction we need to go with our conservation efforts towards declining species, knowing that stopover habitat degradation, hunting pressure or collision risks will affect the entire population using a certain flyway (Willemoes et al., 2014).

This study also showed that not all individuals have the same degree of repeatability in migration routes: it remains to be investigated if the exceptional behaviour showed by Whortle in this study reflects a variability at a broader level or if this is an artifact due to the small sample size of the study. As previously stated, different migration routes can have different effects on the survival of individuals and on the population dynamics (Hewson et al., 2016): it should therefore be investigated if such variability can be found at a population or species level.

6. REFERENCES

- Alcock J. (2013). *Animal behavior: an evolutionary approach*, 10th edition, ed. Sinauer Associates
- Alerstam T., Hake M., Kjellén N. (2006). *Temporal and spatial patterns of repeated migratory journeys by ospreys*, *Animal Behaviour*, vol. 71, pp. 555-566
- Araújo P.M., Da Silva L.P., Paiva V.H., Ramos J.A. (2016). *Reed warblers migrating through Portugal: climatic influence on stopover ecology over the last decade*, *Zoology*, vol. 119, pp. 232-240
- Biebach H. (1990). *Strategies of trans-saharan migrants*, in Gwinner E., *Bird Migration*, ed. Springer-Verlag
- BirdLife International (2016). *Cuculus canorus*. *The IUCN Red List of Threatened Species*. Retrieved from <https://www.iucnredlist.org> on 22nd October 2018
- Birkhead T. (2012). *Bird Sense: What It's Like to Be a Bird*, ed. Bloomsbury Paperbacks
- British Trust for Ornithology (2016). *Cuckoo tracking - What have we learnt so far?*. Retrieved from <https://www.bto.org/cuckoos> on 22nd October 2018
- Calvert A.M., Taylor P.D., Walde S. (2009). *Cross-scale environmental influences on migratory stopover behaviour*, *Global Change Biology*, vol. 15, pp. 744-759
- Chevallier D., Le Maho Y., Brossault P., Baillon F., Massemin S. (2011). *The use of stopover sites by black storks (Ciconia nigra) migrating between West Europe and West Africa as revealed by satellite telemetry*, *Journal of Ornithology*, vol. 152, n. 1, pp. 1-13
- Cramp S., Brooks D.J., Dunn E., Gillmor R., Hollom P.A.D., Hudson R., Nicholson E.M., Ogilvie M.A., Olney P.J.S., Roselaar C.S., Simmons K.E.L., Voous K.H., Wallace D.I.M., Wattel J., Wilson M.G. (1985). *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic*, ed. Oxford University Press, vol. IV- Terns to Woodpeckers, pp. 402-416
- Darwin C. (1861). *On the Origin of Species by Means of Natural Selection*, London, Murray Publishing
- Davies N. (2015). *Cuckoo – Cheating by Nature*, Bloomsbury Publishing

Davies N.B. and Brooke M. de L. (1989). *An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts - I. Host egg discrimination*, Journal of Animal Ecology, vol. 58, pp. 207-224

Douglas D.J.T., Newson S.E., Leech D.I., Noble D.G., Robinson R.A. (2010). *How important are climate-induced changes in host availability for population processes in an obligate brood parasite, the European cuckoo?*, Oikos, vol. 119, pp. 1834-1840

Fossøy F., Antonov A., Moksnes A., Røskoft E., Vikan J.R., Møller A.P., Shykoff J.A., Stokke B.G. (2011). *Genetic differentiation among sympatric cuckoo host races: males matter*, Proceedings of the Royal Society, vol. 278, pp. 1639-1645

Gibbs H.L., Sorenson M.D., Marchetti K., Brooke M. de L., Davies N.B., Nakamura H. (2000). *Genetic evidence for female host-specific races of the common cuckoo*, Nature, vol. 407, pp. 183-186

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

Kishkinev D. (2011). *Long-distance navigation and magnetosensory mechanisms in migratory songbirds*, PhD Thesis – University of Oldenburg

Ktitorov P., Tsvey A., Mukhin A. (2010). *The good and the bad stopover: behaviours of migrant reed warblers at two contrasting sites*, Behavioural Ecology Sociobiology, vol. 64, 1135-1143

Levey D.J., Stiles F.G. (1992). *Evolutionary precursors of long-distance migration: resource availability and movement patterns in neotropical landbirds*, The American Naturalist, vol. 140, n. 3, pp. 447-476

López-López P. (2016). *Individual-based tracking systems in Ornithology: welcome to the Era of big data*, Ardeola, vol. 63, n.1, pp. 103-136

Merom K., Yom-Tov Y., McClery R. (2000). *Philopatry to stopover site and body condition of transient warblers during autumn migration through Israel*, The Condor, vol. 102, pp. 441-444

Møller A.P., Rubolini D., Lehikonen E. (2008). *Populations of migratory bird species that did not show a phenological response to climate change are declining*, PNAS, vol. 105, n. 105

- Newton I. (2008). *The Migration Ecology of Birds*, ed. Academic Press
- Newton I. (2014). *BB eye - Is bird ringing still necessary?*, Retrieved from <https://britishbirds.co.uk/article> on 16th October 2018
- Nilsson C., Klaassen R.H.G., Alerstam T. (2013). *Differences in speed and duration of bird migration between spring and autumn*, *The American Naturalist*, vol. 181, n. 6, pp. 837-845
- Pinzon-Rodriguez A., Bensch S., Muheim R. (2018). *Expression patterns of cryptochrome genes in avian retina suggest involvement of Cry4 in light-dependent magnetoreception*, The Royal Society Publishing, *Interface* 15
- R Core Team (2017). *R: A language and environment for statistical computing*, R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Saino N., Rubolini D., Lehikonen E., Sokolov L.V., Bonisoli-Alquati A., Ambrosini R., Boncoraglio G., Møller A.P. (2009). *Climate change effects on migration phenology may mismatch brood parasitic cuckoos and their hosts*, *Biological Letters*, vol. 5, pp. 539-541
- Thorup K., Bisson I.A., Bowlin M.S., Holland R. A., Wingfield J.C., Ramenofsky M., Wikelski M. (2007). *Evidence for a navigational map stretching across the continental U. S. in a migratory songbird*, *PNAS*, vol. 104, n. 46, pp. 18115-18119
- Thorup K., Vardanis Y., Tøttrup A.P., Willemoes M.K., Alerstam T. (2013). *Timing of songbird migration: individual consistency within and between seasons*, *Journal of Avian Biology*, vol. 44, pp. 486-494
- Thorup K., Tøttrup A.P., Willemoes M., Klaassen R.H.G., Strandberg R., Vega M.L., Dasari H.P., Araújo M.B., Wikelski M., Rahbek C. (2017). *Resource tracking within and across continents in long-distance bird migrants*, *Science Advances*, vol. 3
- Tøttrup A.P., Thorup K., Rainio K., Yosef R., Lehikonen E., Rahbek C. (2008). *Avian migrants adjust migration in response to environmental conditions en route*, *Biology Letters*, vol. 4, pp. 685-688
- Tøttrup A.P., Klaassen R.H.G., Kristensen M.W., Strandberg R., Vardanis Y., Lindström Å., Rahbek C., Alerstam T., Thorup K. (2012). *Drought in Africa caused delayed arrival of European songbirds*, *Science*, vol. 338
- Trnka A., Trnka M., Grim T. (2015). *Do rufous common cuckoos females indeed mimic a predator? An experimental test*, *Biological Journal of the Linnean Society*, vol. 116, issue 1, pp. 134-143

Vardanis Y., Klaassen R.H.G., Strandberg R., Alerstam T. (2011). *Individuality in bird migration: routes and timing*, Biological Letters, vol. 7, pp. 502-505

Vardanis Y. (2016). *Individual consistency in bird migration*, Phd Thesis – University of Lund

Vega M.L., Willemoes M., Thomson R.L., Tolvanen J., Rutila J., Samaš P., Strandberg R., Grim T., Fossøy F., Stokke B.G., Thorup K. (2016). *First-time migration in juvenile common cuckoos documented by satellite tracking*, PloS One

Wikelski M., Tarlow E.M., Raim A., Diehl R.H., Larkin R.P., Visser G.H. (2003). *Costs of migration in free-flying songbirds*, Nature, vol. 423

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, vol. 9, issue 1

Willemoes M., Blas J., Wikelski M., Thorup K. (2015). *Flexible navigation response in common cuckoos *Cuculus canorus* displace experimentally during migration*, Scientific Reports

Wiltshcko W., Traudt J., Güntürkün O., Prior H., Wiltshcko R. (2002). *Lateralization of magnetic compass orientation in a migratory bird*, Nature, vol. 149, pp. 467-470

Winger B.M., Lovette I.J., Winkler D.W. (2012). *Ancestry and evolution of seasonal migration in the Parulidae*, Proceedings of the Royal Society, vol. 279, pp. 610-618

7. APPENDIX 1

Staging site	Individual	Distance from previous year (km)	Stopover duration (days)
Europe-autumn	BB	529.7664636	7
Europe-autumn	BB	11.6086221	17
Europe-autumn	BB	300.6862563	3
Europe-autumn	BB	10.05855825	24
Europe-autumn	Chance	3.164109761	38
Europe-autumn	Chris	81.40032995	13
Europe-autumn	Chris	637.8448884	12
Europe-autumn	Chris	110.0266922	29
Europe-autumn	Chris	223.7540694	8
Europe-autumn	Chris	35.43687019	16
Europe-autumn	Chris	149.3760642	10
Europe-autumn	David	924.8955076	6
Europe-autumn	David	5.822948128	36
Europe-autumn	David	870.8200461	3
Europe-autumn	David	982.0689668	6
Europe-autumn	David	18.4554461	33
Europe-autumn	Derek	9.687506238	14
Europe-autumn	Livingstone	391.1119227	6
Europe-autumn	Livingstone	1.574457805	22
Europe-autumn	Skinner	333.7984018	8
Europe-autumn	Skinner	163.2679469	6
Europe-autumn	Skinner	3.273469134	18
Europe-autumn	Waller	57.62624914	12
Europe-autumn	Waller	3.033833309	8
Europe-autumn	Whortle	257.8599654	10
Europe-autumn	Whortle	879.042411	8
Europe-autumn	Whortle	946.1782283	30
Europe-autumn	36331	35.58588158	28
Europe-autumn	36331	17.11666862	34
Europe-autumn	36328	232.7849728	3
Europe-autumn	36328	112.5072758	7
Europe-autumn	36328	74.76652327	19
Europe-autumn	36487	50.86274861	31
Europe-autumn	36487	43.44429787	6
Europe-autumn	36487	11.65921476	37
Europe-autumn	75	181.1922002	8
Europe-autumn	75	348.8487099	8
Europe-autumn	75	249.0681732	3
Europe-autumn	75	991.8143958	3
Europe-autumn	75	1222.488364	13

Sahel	BB	316.068018	46
Sahel	BB	0.758653049	76
Sahel	BB	82.11156998	5
Sahel	BB	1.385702915	87
Sahel	Chance	73.4741147	3
Sahel	Chance	190.8835744	8
Sahel	Chance	43.93767866	16
Sahel	Chance	10.37571749	25
Sahel	Chance	275.6225337	21
Sahel	Chris	49.9789461	69
Sahel	Chris	388.9114422	31
Sahel	Chris	36.56451276	13
Sahel	Chris	55.35437921	10
Sahel	Chris	137.0895002	3
Sahel	Chris	193.4706515	50
Sahel	Chris	189.4039403	5
Sahel	Chris	71.12019657	4
Sahel	Chris	345.8110387	5
Sahel	David	242.7218183	25
Sahel	David	64.07270756	12
Sahel	David	724.6116855	5
Sahel	David	751.4931338	10
Sahel	David	218.9304968	8
Sahel	Derek	615.0584091	14
Sahel	Derek	725.2413263	3
Sahel	Derek	804.7573109	27
Sahel	Derek	646.5173611	8
Sahel	Derek	675.2651752	14
Sahel	Livingstone	18.73832274	4
Sahel	Livingstone	18.49964091	16
Sahel	Livingstone	17.68552105	20
Sahel	Livingstone	535.7513437	15
Sahel	Skinner	266.3457851	7
Sahel	Skinner	124.1580887	5
Sahel	Skinner	207.1689482	9
Sahel	Skinner	169.908596	3
Sahel	Skinner	104.2855273	17
Sahel	Skinner	686.9319263	15
Sahel	Skinner	355.0096151	3
Sahel	Waller	497.225586	12
Sahel	Waller	384.2556736	3
Sahel	Waller	351.067749	30
Sahel	Whortle	2222.301079	3
Sahel	Whortle	1885.136934	5

Sahel	Whortle	1867.677215	8
Sahel	Whortle	1059.429665	3
Sahel	Whortle	800.9779147	3
Sahel	36331	346.5344434	6
Sahel	36331	112.3049305	7
Sahel	36331	192.5855042	9
Sahel	36331	174.6857901	7
Sahel	36331	274.5449168	21
Sahel	36331	234.213878	22
Sahel	36331	33.12749594	9
Sahel	36328	128.7293534	19
Sahel	36487	23.16264429	20
Sahel	36487	117.3051256	29
Sahel	36487	13.02546631	26
Sahel	36487	6.906375201	36
Sahel	75	517.4038611	3
Sahel	75	420.2672413	8
Sahel	75	410.0610726	13
Winter	BB	28.17063373	27
Winter	BB	13.21874473	45
Winter	Chance	177.5406282	64
Winter	Chance	304.7659481	19
Winter	Chris	51.52872822	68
Winter	Chris	70.64461929	13
Winter	Chris	17.46584697	49
Winter	Chris	34.67483747	70
Winter	Chris	75.20476712	10
Winter	Chris	209.9974448	68
Winter	Chris	74.40721168	60
Winter	Chris	188.2453752	8
Winter	Chris	79.30890996	30
Winter	Chris	128.2328536	8
Winter	Chris	246.3593889	32
Winter	Chris	196.8198005	3
Winter	Chris	298.1582508	3
Winter	David	105.6328718	22
Winter	David	57.68756453	52
Winter	David	43.62674862	8
Winter	David	83.5112747	13
Winter	David	26.19895655	36
Winter	David	124.6921934	20
Winter	David	208.6357472	4
Winter	David	53.89990941	8
Winter	David	73.22733288	24

Winter	David	34.79892047	17
Winter	Derek	2.387254091	33
Winter	Derek	3.335131687	39
Winter	Derek	61.05417002	3
Winter	Derek	12.50820375	42
Winter	Derek	304.6676468	3
Winter	Livingstone	18.23153381	20
Winter	Livingstone	150.7976261	6
Winter	Livingstone	122.7364995	3
Winter	Livingstone	82.03359878	39
Winter	Skinner	524.4854562	5
Winter	Skinner	99.76698957	16
Winter	Skinner	256.1906731	20
Winter	Skinner	308.8615584	16
Winter	Skinner	369.6880726	6
Winter	Skinner	312.5120103	4
Winter	Waller	0.50554011	51
Winter	Waller	138.4377976	6
Winter	Waller	243.701118	8
Winter	Waller	254.0263049	10
Winter	Waller	194.7249211	5
Winter	Waller	256.4737269	17
Winter	Whortle	120.6181331	44
Winter	Whortle	150.1035656	8
Winter	Whortle	92.07613623	13
Winter	Whortle	400.0447259	16
Winter	36331	25.44653707	60
Winter	36331	20.74784984	15
Winter	36331	88.72646436	12
Winter	36331	46.30663065	19
Winter	36331	28.77980427	6
Winter	36331	115.2487181	4
Winter	36331	212.9766255	6
Winter	36331	75.7831366	9
Winter	36331	110.5291466	14
Winter	36331	264.9898876	6
Winter	36331	0.295103596	12
Winter	36331	102.6533746	42
Winter	36331	81.44268385	25
Winter	36328	89.14326991	6
Winter	36328	79.94365644	25
Winter	36328	148.8479368	19
Winter	36328	161.731404	3
Winter	36328	71.68828624	67

Winter	36328	10.2164041	19
Winter	36487	301.0392784	6
Winter	36487	19.03624787	71
Winter	36487	129.5490182	9
Winter	36487	178.986579	4
Winter	36487	108.724813	4
Winter	36487	31.4677478	4
Winter	36487	618.867007	28
Winter	36487	627.7707251	10
Winter	75	91.71627846	88
Winter	75	155.3192928	11
Winter	75	185.5866186	3
Winter	75	112.2645592	4
W-Africa	BB	494.6608512	16
W-Africa	BB	1098.914904	8
W-Africa	Chris	183.0993118	3
W-Africa	Chris	328.8268942	18
W-Africa	Chris	114.4403943	17
W-Africa	David	1.135831417	4
W-Africa	36331	178.4488384	3
W-Africa	36331	30.41319415	6
W-Africa	36331	28.43317531	17
W-Africa	36328	39.35920733	8
W-Africa	36328	129.0346308	4
W-Africa	36328	219.1639319	6
W-Africa	36328	201.406296	6
W-Africa	36487	47.87371834	26
W-Africa	36487	44.88647748	12
W-Africa	36487	6.318960157	12
W-Africa	36487	118.8454736	10
W-Africa	75	578.7363359	6
Europe-spring	BB	102.1947701	5
Europe-spring	Chris	533.0103581	18
Europe-spring	Chris	474.2915918	3
Europe-spring	Chris	229.4298218	14
Europe-spring	David	651.2903762	6
Europe-spring	David	133.7729129	8
Europe-spring	36331	1162.088373	6
Europe-spring	36328	291.5115129	4
Europe-spring	36487	72.68657549	7
Europe-spring	36487	628.6542379	6
Europe-spring	75	695.5634077	4
Europe-spring	75	1150.407152	3

8. APPENDIX 2

When not considering Whortle in the statistical analyses, the best model was a linear model considering only staging site, stopover duration and their interaction as predictors of the response variable (AIC= 600.89). We ran the same models as we did considering all individuals, but in this case the models considering the effect of individual, either as a random effect (AIC= 602.31) or as a fixed effect (AIC= 605.36), had a higher score. All AIC scores from the models ran using a database not considering Whortle are shown in **Table 4** and the summary of the best model is shown in **Table 5**.

Model	AIC – no Whortle
lnAvgMinDist ~ Days	616.45
lnAvgMinDist ~ Days + (1 ID)	617.07
lnAvgMinDist ~ Days + ID	619.02
lnAvgMinDist ~ Region + Days	615.77
lnAvgMinDist ~ Region + Days + (1 ID)	615.50
lnAvgMinDist ~ Region + Days + ID	615.79
lnAvgMinDist ~ Region + Days + Region * Days	600.89
lnAvgMinDist ~ Region + Days + Region * Days + (1 ID)	602.31
lnAvgMinDist ~ Region + Days + Region * Days + ID	605.36

Table 4: Summary of AIC values from the different models tested.

Covariate	Estimate	Std. Error	t value	p-value
Intercept (Europe autumn)	6.01494	0.37355	16.102	0 (***)
Sahel	-0.34320	0.44958	-0.763	0.45
Winter	-1.16110	0.43312	-2.681	0.008 (**)
Days	-0.11237	0.02009	-5.594	0 (***)
RegionSahel:Days	0.06650	0.02246	2.960	0.004 (**)
RegionWinter:Days	0.09047	0.02134	4.240	0 (***)

Table 5: Summary of the best model (lnAvgMinDist ~ Region + Days + Region * Days).

Figure 6 shows the routes used by Whortle until the signal stopped in Central Africa, during the second wintering period tracked. The map clearly shows how the first migration route used to reach the wintering grounds is

completely different from the one used in the second year, with completely different stopovers both at the European staging site in autumn and in the Sahel region. None of the other 12 birds showed such a pronounced variability in their routes.



Figure 6: Whortle's routes. First year is shown in orange, second year in yellow. The satellite tracker stopped transmitting during the winter of the second year, when the bird was staying in Central Africa (Democratic Republic of Congo).

As shown in **Figure 7**, the general distribution did not change drastically when not considering Whortle. A stronger relationship between stopover duration and distance from previous position is still evident in the European staging site in autumn, the Sahel region has an intermediate relationship and a weaker relationship is still present at the wintering sites.

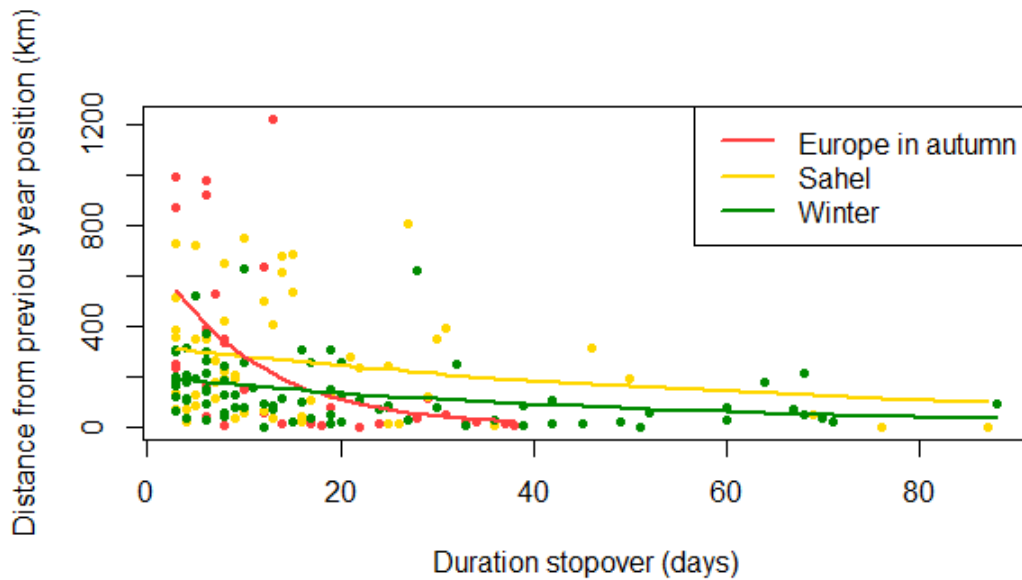


Figure 7: Graph obtained not considering Whortle. It shows the relationship between stopover duration (days) and the average minimum distance from the sites visited in the previous year (km) in the three staging regions. The pattern is similar to the one showed in **Figure 6**, even if the average site fidelity is higher, since here we are not considering the only individual that was following two completely different routes in consecutive years.

9. ACKNOWLEDGEMENTS

I would like to thank prof. Matteo Griggio for accepting once again to be my supervisor and helping me with the writing part of my thesis.

I am particularly grateful to all the staff of the Bird Corridor at the Zoological Museum of Copenhagen, for hosting me during my traineeship and for giving me this great opportunity. To Kasper and Mikkel for giving me this project and helping me with their supervision and useful opinions and advices; to Sissel for taking me to some great fieldwork trips; to Kat and Rien for their incredible availability when I needed some help; to Filippo for sharing all his coffee breaks with me and giving me some Italian vibes when I was missing home; to Bela for her advices, not only about work, and in general for her friendship; to Jesper for making me feel welcome when I had just arrived; to Jon, Jan and Jens, for being so kind and friendly, even if I will never get their names right.

Finally, thanks to my mom and dad and to my brother, my role model and my best friend, who made me understand that love will give you the strength to go everywhere and appreciate life, that there is something to discover and to learn from every place and that no place is like home.