

Common Whitethroats *Curruca communis* show a continuum of residency duration but a high degree of between-years site fidelity at non-breeding grounds in Nigeria

Claudia Tapia-Harris¹ and Will Cresswell¹

¹University of St Andrews

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Abstract

The non-breeding period represents a significant part of an Afro-Palearctic migratory bird's annual cycle. Decisions such as whether to remain at a single site and whether to return to it across years have important effects on aspects such as survival, future breeding success, migratory connectivity, and conservation. During this study, we colour-ringed > 300 Common Whitethroats *Curruca communis* and undertook daily resightings to understand site persistence and the degree of site fidelity throughout three non-breeding periods (November – April) in Nigeria. The probability of detecting a colour-ringed Whitethroat when it was present, was 0.33. Site persistence varied widely across individuals (1 – 165 days) and did not differ significantly with sex or year, though first-year birds remained for significantly shorter periods than adults. We believe that shorter residencies are likely due to the use of multiple stationary non-breeding sites rather than low winter survival. A minimum of 19% of individuals returned to the study site the following year and shifted, on average, 300 meters, suggesting that Whitethroats have a relatively high degree of between-years site fidelity at a very fine scale. An individual's previous residency duration did not seem to determine its residency duration the following year. We suggest that spatial fidelity is high and constant through years, but temporal fidelity is not, and individual residency patterns vary, probably according to yearly and seasonal conditions. Our results highlight the complexity of the annual cycle of a single species and the importance of carrying out in situ, small scale research throughout a migrant's annual cycle over several years.

Introduction

Over 60% of an Afro-Palearctic migrant's annual cycle occurs at non-breeding grounds (McKinnon, Fraser, et al., 2013), where migrants experience unstable and challenging environmental conditions. What ensues during this period will have significant carryover effects on many aspects of their survival and reproduction (Both et al., 2006; Pulido, 2007) and on the overall population dynamics of a species. Nevertheless, this period has been insufficiently studied (Marra et al., 2015) and details regarding fine-scale spatio-temporal movements are lacking. Understanding site persistence and the degree of between-years site fidelity will contribute to a better understanding of migratory connectivity and of how birds may respond to longer-term habitat and climate changes that, in turn, can lead to appropriate conservation efforts (Sanderson et al., 2006).

For many years, there was a largely evidence-free assumption that small migrants tended to move across Africa, tracking changing seasonal conditions in a generally itinerant way (Moreau, 1972). More recently, there has been increasing evidence that this is strongly species- and population-specific (Bulluck et al., 2019), with some species visiting several sites, others spending longer periods at fewer sites, establishing and defending territories, and, in some cases, showing both strategies (Belda et al., 2007; Blackburn & Cresswell,

2016; Catry et al., 2003; Thorup et al., 2019). To remain at a single site and maintain a territory confers advantages regarding local knowledge such as foraging locations, competitor densities, resource fluctuations, and predators (Catry et al., 2004; Piper, 2011), and avoids high costs and unpredictability associated with moving long distances, likely leading to higher survival rates (Cresswell, 2014; Yoder et al., 2004). On the other hand, itinerant individuals track ephemeral resources over a large area and are likely to move as environmental conditions change with the progression of the season, to optimise food availability (Ruiz-Gutierrez et al., 2016).

Many Afro-Palearctic migrants not only remain for prolonged periods at non-breeding sites but return to them year after year, especially territorial individuals (Blackburn & Cresswell, 2016; Cuadrado, 1992). Familiarity with these sites confers similar advantages as longer residency. Furthermore, fidelity has also been detected at a temporal scale, where individuals return to the same sites during similar times of the year (Stanley et al., 2012; van Wijk et al., 2016).

According to the serial residency hypothesis (Cresswell, 2014), many Afro-Palearctic migrants are likely to be faithful to any site(s) that promotes their survival, thus we expect strong residency differences and return rates amongst individuals of different ages. This hypothesis predicts that first-years, which lack knowledge of small- and medium-scale locations of where to arrive, will reach the non-breeding grounds stochastically. Some will find a site and remain at it until migration, while others will continue their search elsewhere, many of them arriving at less suitable sites or even discovering new unknown suitable habitats. Individuals will then reuse those successful sites during subsequent years as adults. Therefore, if an individual gets older, it becomes more site faithful because of natural selection removing those that did not locate suitable sites. In any population therefore, older birds will be more site faithful.

Studying site persistence and between-years site fidelity, however, is problematic. First, few species are likely to be so noticeable that they will always be detected at a site when present, leading to false negatives, particularly with low sampling effort. Second, determining site persistence and return rates greatly depends on when individuals are first marked and on their duration of stay, because passage birds will have lower detection and overall capture probabilities than more resident birds. Third, data is highly dependent on the methods used (*e.g.* . ringing schemes, geolocators, resightings). Ringing studies, for example, are usually undertaken at the beginning and end of the season at constant sites. This increases a birds' 'net-shyness' and reduces capture probability and makes it difficult to detect short duration stays. Results from tracking studies, on the other hand, are potentially the solution, except that small passerines can only be tracked with archival tags, where data is only recovered if an individual has some degree of site fidelity and at a very low spatial resolution.

The Common Whitethroat *Curruca communis* (henceforth 'Whitethroat') is a widely distributed small Afro-Palearctic migrant. Studies based on ringing recoveries and sporadic encounters have speculated that Whitethroats are faithful to their non-breeding grounds and remain there for a considerable period. Whitethroats inhabit dense thickets, show inconspicuous behaviour, and are relatively quiet during the non-breeding period (Zwarts & Bijlsma, 2015), all of which make them hard to detect. In this study, we use intensive resighting efforts throughout three non-breeding periods at a single site in Nigeria to understand, at an individual level, how Whitethroats use the non-breeding grounds at a fine spatial and temporal scale. We first calculate the probability of detecting an individual during a resighting visit and investigate site persistence of individuals of different age and sex groups. We then describe return rates and the degree of between-years site fidelity and determine whether individuals depart the area at similar times every year. To our knowledge, this is the first study to research winter residency and site fidelity of Whitethroats at a very fine spatial scale during the entirety of multiple non-breeding seasons.

Methods

Study site

The study took place over three consecutive non-breeding periods, hereby referred to as year1 (November 2017 – April 2018), year2 (September 2018 – April 2019), and year3 (November 2019 – March 2020) at a guinea savannah site on the Jos Plateau, Nigeria in West Africa (09°52'N, 08°58'E). This region experiences single pronounced wet and dry seasons lasting six months each, from May to October and November to April, respectively. Sites were primarily open scrubland with different and varying degrees of anthropogenic activities, *e.g.* farming, livestock grazing, tin mining, and fires (Hulme & Cresswell, 2012). These sites represent typical African dynamic habitats, where anthropogenic activities are constant and continuously changing throughout the year.

Mist-netting and resightings

Birds were captured using 9m, 12m, and 18m x 2.5m 5-shelf (16 x 16mm mesh) mist nets and conspecific playback. During year1, nets were set up in the morning between mid-November 2017 and mid-February 2018 (mean of four nets per day, open for 2h 50m), totalling 70 visits. In year2 nets were set up in the morning and/or evening from late October 2018 to mid-April 2019 (mean of 4.5 nets per day for 3h 24m), totalling 69 visits. Few additional birds were caught in year3 between mid-November 2019 and mid-February 2020 but were excluded from return rates and between-years site fidelity analyses. All individuals were sexed as either female, male or unknown, and aged as either first-year, adult, or unknown (Svensson, 1992). Each individual was given a unique combination of coloured leg rings (three colour rings and a metal ring). In total, 212 individuals were colour-ringed in year1, 115 individuals in year2, and 10 in year3. This work was conducted under the ethical guidelines of the AP Leventis Ornithological Research Institute Scientific Committee and all methods were approved by the School of Biology Ethics Committee of the University of St. Andrews (SEC17028).

Resightings were carried out at least once a week between sunrise and ~1030 hrs and/or between ~1500 hrs and sunset throughout the fieldwork period. Two observers undertook all observations. We interspersed starting points to avoid biases as a product of the time of day and air temperature. Resightings were not carried out during days of heavy rain. Once an individual was detected we proceeded to identify its complete colour combination using 10 x 40 binoculars. GPS points were recorded with a Garmin eTrex10 GPS where individuals were first detected and/or captured. Due to the skittish and shy behaviour of Whitethroats, conspecific playback was used. In some cases, individuals were first detected and playback was then used to help reveal the complete colour-combination. In most cases, however, when there were no signs of activity, playback was used before detection. This did not seem to induce any significant movement in individuals, and we believe that most recorded GPS points reflect unbiased locations where the individuals would be without any interaction with observers. We tried to spend the same effort resighting all individuals, but we acknowledge that this may not have been always the case. 135 individuals were seen at least once after capture. Because of the high resighting effort, we are confident that departure months and site persistence were determined accurately.

Radio tag deployment

Between 25 October 2019 and 28 November 2018, 11 individuals were fitted with “LifeTags”, a 0.45 g solar-powered and battery-free radio transmitter from Cellular Tracking Technologies. Tags were attached to birds’ backs using an elastic leg-loop harness (Rappole & Tipton, 1991). Devices weighed approximately 0.51 g with the harness, corresponding to 3.4% (3.2 – 3.8%) of an individual’s body mass. As individuals were fitted with radio tags, an effort was made to seek them at least twice a week after tag deployment until 8 December 2019. All birds were observed for at least three days after tag deployment. When individuals were detected, efforts were made to observe and corroborate its ring combination. GPS coordinates were recorded where

individuals were first seen or heard or when detection was strong. To determine whether radio tags had any negative effect on individuals, the residency period (number of days between when an individual was caught and the last time it was detected) and return rates (proportion of individuals that returned the following non-breeding period) was compared between 11 radio-tagged individuals and 11 randomly selected control birds, ringed during the same period. No significant differences were found regarding residency periods ($F_{(1,20)} = 0.05$, $p = .82$) or return rates ($\chi^2 = 0.26$, $df = 1$, $p = .61$) between radio-tagged individuals and controls.

Detection probabilities

The probability of detecting an individual directly affects how we calculate and categorise site persistence. Therefore, to estimate detection probability we used multiple datasets and methods.

1. *Manually* : Detection probabilities were calculated by dividing the number of times a bird was detected (number of encounters) by the total visits to its home range between its first detection (excluding the date it was ringed) until its last detection for each year. We used data obtained from individuals that we knew were present at the study site during each visit (*i.e.* obvious long-term winter residents, see below) to be certain that their non-detection was due to detectability factors and not due to absence or death. This assumes that birds did not leave their home range at any time and that all birds, if present, had the same probability of detection. We used information collected from 20, 16, and 15 individuals during years 1, 2, and 3, respectively. All data were analysed separately by year and returning individuals were included in every year they were detected: excluding them would otherwise bias estimates by preferentially sampling first winter birds.
2. *MARK* : With the same data, we proceeded to calculate detection probabilities using Cormack–Jolly–Seber (CJS) models in MARK software (White & Burnham, 2009). CJS models estimate both apparent survival (ϕ) and detection probability (p), where the former is the probability that an individual survives from one sampling occasion to the next, and the latter is the probability that, given that the individual is alive and in the sample, it is encountered (Hammond, 2018). Given that we used capture histories from individuals which we knew were present and alive ($\phi = 1$), we were only interested in obtaining the detection probability for each year. We assumed that detection was constant throughout all encounters ($\phi(.)p(.)$).
3. *Radio tags* : Detection probabilities were calculated for three radio-tagged individuals that were detected at least during three visits in year2. Every time a radio-tagged individual was detected with the antenna, we proceeded to find it in the same manner that we would normally do during resightings. We then estimated detection probabilities by dividing the number of visits during which an individual was detected in ‘resighting’ conditions by the total number of visits that same individual was detected with the radio tag antenna.

The final overall detection probability was obtained by averaging all seven estimates: detections obtained manually and in MARK for all three seasons (total of six detections), and a detection obtained through radio-tagged individuals.

Site persistence

Once established that individuals undertook different residency strategies (see Appendix 1), we estimated the number of days individuals spent in the study area (days between when individuals were first and last detected). To facilitate further comparisons, however, individuals were grouped into residency categories as seen in Table 1. Individuals detected across more than one year were categorised independently each year.

Between-years site fidelity

Return rates were estimated by dividing the number of individuals that were seen in year $i + 1$ by the total number of individuals ringed in year i . To determine the degree of between-years site fidelity of individuals that returned for at least two non-breeding seasons – how far an individual moved from year i to year $i + 1$ – we calculated the centroid coordinate for each individual in each year and estimated the distance between centroids using the “*distHaversine*” function from the “*geosphere*” package version 1.5.10 in R (Hijmans, 2019; Fig. 1). Individuals were grouped into group A, individuals detected in years 1 and 2, group B, individuals detected in years 2 and 3, and group C, individuals detected in years 1 and 3 but not in year 2. Individuals that were seen during all three seasons were not excluded from the analysis and were added to groups A and B.

Departure dates

We tested departure date repeatability of individuals seen for at least two non-breeding periods. Year 3 birds were excluded from this analysis because resightings that year ended earlier, and final resightings were not likely to reflect true departure dates. We excluded records of all birds that were seen after 25 February (three weeks before the end of observations) to exclude birds that were highly likely to have not left before our last resighting effort of that year. We estimated repeatability using the “*rpt*” function in the “*rptR*” package (Stoffel et al., 2017). This uses a linear mixed model framework where the groups compared for repeatability are specified by a random effect (*i.e.* individuals). Confidence intervals were estimated by running 1000 bootstraps. We calculated repeatability for adults and first-year birds, as well as for each residency category (*i.e.* long-term, short-term, and passage birds).

Statistical analyses

All data were analysed using R version 3.6.3 and RStudio version 1.1.456 (R Core Team, 2020) and a statistical significance level of $p < .05$ was chosen to reject the null hypotheses.

Detection probabilities

To compare whether detection probabilities were constant between non-breeding periods and methods, General Linear Models (GLMs) were performed.

Site persistence

We performed GLMs to understand whether site persistence, defined as the number of days an individual was present and detected in the area, varied across years, age, and sex. Birds that could not be aged or sexed were excluded from models that included these variables as predictors. First-year Whitethroats are difficult to sex accurately (Waldenström & Ottosson, 2000), so models using sex as an independent variable only include adults. Because of this, modelling for the effects of age and sex in residency periods was undertaken separately. Data from year 3 were excluded from these analyses as well as those individuals whose age and sex were unknown.

We used a model averaging approach for models that had the same sample size using the “*dredge*” and “*model.avg*” function from the “*MuMin*” package in R (Barton, 2020). This procedure entails carrying out all possible models from a base model (*i.e.* ‘days ~ age + year’ and ‘days ~ sex + year’), and calculating a weighted average of parameter estimates, such that parameter estimates from models that contribute little information about the variance in the response variable are given little weight (Grueber et al., 2011).

Between-years site fidelity

Chi-squared tests (χ^2) were performed to determine the effects of year, age at year i (‘previous age’), sex, and residency at year i (‘previous residency’) on return rates. A model averaging approach was also

undertaken to explore whether the distance moved from one year to another was dependent previous age, sex, and previous residency (base model: ‘dist ~ preage + sex + group + preres + preage*preres + preage*group’). All birds that could not be aged were excluded from models that included age as a predictor.

Residency repeatability

To explore whether individuals remained for similar periods across different years, or whether they repeated residency categories the following years, we estimated the percentage of individuals that remained (or changed) in each residency category. We carried out a linear model and estimated the correlation between the number of days spent in year i with the number of days spent in year $i + 1$.

Departure dates

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

Results

Detection probabilities

The mean of all seven detection probabilities (manual detections from years 1, 2 and 3, MARK detections from years 1, 2 and 3, and detection from radio-tagged birds in year2) was 0.33 (se = 0.02); the probability of detecting a Whitethroat at our study site when it is present was once every three visits (Fig. 1). Detection probabilities were similar between years when undertaken manually (mean = 0.36, se = 0.02, $F_{(2,48)} = 0.13$, $p = .88$) and in MARK (mean = 0.29, se = 0.03, $F_{(2,48)} = 1.48$, $p = .24$) and were similar across methods during all three years (year1: $t_{(38)} = 0.88$, $p = .38$; year2: $F_{(2,32)} = 2.44$, $p = .10$; year3: $t_{(28)} = 1.18$, $p = .25$).

Site persistence

Site persistence, defined as the number of days an individual was present and detected in the area, varied widely across individuals, ranging from one day to 165 days (mean = 31 days, se = 3 days, $n = 341$) but did not seem to differ significantly between years and between adult female and male birds (Table 2). First-years, however, remained for significantly shorter periods when compared to adults (Table 2).

Between-years site fidelity

Return rates

Overall return rates were similar across years but varied between age groups dependent on year and residency category, with more long-term and short-term winter residents returning than passage birds. A similar proportion of individuals returned between years ($\chi^2 = 0.56$, df = 1, $p = .45$): 36/182 (20%) individuals returned from year1 to year2 (group A), and 24/145 (17%) individuals returned from year2 to year 3 (group B). Seven individuals from year1 failed to return in year2 but then returned in year3 (group C). Only 12 individuals were seen during all three fieldwork seasons. In group A, a similar proportion of individuals of adults and first-year birds returned the following year: 13/62 (21%) adults and 22/96 (23%) first-years ($\chi^2 = 0.08$, df = 1, $p = .77$). In group B, however, there were clear differences between individuals of different

ages: 20/90 (22%) adults and 3/50 (6%) first-years returned ($\chi^2 = 6.16$, $df = 1$, $p = .01$). Most individuals from group C were first-year birds in year1. Female and male adults had similar return rates in group A (females = 5/21, 24%, males = 6/28, 21%; $\chi^2 = 0.04$, $df = 1$, $p = .84$) and in group B (females = 9/35, 26%, males = 8/42, 19%; $\chi^2 = 0.49$, $df = 1$, $p = .48$). When comparing return rates amongst residency categories in group A, long-term winter residents (14/43, 33%) and short-term residents (2/7, 29%) had higher return rates than passage birds (10/90, 11%) ($\chi^2 = 9.34$, $df = 2$, $p = .009$). A similar trend was seen in group B ($\chi^2 = 6.98$, $df = 2$, $p = .03$); 12/31, 39% of long-term winter residents returned; 3/16, 19% short-term residents; 5/40, 13% passage birds.

The distance moved from one year to another varied among individuals (Fig. 2) but, on average, individuals moved less than 300 meters (Fig. 2; Appendix 2). This figure was similar amongst groups A, B, and C ($F_{(2,51)} = 0.006$, $p = .99$).

The distance shifted between years did not vary significantly according to previous age ($F_{(1,45)} = 2.1$, $p = .16$), sex ($F_{(1,33)} = 0.58$, $p = .45$) or previous residency ($F_{(2,47)} = 1.61$, $p = .21$; Fig. 3; Appendix 2). Results from the averaging model, however, show that first-years in group A (seen from year1 to year3) shifted longer distances than adults (Table 2). All other variables were NS (Table 2).

Residency repeatability

The degree of residency category repeatability, *i.e.* whether individuals remained in the same residency category through different years, varied across individuals (Fig. 4). 68% of long-term winter residents remained as such the following year, and 32% remained for similar or shorter periods. Most of the short-term winter residents (66%), when they returned the following year, were categorised as passage birds, 17% remained for similar periods and 17% remained for longer. Half of the passage birds remained as such the following year, while the other half remained for longer periods: 31% were categorised as long-term winter residents and 19% as short-term winter residents (Fig. 4).

When comparing the duration (in days) spent at the site of individuals from one year to another, we found that there was a significant somewhat positive correlation between the duration in year i and the duration in year $i + 1$ (correlation $R = 0.32$, $p = .026$): individuals that remained for longer periods in year i remained longer periods in year $i + 1$ but, overall, individuals remained for shorter periods the following year (Fig. 5). The latter is especially true for short-term and long-term winter residents. Passage birds, however, remained longer periods during year $i + 1$ compared to during year i (Fig. 5).

Departure dates

Departure dates for individuals seen between January and April during years 1 and 2 did not vary between years ($F_{(1,179)} = 0.02$, $p = .90$), between adults and first-years ($F_{(1,179)} = 0.002$, $p = .89$), or between males and females ($F_{(1,137)} = 0.03$, $p = .31$). Individuals that were seen during at least two years showed relatively low repeatability values ($r = 0.15$, Table 3). The difference (in days) between the departure date in year i that of year $i + 1$ was statistically significant when categorising individuals by their residency at year i ($F_{(2,37)} = 4.3$, $p = .02$). This means that long-term birds departed at more similar dates across years compared to passage birds (Table 3). When categorising individuals by their previous age, we found that there was no significant difference in departure dates between adults and first-year birds ($F_{(1,37)} = 0.27$, $p = .61$).

Discussion

Detection probabilities

The probability of detecting a colour-ringed Whitethroat at our study site, when it was present, was 33%. Our results are consistent with the *Sylviiidae* family having relatively lower detection rates than other passerine

birds (Johnston et al., 2014; Zwarts & Bijlsma, 2015) and are similar to detection probabilities at their breeding sites in the UK (30%; Johnston et al., 2014). This rate is relatively low when compared to detectability at the non-breeding grounds of other Afro-Palearctic migrants such as Whinchats *Saxicola rubetra* (63% detection probability; Blackburn & Cresswell, 2016b) and Chiffchaffs *Phylloscopus collybita* (recapture probability 66%; Catry et al., 2003), though there are few studies that have addressed and calculated detection probabilities during this period (e.g. Zwarts & Bijlsma, 2015). Nevertheless, despite Whitethroats having relatively low detection probabilities, we consider that our high sampling effort (sites were visited at least once a week, for over 20 weeks each year) was sufficient to compensate for this.

Site persistence

Site persistence varied significantly amongst individuals, ranging greatly between one and 165 days. Because of the high sampling effort as well as similar return rates between individuals of different residency categories, our evidence is fairly compelling that shorter stays truly reflect shorter residencies and not detectability issues or mortality. Overall, the mean persistence duration was similar throughout years, so residency dynamics at a species level may not be changing strongly with time. In the Gambia, Whitethroats were also observed to have different degrees of site persistence with 45% of captured individuals remaining in the area between two and 84 days, though most individuals were caught less than a month after ringing (King & Hutchinson, 2001). In Senegal, however, most individuals were on passage (King & Hutchinson, 2001).

Different wintering strategies of individuals at the same site have also been recorded for other long-distance migrants: 27% of Blackcaps *Sylvia atricapilla* in Spain (Belda et al., 2007) and 8% of Chiffchaffs in Portugal were winter residents (Catry et al., 2003), whilst the rest were categorised as transients. This could have several explanations. First, individuals could have genetic differences due to parallel evolution of morphological and behavioural adaptations, making some individuals more inclined to lead either a nomadic or a resident lifestyle (Senar & Borrás, 2004). However, we cannot be certain whether individuals that were categorised as “passage” or “unknown” at our study site remained itinerant throughout the season, if they were in fact *en route* to a stationary non-breeding site elsewhere, or if they died during the period. These genetic differences could also reflect individuals from different breeding populations although this seems highly unlikely because individuals switched strategies across years, and Whitethroats seem to have a somewhat low migratory connectivity (Tapia-Harris et al., n.d.). A second explanation could be due to habitat quality changes throughout the season. The broad residency spectrum, from continual and variable movement to winter residency, appears to reflect a gradient in predictability in food supplies (Newton, 2008). As time passes, habitats dry and resources change (Moreau, 1972), so competition could increase. Some individuals may decide to leave the area to find other more suitable habitats elsewhere, while others may risk staying (for example those that are better competitors or are already in the best territories).

Short-term residencies, during both autumn and spring, may indicate the use of multiple important non-breeding sites. Nigerian Whitethroats deployed with geolocators remained at a first stationary non-breeding site in the Sahel before arriving at our study site in November (Tapia-Harris et al., n.d.). If some of these birds were then to be short-term residents, individuals could have more than two important stationary non-breeding sites. Multiple site use by individuals has been well described for several migrants in the Palearctic systems (McKinnon, Stanley, et al., 2013).

Adult birds’ site persistence was longer than first-year birds likely due to their previous experience and potential dominance. Many first-year birds probably arrive stochastically at non-breeding sites looking for suitable habitats. Many will need to explore the terrain and scout for resources, and whilst some will remain at it until migration to a second site later in the non-breeding season, or back to Europe in the spring, others may continue their search elsewhere, making a relatively immediate migratory scale movement.

Between-years site fidelity

Many long-distance migrants return to the same non-breeding sites year after year both in the Nearctic-Neotropical and Afro-Palearctic systems (Blackburn & Cresswell, 2016; Moreau, 1969; Salewski et al., 2000). Here we found that a minimum of 19% of individuals returned from one year to the next, an intermediate return rate in comparison to other Palearctic migrants in Africa (Kelsey, 1989; Salewski et al., 2000; Thorup et al., 2019) and Whitethroats at their breeding grounds (0–64%; da Prato & da Prato, 1983, 14.5%; Boddy, 1992). Not only did a significant proportion of individuals return the following year, but individuals moved, on average, only 300 m. These results suggest that many individuals have a high degree of between-years site fidelity at a very small spatial scale, though less than Whinchats at the same study site, which moved < 30 m (Blackburn & Cresswell, 2016). Fidelity across years confers the same advantages as longer residency patterns, especially regarding knowledge of local and fluctuating food sources, competitor densities, and location of refuges, and this seems to secure and increase an individual's survival.

Return rates were different amongst individuals from different age categories: first-years had lower return rates than adults, at least from year2 to year3. First-year birds lack knowledge of small and medium scale locations of where to arrive, thus their first non-breeding period is full of uncertainty and stochasticity (Cresswell, 2014). Some individuals will find a suitable site immediately and remain at it until spring migration, while others will continue their search elsewhere, many of them arriving at less suitable sites or even discovering new unknown suitable habitats. Older birds will tend to reuse non-breeding sites, so becoming more site faithful over time. Some studies have argued that higher return rates in adults could be due to greater survival from the previous year. Though this may be true for a few individuals, we think that because individuals had already undertaken a first migration, when high mortality rates occur, then overall, age-related survival differences are unlikely at this stage.

Even though most of the long-term winter residents remained as such the following year, some remained at the site for less time the following year. We expected individuals with a successful previous experience to repeat the same behaviour in the following years to guarantee their winter survival. When we further investigated these individuals, we found that most of them were seen in spring of the following season. Individuals may have remained longer at their previous wintering site due to better yearly habitat conditions that year and delayed the return to our site. If this were correct, we would expect that many individuals do not return to our study site when conditions are better further north and only return when conditions are suboptimal. On the other hand, passage birds increased the duration of their stay the following year. Given many of them were first-year birds, the lack of experience and dominance would have become a disadvantage, arriving at non-breeding grounds after adults, by which time fewer sites will have been available. By the following year, returning earlier in the season and as adults, they could occupy empty territories that allowed them to remain for longer periods.

Departure dates

Individuals did not seem to change their departure timing from year1 to year2, although further information over a span of many years is needed to draw stronger conclusions. Timing of migration is of critical importance in migratory species and is key for securing fitness (Drent et al., 2003; Kokko, 1999). Departure from the non-breeding grounds has been seen to correlate with arrival at breeding sites (Kristensen et al., 2013; Ouwehand & Both, 2017), though later departing individuals can migrate faster to compensate for lost time (Yohannes et al., 2009). As our study site is located at the southern part of the distribution and individuals have different breeding sites, the first individuals to depart are not necessarily the first to arrive at their respective breeding grounds (Tapia-Harris et al., n.d.).

Individuals at our study site showed lower intra-class correlation departure coefficients ($r = 0.15$) than most other Afro-Palearctic migrants (range 0.06 – 0.82, Both et al., 2016). Low repeatability fits well with the idea that individuals do not always remain for similar periods across years, and therefore it is perhaps not surprising that some individuals left the area on different dates, but there are a few things to consider with

these results. Firstly, repeatability indicates how consistently individuals differ from each other and is not necessarily a measure of individual repeatability across years (Conklin et al., 2013). Secondly, departure from our study site does not necessarily imply that individuals commenced spring departure, they could have moved to another non-breeding site.

Conclusion

Our results are consistent with the serial residency hypothesis (Cresswell, 2014) but also suggest small modifications. Instead of individuals repeatedly settling at the same wintering sites during the same periods year after year, we hypothesise that individuals may vary their timing at the sites depending on yearly conditions. We predict that spatial site fidelity and repeatability are high with little variation across individuals, but temporal fidelity varies individually and according to yearly conditions. Individuals stay stationary at a suitable site and remain there for as long as possible. Some proportion of the population will stay there all the northern winter, most likely those that are better competitors and are at overall higher quality sites and better environmental conditions, whilst others will move to a second site. This might never happen to an individual, and for some individuals this might only happen in their second or third autumn non-breeding season, depending on the specific year's conditions. The following year the same first site will be revisited; if conditions are stable and the site adequate to secure its survival throughout the period then there would be no need to migrate elsewhere. If not, then it would migrate to the same second site, and so on. When individuals reach the limits of their potential distribution, such as our study site, then they will return only in occasional years of widespread food shortage or suboptimal conditions in the previous sites (Newton, 2008). We would therefore predict that apparent survival at a sub-Saharan non-breeding site will correlate positively with latitude. Some individuals may get unlucky and will need to change sites several times, which makes them appear itinerant, whilst others will remain as long-term winter residents at few sites. Regardless of any particular year's conditions, the number of migration steps and distance of migration is minimised and matched to environmental conditions.

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

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Tables

Table 1. Description of residency categories and the number of individuals within each category per year. Percentages, excluding unknown birds, are shown in parenthesis.

Residency category	Description
Long-term winter residents	Remained ≥ 60 days at the study site, was detected two or more times after ringing, and seen again
Short-term winter residents	Remained between 8 and 59 days at the study site*.
Passage birds	Ringed between October and December. Only detected when ringed and remained ≤ 7 days
Unknown	Ringed between January and April. Only detected when it was ringed, or pattern was not clear
Total	

* If individuals were ringed during January or February, they could potentially be long-term winter residents.
All categories could include an unknown number of individuals that may not have migrated beyond our study

site but could have settled close by and gone undetected. Note that these categories do not differentiate between departures and mortality.

Table 2. General Linear Model results of site persistence and distance shifted between years predictors. In models, age = adult, sex = female, year = 1, group = A, residency = long-term were the base categories. Significant *p* values are highlighted in bold and italics. All interactions were NS.

<i>Site persistence</i>	<i>Site persistence</i>
AGE <i>n</i> = 204	AGE <i>n</i> = 204
Full model average (days ~ age + year)	Full model average (days ~ age + year)
Variable	Estimate
(Intercept)	40.9
Age First-year	-15.25
Year 2	10.17
SEX <i>n</i> = 81	SEX <i>n</i> = 81
Full model average (days ~ sex + year)	Full model average (days ~ sex + year)
Variable	Estimate
(Intercept)	48.43
Year 2	10.75
Sex Male	8.1
<i>Distance shifted between years</i>	<i>Distance shifted between years</i>
<i>n</i> = 47	<i>n</i> = 47
Full model average (dist ~ preage + sex + group + preres + preage*preres + preage*group)	Full model average (dist ~ preage + sex + group + preres + preage*preres + preage*group)
Variable	Estimate
(Intercept)	345.30
Group B	-243.58
Group C	-235.04
Preage First-year	-135.23
Group B: Preage First-year	1975.10
Group C: Preage First-year	528.83
Preresidency Passage	180.12
Preresidency Short-term	2.69
Sex Male	86.32
Sex Unknown	215.19
Preage First-year: Preresidency Passage	40.20
Preage First-year: Preresidency Short-term	-75.23

Table 3. Differences in departure dates between year1 and year2 according to age and residency category.

Intra-individual variability (Individuals seen during at least 2 years).			Intra-individual variability (Individuals seen during at least 2 years).
<i>n</i>			Mean ± SE
Age	Adult	21	46 ± 8.8
	First-year	18	52 ± 8.6
Res	Long-term	20	36 ± 8.4
	Short-term	6	33 ± 10
	Passage	14	71 ± 10.3

Figure legends

Fig. 1. Mean detection probabilities ± 1 standard error of known long-term resident birds in each year using distinct methods (red = manually, green = MARK, blue = manually from radio-tagged birds). Sample sizes during each year are shown on the top. In year2 “($n=3$)” represents the sample size of radio-tagged birds. Dashed line shows the overall mean detection (0.33). There were no clear differences in detection probabilities across years or methods.

Fig. 2. Distances moved between year i and year $i+1$ by individuals that moved above the average ($> 300\text{m}$; A) and below the average ($< 300\text{m}$; B). Sample sizes are shown on each map. A subset of individuals is shown with a higher definition in map C. Here, each colour represents a different individual. Individuals that do not have a line moved out of the confines of the box. Overall, individuals had a high degree of between-years site fidelity.

Fig. 3. Distance (meters) moved from year i to year $i+1$ according to previous age, sex, and previous residency.

Fig. 4. Change of individuals’ residency category from one year to the following year it was detected. Percentage in the square represents the proportion of individuals in each residency category at year $i+1$, as is observed by the width of the bands. Colours represent previous residency category.

Fig. 5. Linear correlation between the number of days an individual spent at the study site in year i and the number of days an individual spent at a location in year $i+1$. Colours represent residency category during year i . The dotted line represents a constant residency period during both years. Points above the dotted line represent individuals that remained longer in year $i+1$ than the previous year and points below the line represent individuals that remained a longer period in the previous year. R = correlation between variables and the p -value shows a significant positive trend.

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Appendix

Appendix 1: Proving different residency categories

To prove that individuals remained for different periods throughout the non-breeding season at our study site – that individuals have different within-winter residency strategies – we compared the observed frequencies of the number of visits individuals were detected each year, with that expected by chance assuming that all individuals were long-term winter residents. To do this, we first calculated the number of individuals seen *per* year and the respective mean number of visits. We ran 50 iterations to obtain a representative mean of birds detected each visit, assuming that (1) birds were present in the area throughout the study, *i.e.* long-term winter residents, and (2) that the detection rate *per* visit was 0.33 (see manuscript). We then compared these estimates with our observed data using a two-sample t -test. We expect that if our observed frequencies match those expected by chance, then all individuals are long-term winter residents.

If frequencies do not match, however, we assume that individuals have different duration residency periods. All years were analysed separately. Individuals seen in multiple years were not excluded from any analyses.

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

We found that the expected frequencies of the number of visits that individuals were predicted to be detected at was statistically different from what was observed when analysing both the data set with information from all individuals and the data set with individuals that were detected at least twice during the year (Fig. A.1; Table A.1). These results are similar across years. With this, we confirm that not all birds seen at our study sites are long-term winter residents.

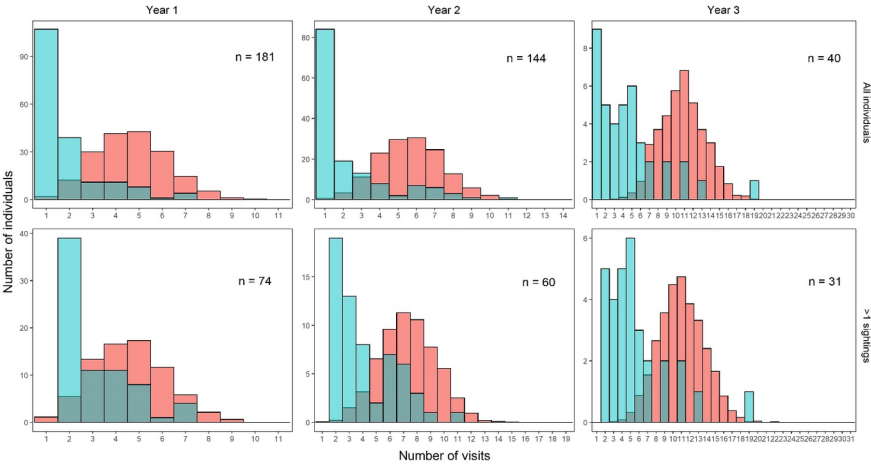


Fig. A.1. Expected (red) and observed (blue) frequencies of the number of individuals that were detected at different number of visits. Graphs in the first row were obtained from data gathered from all individuals and graphs from the second row were obtained from data of individuals that were seen at least twice during the year. In all graphs, blue bars (observed data) and red bars (expected data) rarely overlap. We observed many more individuals than expected only once or twice if all were long-term residents when detectability rate was assumed to be 0.33.

Table A.1. Statistical summary of the expected and observed number of visits at which individuals were detected during all three years and using two data sets: (1) “all data”, information from all detected individuals, and (2) “> 1 sightings”, information from individuals detected at least twice during the year. All the expected mean visits were statistically different from the observed mean visits.

Year	Data set	n	Expected mean visits	se	Observed mean visits	se	Results from <i>t</i> -tests
1	all data	181	4.64	0.12	1.86	0.1	$t_{(360)} = 18, p < .001^{***}$
1	> 1 sightings	74	4.62	0.19	3.09	0.17	$t_{(146)} = 6.1, p < .001^{***}$
2	all data	144	5.67	0.14	2.3	0.18	$t_{(286)} = 14.9, p < .001^{***}$
2	> 1 sightings	60	7.3	0.27	4.12	0.29	$t_{(118)} = 8.1, p < .001^{***}$
3	all data	40	10.8	0.39	4.62	0.61	$t_{(78)} = 8.6, p < .001^{***}$
3	> 1 sightings	31	10.8	0.46	5.68	0.68	$t_{(60)} = 6.3, p < .001^{***}$

Appendix 2. Distances shifted between years

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

Variable	Variable	<i>n</i>	Min distance	Max distance	Mean distance	se	Median distance
Group	A	28	6.3	2106.9	298	101	99.2
	B	21	7.8	2239.6	285	129	71.7
	C	5	80.1	942.7	273.1	167	120.1
Previous age	Adults	28	7.8	1790.8	203.8	73	81.3
	First-years	19	6.3	2239.6	441.7	169	99.7
Sex	Females	20	6.3	1018.1	148.1	50	99.7
	Males	15	13	1790.8	241.7	125	71.7
Previous residency	Long-term	28	6.3	2239.6	207	179	55.9
	Short-term	6	71.7	288.1	130.3	32	106.8
	Passage	16	17.5	2106.9	481.4	178	132.5



