

JOURNAL OF AVIAN BIOLOGY

Research article

Recurrence, fidelity and proximity to previously visited sites throughout the annual cycle in a trans-Saharan migrant, the common cuckoo

Carlotta Bonaldi^{1,*}, Yannis Vardanis^{2,*}, Mikkel Willemoes², Chris M. Hewson³, Philip W. Atkinson³, Jan-Åke Nilsson², Raymond H. G. Klaassen⁴, Roine Strandberg², Anders P. Tøttrup⁵, Paul W. Howey⁶, Thomas Alerstam² and Kasper Thorup²  ^{1,7}

¹Center for Macroecology, Evolution and Climate, Globe Institute, University of Copenhagen, Copenhagen, Denmark

²Department of Biology, Lund University, Lund, Sweden

³British Trust for Ornithology, The Nunnery, Thetford, Norfolk, UK

⁴Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, the Netherlands

⁵Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

⁶Microwave Telemetry Inc, Columbia, MD, USA

⁷Department of Migration, Max Planck Institute of Animal Behavior, Radolfzell, Germany

Correspondence: Kasper Thorup (kasper.thorup@sund.ku.dk)

Journal of Avian Biology

2024: e03183

doi: [10.1111/jav.03183](https://doi.org/10.1111/jav.03183)

Subject Editor: Christiaan Both

Editor-in-Chief: Staffan Bensch

Accepted 14 February 2024



www.avianbiology.org

Most migratory birds return every year to the same breeding sites and some species show a similarly high fidelity to wintering grounds as well. Fidelity to stopover sites during migration has been much less studied and is usually found to be lower. Here, we investigate site fidelity and distance to previously visited sites throughout the annual cycle in the common cuckoo, a nocturnal trans-Saharan migrant, based on satellite-tracking data from repeated annual migrations of thirteen adult males. All birds (100%) returned to the same breeding grounds, with a median shortest distance of only 1 km from the locations in previous year. This was in strong contrast to a much lower and much less precise site fidelity at non-breeding sites during the annual cycle: In only 18% of the possible cases in all non-breeding regions combined, did the cuckoos return to within 50 km of a previously visited non-breeding site, with no significant differences among the main staging regions (Europe in autumn, Sahel in autumn, wintering in Central Africa, West Africa in spring, Europe in spring). The shortest distance to a previously visited non-breeding site differed among the staging regions with median shortest distances for the longest stopovers of 131 km [2;1223] (median [min;max]) in Europe, 207 km [1;2222] in Sahel in autumn and 110 km [0;628] in Central Africa. The distance to a previously visited staging site decreased with the time spent at the stopover in a previous year. Understanding the drivers of recurrence and site selection in migratory birds are important for guiding conservation efforts in this group but further studies are needed to establish whether the patterns observed in cuckoos are general among terrestrial migrants with continuous distribution of habitat.

Keywords: common cuckoo, migration, satellite tracking, site fidelity

© 2024 The Authors. Journal of Avian Biology published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

*Contributed equally.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Introduction

Seasonal migration is wide-spread across animal taxa, allowing animals to exploit favourable resources over the course of the year as well as avoiding unfavourable conditions or predators and diseases (Alerstam et al. 2003). In such animals, the annual cycle consists of alternating periods of residency and travel. Birds are generally restricted to one site during breeding but even outside this period the main part is spent residing rather than travelling. Because travel is costly in terms of fuel, storing fuel is necessary for travel and even for time-minimised travelling between sites the necessary fuelling for travel exceeds the time taken to travel (Hedenström and Alerstam 1997). The optimal balance between stopping over and travel depends on many factors and there are many other reasons than fuelling for stopping over, including recovery, moulting or benefits of survival (Linscott and Senner 2021).

Site fidelity, the return to previously visited sites, is common in obligate long-distance migratory birds (Holland 2014, Mettke-Hofmann 2014). During both breeding and winter, return rates are between 30–60% for passerine species and between 60–90% for non-passerines (Newton 2012, Monroy-Ojeda et al. 2013), indicating that most individuals return to the same breeding and wintering sites in successive years (Newton 2012). Site fidelity as a behavioural adaptation provides benefits such as reduced costs for foraging, breeding and migration in predictable environments but also requires potentially costly spatial memory, additional travel costs (for example less effective exploration of wind, Catry et al. 2004) and could reduce survival and reproductive prospects when conditions change between years if behaviourally restrained by fidelity (Newton 2008).

Site fidelity occurs at various scales. At the home range scale, intimate familiarity of a site might be beneficial while at the larger scale, suitability of general areas might play a role. While site fidelity patterns are generally attributed to memory (Merkle et al. 2022, Picardi et al. 2023), it might also arise by random or by repetition of behaviours without involving memory. Therefore, Picardi et al. (2023) argue that testing patterns against a null model of no site fidelity is necessary to infer memory-based processes.

In some migratory species, migration takes the form of to-and-fro migration between breeding and wintering areas (where a strategy of time-minimisation is likely) but in other migrants the non-breeding period includes several long, spatially separated stopover sites. The reasons for stopping over likely varies among those sites from recovering and fuelling as fast as possible to sites with seasonally appropriate survival conditions. In the first case, optimal conditions will enable a short stay whereas in the last case, good quality habitat will favour long stays (Ktitorov et al. 2010).

Patterns of site fidelity across the annual cycle have been well described in long-distance migratory species associated with patchily distributed wetland sites such as waders with accurate locations attained by GPS loggers or satellite tags. A general high site fidelity throughout the annual

cycle was reported in black-tailed godwits *Limosa limosa* (Verhoeven et al. 2021) and red knots *Calidris canutus* were often faithful even to specific mudflat areas within estuaries at staging sites (Buchanan et al. 2012). However, in whimbrels *Numenius phaeopus*, despite generally high site fidelity, for staging sites it was only high at sites used prior to long, nonstop flights (Ruthrauff et al. 2021).

Less is known about site fidelity across the annual cycle in terrestrial species with presumably more continuous habitat, less concentrated routes and ill-defined stopover regions. In migratory songbirds, annual returns to specific wintering sites have shown high site fidelity to be common across a variety of species. For example, American redstarts *Setophaga ruticilla* and black-throated blue warblers *Dendroica caerulescens* had high annual return rates to sites in Jamaica (51 and 46%, respectively) with little difference between sex and age classes in a study by Holmes and Sherry (1992) and they considered more than 50% annual return rates in Nearctic songbirds in winter to be common. Such a high return rates was found even at the territory scale in whinchats *Saxicola rubetra* wintering in Nigeria (Blackburn and Cresswell 2016). Furthermore, differences between residents and wanderers (wood thrushes *Hylocichla mustelina*; Rappole et al. 1989) and among habitats (American redstarts; Wunderle and Latta 2000) have been reported.

In contrast to breeding and wintering sites, year-round patterns including migratory stopovers have rarely been reported for terrestrial species. Migratory species exhibit a range of strategies during the non-breeding season, from having short migration periods and one long sedentary winter stay, to itinerancy, having multiple winter stays, to a sequence of sedentary stays during the non-breeding season. Most studies showing high fidelity have dealt with non-itinerant wintering but also for example Montagu's harriers *Circus pygargus* and lesser kestrels *Falco naumanni*, two species that move during winter and show some degree of social gathering, have high site fidelity (Trierweiler et al. 2013, Lopez-Ricaurte et al. 2023).

High small-scale return rates to specific stopover sites during migration, where birds might spend short periods of a few days to refuel, is typically rare among solitary migrating land birds (Catry et al. 2004), where available habitat is evenly distributed in most parts of the annual cycle. This could potentially result from site fidelity estimates based on return rates in site-based studies being biased because of returning individuals not being detected or because the sites investigated (typically migration hotspots) were not representative. In a study of hoopoes *Upupa epops*, based on geolocation and thus relatively imprecise locations, van Wijk et al. (2016) found that individuals were likely to use the same overall migration routes (69% of adults and 75% of second-year migrants) but winter site fidelity was low with 21% adults and 33% second-year migrants wintering within 150 km from the previous winter site, and for some individuals sites were more than 1000 km from the site occupied in the previous winter.

Few studies have investigated causes of variation. For example, while other activities could also be drivers of site fidelity, effects of moult activity were only found in one out of 16 species of songbirds (dark-eyed junco *Junco hyemalis*; Figueira et al. 2020).

Here, we study return to previously visited sites across the annual cycle in the common cuckoo, a long-distance Afro-Palaearctic migrant (Cramp et al. 1985). The common cuckoo has been intensively studied as a model species for avian brood parasitism (Stoddard and Kilner 2013) but little data exist on site fidelity and all is restricted to the breeding grounds: indirect genetic evidence for weak natal philopatry (Gibbs et al. 2000), and two multi-year radio-telemetry studies on breeding localities (Honza et al. 2002, Nakamura et al. 2005). One study showed 50% of adult cuckoos being recovered within 20 km of the ringing site (Lindholm 1999) and another study estimated adult mortality as 48% (Brooke and Davies 1987), both indicating that a large proportion of surviving cuckoos return to the same site the following year.

We expect that cuckoos, being terrestrial and insectivorous, would show similarities in migratory habits to passerine migrants. In general, migratory species experiencing more evenly distributed potential stopover sites, as shaped by the landscape and habitat properties, are more likely to show weak fidelity to specific sites (Catry et al. 2004). However, in contrast to the passerines, which spend typically only short periods in the stopover sites, the common cuckoos remain several weeks, or months, in their staging areas (Warnock 2010). This variation in the duration of the stay, in relation to the annual cycle may then reflect the importance of each stationary period, thus promoting site fidelity. Consequently, we predict a positive effect of the duration of the period of residency on the probability of returning to the same site.

By using long-term satellite tracking data of birds breeding in different European populations, we identify the location and duration of their individual residency periods and measure the minimum distances to sites visited during previous years' residency periods. We estimated proportions of likely revisits and reuses of previous sites as well as to the general areas of the familiar sites based on different distance criteria. Furthermore, we considered the proximity to previously visited sites and used this continuous variable to analyse potential factors affecting the return to familiar areas. Our main questions are: 1) To what degree are cuckoos faithful to sites in the main residency regions of their annual migration cycle (breeding, staging on northbound and southbound migrations and wintering sites)? 2) What is the scale of dispersal between years at the revisited areas, and how is this affected by annual stage? 3) Are cuckoos more likely to revisit sites where they stayed for longer periods compared to sites where they stayed for shorter periods? The differences in site fidelity among stages and scales support our understanding of the drivers of and variation in staging behaviour and the importance of these behaviours in the annual routine of a long-distance migrant.

Material and methods

Tracking data

We analysed satellite-tracking data from 13 adult common cuckoos that were tracked during two, three or four successive years, from June 2010 to February 2015 (Willemoes et al. 2014, Hewson et al. 2016). During the annual cycle the cuckoos visited overall the same regions and at least moved onward from the first region visited on migration after breeding in the second year of tracking. Three individuals originated from a population breeding in Denmark (55.61–56.09°N, 12.12–12.59°E), nine from Great Britain (50.49–57.39°N, –5.82–1.97°E) and one from 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 3–1 have the highest accuracy with an error ellipse of less than one kilometre, Z has the lowest, unspecified, accuracy and 0, A and B are also unspecified but normally within 10 s of kilometres): we excluded all positions of class Z. Each transmitter was programmed to operate on a duty cycle of 10 h on and 48 h off, aiming to optimise 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 10 h transmission period.

Stationary 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 (Fig. 1). Birds stayed for longer periods in the following six broader regions during the annual cycle: 1) breeding area (50.49–68.48°N, –5.82–18.80°E), 2) staging sites in Europe during autumn migration (39.71–67.42°N, –3.38–30.41°E), 3) staging sites in the Sahel and Savannah zones 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 sites in West-Africa during spring migration (6.21–11.32°N, –12.12–5.27°E), 6) staging sites in Europe during spring migration (33.16–49.12°N, –6.86–14.65°E).

We distinguished between a visit to a site, which could be of only short duration (potentially just flying over), and use of a site, which would require staying for a number of days. Revisiting or reusing a site would require the same smaller range (5 km) to be visited or used as in a previous year. Revisiting or reusing a general area would require the same larger area (25 or 50 km) to be visited or used. Based on stationary sites defined as locations within 25 km over a minimum of three days (period including at least two transmission intervals, i.e. 10 h on + 48 h off + 10 h on), we identified likely revisits when the observed proximity of locations was within 5 km from a previous stopover, and potential reuses of previous sites when the distance between centroids of stopovers of previous and following years was less than 5 km.

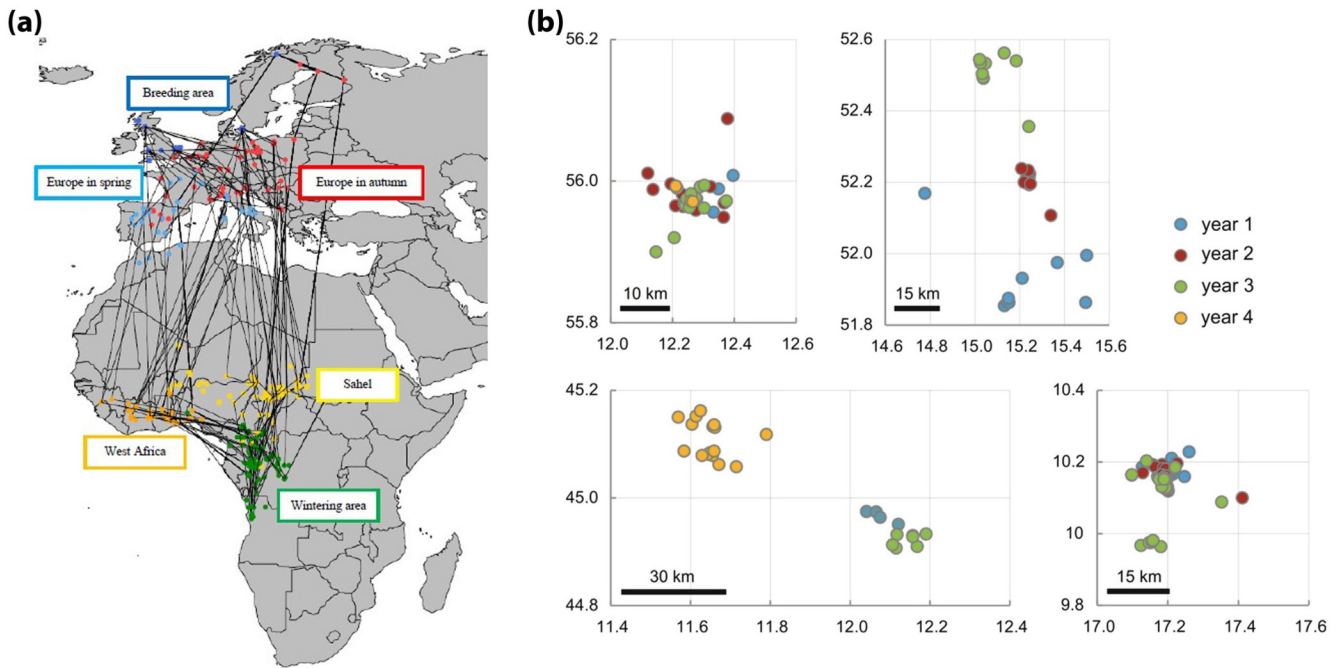


Figure 1. (a) Migratory routes of satellite-tracked adult common cuckoos ($n=13$). For each individual cuckoo, lines connect the longest stationary period in each region. Sites used by cuckoos during stationary periods (Duration ≥ 3 days) throughout the annual loop migration are indicated with different colours (Breeding = blue, Europe-Autumn = red, Sahel = yellow, Winter = green, West-Africa = orange, Europe-Spring = light blue). Positions within a 25 km radius were considered as the same stopover. (b) Examples of the variation in geographic distribution of locations (latitude and longitude according to y- and x-axes, respectively) in different years at revisited sites (definition of site in methods). Symbols show one location as recorded by satellite telemetry from each 10 h transmission period during the bird's stay (≥ 7 days) at the site, with different colours for locations from different years. (a) no. 36487, breeding site, (b) no. 36332, Europe autumn, (c) no. 62608, Europe autumn and (d) no. 115591, Sahel. Note that in (c) the site was not visited in year 2, representing a case of a gap year (in b and d birds were only tracked for three years 1–3).

Additionally, we identified visits to and uses of the general areas used previously occurring within 25 or 50 km of these stationary sites.

Definition of individual stationary sites

Our definition of stationary sites was largely dictated by the duty cycle of the transmitters and the (low) precision of location estimates. We only considered stopovers of minimum three days (two transmission periods) to avoid including occasions of a bird being forced to stay for example from conditions not being suitable for onward migration (birds usually leave a stopover within one day from their arrival if its quality is suboptimal; Ktitorov et al. 2010).

Williams et al. (2016) estimated cuckoo stopover ranges as on average 12 km². Allowing for uneven shape, we equate this to an approximate 5–10 km range (daily commuting was reported in breeding cuckoos increasing daily ranges considerably which might also occur outside of breeding; Nakamura and Miyazawa 1997). In any case, the uncertainty of location estimates is beyond this range, and we therefore used a 25 km distance criterion (i.e. grouped all the positions within a 25 km radius as part of the same stopover) as has been used in other studies for defining stopover periods (Strandberg et al. 2008).

Furthermore, given the low site fidelity based on the shorter stopovers (results), we also investigated longer-term stopovers including at least three entire transmission periods (≥ 7 days) that are unlikely to include shorter-term recovery behaviours. During longer stays, individuals tended to move more around locally and to avoid classifying such general areas as separate stopovers, we used a 50 km range criterion.

Spatial scales and measures of recurrence

We investigated recurrence at several different spatial scales and also investigated different measures of revisitation. Memory of for example foraging spots at specific sites is likely only possible within the relatively small normal range size – here estimated as potentially up to 5 km from the centre. Thus, we considered this range as evidence of birds using intimate knowledge of a site (i.e. ranges largely overlapping) familiar from a previous year and estimated the proportion of revisits (proximity) within this range and the proportion that had a stationary site within this range (reuse). Proximity within 25 or 50 km and stays of at least 3 or 7 days were considered evidence of familiarity of the general area. We based fidelity to staging sites on proximity within 50 km. For any given site visited by an individual, the number of possible visits to the same site was counted as the number of

following years where the individual was tracked through the same stage/regions (breeding, Europe autumn, Sahel, wintering, West Africa, Europe spring). Site fidelity was calculated as the number of observed visits to the site divided by the number of possible visits to the site, which corresponds to the average probability for an individual of revisiting a given site.

Unfortunately, the rather imprecise and temporally separated data do not allow for sensible calculation of range overlap between years.

Test for revisitation occurring by chance

Revisitation could simply be a result of random events rather than a behavioural decision based on memory. Picardi et al. (2023) propose that site fidelity should be defined as 'patterns of return that deviate from a null expectation derived from a memory-free movement model'. For the cuckoo stopovers, it is highly improbable that repeated use during different years of sites would occur by chance even within 50 km: The fraction of sites used by different individuals that are situated within 50 km from each other within a given non-breeding region was as low as 0.7% (based on 2760 pairwise comparisons of sites used by all different individuals in this study) or 0.3% (based on 1155 pairwise comparisons of sites used by different individuals from the same breeding population, either UK or DK birds). The frequency distribution of pairwise distances between sites used by different individuals within the given non-breeding staging regions is shown in Supporting information.

Distance between sites used in different years.

To investigate whether choice of sites were affected by the duration of previous stays, we identified the minimum distance between all positions in one year and those in the following year. For each staging site in year t , we then calculated the average of the minimum distances to positions in year $t+1$ for each position during the duration of the stay. Finally, we used the duration of each stay in year t in days as a measure of previous experience. Thus, each data point used for analysing effects of duration of stays in previous years consists of the duration of a stay in year t and the average distances to positions in the following year. We tested both linear and linear mixed models of average distances, using staging region, duration of stopover in the previous year and individual as explanatory variables.

Individual route repeatability

All individuals were faithful to their previous tracks among the years, following a common pattern, except for one British individual (no. 128297), which used two completely different routes during the first and second migration from the breeding area to the wintering grounds. Overall results were not affected by excluding this individual and here we show the results considering all individuals, because the variability given by no. 128297 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 artefact due to the small sample size used in this study.

Statistical analyses

We tested different models to assess whether the distance between stopovers in consecutive years could be predicted by the duration of the stopover, and if this relationship differed between different staging regions. Because repeated tracks were often incomplete, few data from a small number of individuals were available from the West-African and European spring stopover regions and these were excluded in the complex models. We ran a combination of linear mixed models, considering the average minimum distance between stopovers in consecutive years as the dependent variable. Distances were log transformed to adjust for the skewed distribution with rare longer distances. We included the duration of the stopover (Days), staging site (Region) and the interaction as a fixed effects. Individual (ID) was included as a random effect (intercept). Models were compared based on AIC (Akaike Information Criterion) scores to identify the best model for our data. Models with Individual (ID) included as fixed effect in fact improved model fit compared to the random factor primarily because of the aberrant route in individual no. 128297. Whether individual ID was included as a random or fixed effect did not influence ranking of models and we report only the more general results based on a random effect.

Statistical analyses were performed using R ver. 3.4.3 (www.r-project.org).

Results

Overall, spatiotemporal schedules were similar across individuals with stationary periods during breeding, in Europe and Sahel in autumn, in Central Africa in winter and in West Africa and Europe during spring (Fig. 1a). Individuals frequently visited sites close to those visited previously (< 50 kms, Fig. 2) but with variation across individuals and years (Fig. 1b). At the non-breeding sites, we found various types of visits in following years, with 1) extensive spatial overlap in its locations between years, 2) partial overlap in ranges between years, 3) one or two locations within previous year's range, but staying within a new range nearby, or 4) separate ranges without any recorded instances of contacts, or overlap between years (but with the ranges within 50 km distance; see examples in Fig. 1b). Many of these cases indicate that despite the cuckoos knowing their previous sites, they did not use the same range, but established a new one in the vicinity.

Across the whole annual cycle, individual cuckoos rarely revisited sites (i.e. were located within 5 km) or potentially reused a previously visited site (13 and 4%, respectively). However, site fidelity was common on the breeding grounds and much less so outside of the breeding area (Fig. 2a,

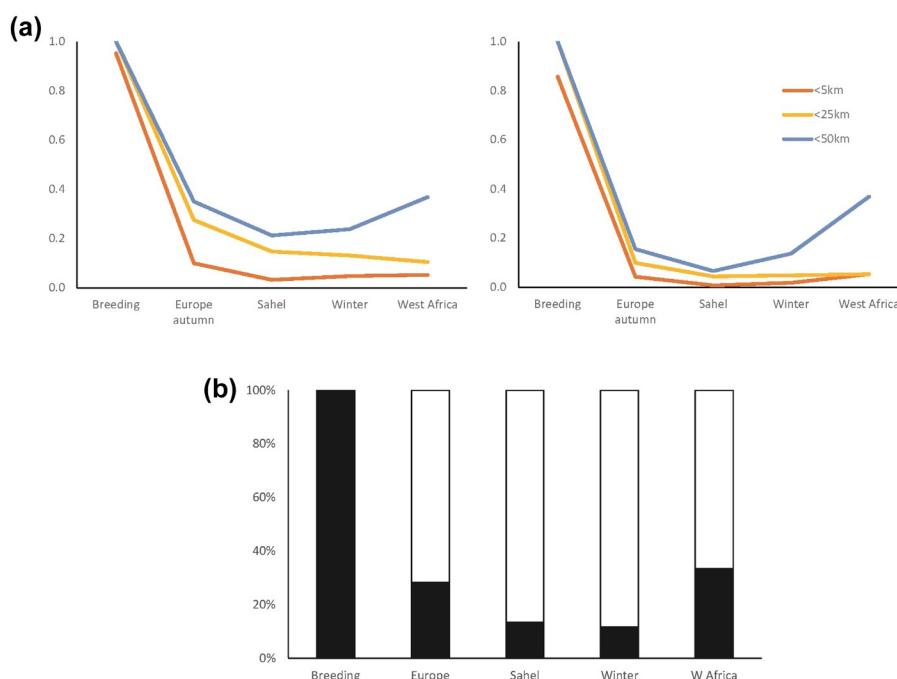


Figure 2. (a) Proximity to previously used sites across different regions. Proportion of individuals (a) visiting and (b) using a site within a certain distance (5, 25, 50 km) from a site used in a previous year (three days duration; 25 km range). (b) Variation across regions and phases of the migratory cycle in the probability of adult common cuckoos staying on average within 50 km from a site visited (Duration ≥ 7 days) in a previous year. Black bars show the proportion of cases when a site was revisited out of the total number of possible revisits.

Supporting information; $\Delta AIC > 100$ between linear models with and without Region including breeding; no overlap between confidence intervals for breeding and other regions). Here, 95% revisited the same breeding site (i.e. positions within a 5 km distance) and 86% reused (i.e. centroids separated by less than 5 km) the same site in a later year. And all individuals returned to the same breeding area (i.e. within 25 km of the previously used breeding site).

Away from the breeding area, visits to the same site (within 5 km) occurred between 10% (Europe autumn) and 0% (Europe spring) with 5% in the wintering area, and use of the same site occurred between 5% (West Africa) and 0% (Europe spring) with 2% in winter (Fig. 2a, Supporting information). Revisits and reuse of the same general area were more frequent than to the same site (Fig. 1; except for stopovers in Europe in spring where no visits were within 50 km of a previous site).

Depending on the region, between 37 and 21% came within and between 37 and 7% used sites within 50 km from those used in previous years. The return rate to non-breeding staging sites for longer stays only (minimum 7 days) ranging up to 50 km was on average 18% within 50 km in location (Fig. 2b; range 12–33% in different non-breeding regions; no significant differences between non-breeding regions).

Differences in distance to previously visited sites among regions (Fig. 3) were strongly supported ($\Delta AIC = 6.48$ between linear models with and without Region excluding breeding). Overall birds tended to winter not very far from the previous site (median 110 km; Fig. 3, Supporting

information) and also in Europe in autumn and in West Africa in spring birds were staying consistently closer to a previous site (131 and 119 km, respectively) than in the Sahel and in spring in Europe (207 and 504 km, respectively).

Effects of duration of previous stays on proximity of sites visited in a later year were strongly supported. The best model of average minimum distance across Europe autumn, Sahel and winter regions was the full model considering the effect of both staging site, stopover duration and the interaction between the two, and ID ($\Delta AIC = 3.53$ to the second best model; Table 1). In general, birds stayed closer to a previously visited site if the previous stay had been longer ($\Delta AIC = 33.38$ when removing Duration from the model Region + Duration + (1|ID); Table 1). In Europe during autumn, this relationship was the strongest, slightly less in the Sahel and only a weak relationship on the wintering grounds (Fig. 4). Also when not considering no. 128297, we found a significant effect of both stopover duration, staging site and their interaction on site fidelity. The long distances in the Sahel region are all from individual no. 128297 that undertook two completely different migration routes during consecutive years (indicated in Fig. 4).

Discussion

Our analysis of satellite tracking data from individual-based repeated annual migratory cycles demonstrates that the cuckoos have a high site fidelity to their breeding sites but a much

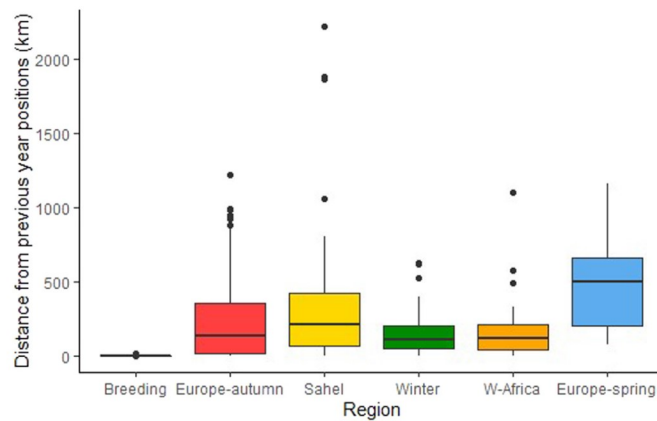


Figure 3. Variation across regions and phases of the migratory cycle of adult common cuckoos in the distance to a previous year's position. Lower values of distance from previous year position indicate a stronger site fidelity and vice-versa. All study individuals are included ($n=13$) and each individual often had more than one separate stay in each region. The sample size of stopover positions (where the bird stayed ≥ 3 days) for which site fidelity was calculated differed between the stationary periods (Breeding=21, Europe-Autumn=40, Sahel=61, Winter=84, West-Africa=19, Europe-Spring=12). Boxplots show minimum values, first quartile, median, third quartile and maximum values.

lower degree of fidelity to sites used during the non-breeding part of the annual cycle (autumn, winter and spring). We observed a few cases where cuckoos revisited non-breeding sites two years after their previous visit (not having visited the site in the intervening year). Observed cases of individuals revisiting sites very briefly, after which they moved and settled at a more distant new site, indicate that the cuckoos remember and recognize sites where they have stayed in earlier years, but in these cases choose not to use them for a longer visit again. Given that tags are only transmitting for shorter periods (10 h on and 48 h off), it is reasonable to

assume that more such cases of brief revisits have occurred during periods with no transmission, but that they have thus remained unnoticed in this analysis. We also find that individuals spending more time at a stop-over site in one year have a higher probability to return the next year and that this relationship varied among regions.

In accordance with the literature, all the 13 individual cuckoos we tracked for 2–4 years returned to their previous breeding territories, showing an apparent 100% return rate, which can only be compared with levels shown in long-lived species with very high adult annual survival (c.f.

Table 1. AIC statistics of models explaining variation in distance to previous years' position ($\log(\text{AvgMinDist})$) in all individuals from Europe in autumn, Sahel and winter area. Parameters of the best model shown below.

Model	K	ΔAIC	AIC	Deviance
Region + Duration + Region \times Duration + (1 ID)	8	0	647.61	631.61
Region + Duration + Region \times Duration	7	3.53	651.14	637.14
Region + Duration + (1 ID)	6	10.26	657.87	645.87
Duration + (1 ID)	4	13.36	660.97	652.97
Region + Duration	5	16.54	664.15	654.15
Duration	3	18.20	665.81	659.81
Region + (1 ID)	5	43.64	691.25	681.25
1 + (1 ID)	3	47.45	695.06	689.06
Region	4	52.12	699.73	691.73
1	2	54.79	702.40	698.40
Best model				
Random effects	Groups	SD		
	(Intercept)	0.441		
	Residual	1.290		
Fixed effects	Parameter	Estimate		
	(Intercept)	5.878		
	Region: Sahel	-0.080		
	Region: Winter	-0.981		
	Duration	-0.097		
	Region: Sahel \times Duration	0.051		
	Region: Winter \times Duration	0.075		

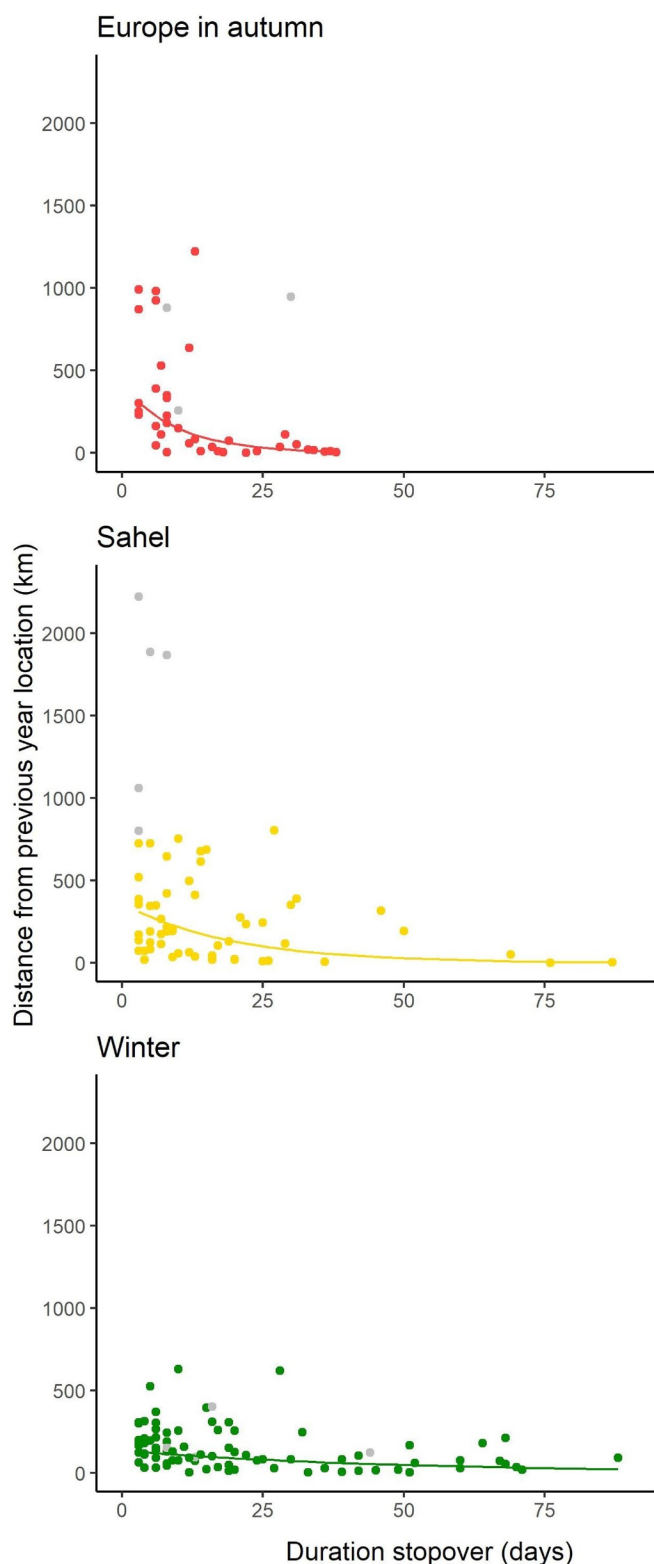


Figure 4. Relationship between duration of a stopover (days) used by adult common cuckoos and distance from a previous year's position in the three staging areas considered for the analyses (Europe-Autumn, Sahel, Winter). Each data point consists of the duration of a stay in a previous year and the average minimum distances between positions in the two years during the duration of the

Newton et al. 2016). Site fidelity was generally much lower and the distances to previously visited sites longer outside the breeding season. Site fidelity is generally low for short staging sites (Catry et al. 2004) but at longer-term wintering sites many species of long-distance migrant passerines show high levels of philopatry (Catry et al. 2004, Newton 2008). During the non-breeding season, staging periods in cuckoos are generally quite long (weeks to months) with movements in response to rainy seasons and the large-scale seasonal availability of food (Cramp et al. 1985, Thorup et al. 2017). Thus, it might be more important for them to find the same general area in subsequent years than to locate the exact position that they occupied in the previous years. The much higher recurrence in other species such as wintering pied flycatchers *Ficedula hypoleuca*, but also itinerant willow warblers *Phylloscopus trochilus* (Salewski et al. 2002), may be explained by different foraging strategies and movement patterns, with specialist species such as the cuckoo having to track their seasonally changing food resources. Nevertheless, the low degree of non-breeding site fidelity reported in hoopoes (van Wijk et al. 2016), a species with relatively short migration and a long sedentary winter stay, appears similar to our estimates in cuckoos. Because both cuckoos and hoopoes are larger insectivores with low fidelity one might speculate that intimate knowledge of foraging opportunities is less important when foraging on larger insect food items, or that foraging locations are less spatially consistent between years.

Though fidelity at non-breeding compared to breeding sites was low, we found staging sites to be closer to previously visited sites during winter than during autumn migration. This is potentially caused by differences in the spatial heterogeneity of suitable habitat. Furthermore, the relationship between stopover duration and site fidelity was strongest during the European autumn staging sites, intermediate in the Sahel region in autumn, and weakest on the wintering grounds. It might be better for birds to stop in areas they already visited for a long time, in order to take advantage of the familiarity of the site, minimising the energy costs deriving from stopping in an unfamiliar site (Wikelski et al. 2003) and spending proportionally longer time at a site could potentially reflect stopover habitat quality. Whilst, however, in time-minimised migration, high quality habitat might result in faster onward migration (Davies et al. 2023), preferential occupation of high quality sites within a migration stage might still result in a positive relationship between stopover duration and recurrence and for example in resident herring gulls *Larus argentatus* the variation in feeding site fidelity

stopover in the previous year. All study individuals are included ($n = 13$) and each individual often had more than one separate stay in each region. Lower values of distance from the sites visited in the previous year by the individual indicate a stronger site fidelity at a stopover site (where the bird stayed for ≥ 3 days); positions within a 25 km radius were considered as one stopover. Points from individual no. 128297 are shown in grey.

appeared not to be related to time or energy budgets that could indicate good foraging habitat (Van Donk et al. 2020).

Compared to spring migration strategies, autumn migration strategies might be more dependent on food availability at stopover sites (Nilsson et al. 2013). Thus, the need for good quality habitat during stopover in Europe could partly explain why site fidelity is more strictly related to previous experience here. The weaker relationship found in the Sahel region might be because resources are less spatially aggregated (Willemoes et al. 2014) and that less fuelling is required resulting in a lower need to find the same sites among different years. Species that migrate using routes that cover more evenly distributed potential stopover sites, like many long-distance migrant passerines, are indeed more likely to show weak fidelity to these sites (Catty et al. 2004, Newton 2008). Alternatively, conditions in the Sahel are overall more variable and less predictable.

While breeding site fidelity is also high for cuckoos, it is lower during non-breeding than reported during both wintering and staging sites in waterbirds and for wintering in many land bird migrants. The patterns reported here might be more characteristic of species with less dependence on long-term breeding and winter residency though the similarly low fidelity found in hoopoes (van Wijk et al. 2016) might point to foraging or food choice as another potential explanation. Further high-resolution tracking across the annual cycle of terrestrial migratory species will be required to determine the causes of variation.

Funding – KT acknowledges support from The Danish Council for Independent Research (grant ID: 10.46540/2032-00171B).

Conflict of interest – Paul Howey is the director of Microwave Telemetry, the company that makes the satellite tags used for tracking the birds. There are no patents, products in development or marketed products to declare. This does not alter the authors' adherence to all the Journal policies on sharing data and materials. The remaining authors declare no competing interests.

Permits – No additional birds were tracked for this study.

Author contributions

Carlotta Bonaldi: Formal analysis (equal); Investigation (equal); Methodology (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Yannis Vardanis: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Mikkel Willemoes: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Writing – review and editing (equal).

Chris M. Hewson: Conceptualization (equal); Data curation (equal); Writing – review and editing (equal).

Philip W. Atkinson: Conceptualization (supporting); Writing – review and editing (equal).

Jan-Åke Nilsson: Investigation (equal); Writing – review and editing (equal).

Raymond H. G. Klaassen: Conceptualization (equal); Writing – review and editing (equal).

Roine Strandberg: Conceptualization (equal); Writing – review and editing (equal).

Anders P. Tøttrup: Conceptualization (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/jav.03183>.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.r4xgxd2mv> (Bonaldi et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Alerstam, T., Hedenström, A. and Åkesson, S. 2003. Long-distance migration: evolution and determinants. – *Oikos* 103: 247–260.
- Blackburn, E. and Cresswell, W. 2016. High winter site fidelity in a long-distance migrant: implications for wintering ecology and survival estimates. – *J. Ornithol.* 157: 93–108.
- Bonaldi, C., Vardanis, Y., Willemoes, M., Hewson, C. M., Atkinson, P. W., Nilsson, J.-Å., Klaassen, R. H. G., Strandberg, R., Tøttrup, A. P., Howey, P. W., Alerstam, T. and Thorup, K. 2024. Data from: Recurrence, fidelity and proximity to previously visited sites throughout the annual cycle in a trans-Saharan migrant, the common cuckoo. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.r4xgxd2mv>.
- Brooke, M. D. L. and Davies, N. B. 1987. Recent changes in host usage by cuckoos (*Cuculus canorus*) in Britain. – *J. Anim. Ecol.* 56: 873–883.
- Buchanan, J. B., Lyons, J. E., Salzer, L. J., Carmona, R., Arce, N., Wiles, G. J., Brady, K., Hayes, G. E., Desimone, S. M., Schirato, G. and Michaelis, W. 2012. Among-year site fidelity of red knots during migration in Washington. – *J. Field Ornithol.* 83: 282–289.
- Catty, P., Encarnação, V., Araújo, A., Fearon, P., Fearon, A., Armelin, M. and Delaloye, P. 2004. Are long-distance migrant passerines faithful to their stopover sites? – *J. Avian Biol.* 35: 170–181.
- 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. and Wilson, M. G. 1985. Handbook of the birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic, vol. IV: terns to woodpeckers. – Oxford Univ. Press, pp. 402–416.
- Davies, J. G., Kirkland, M., Miller, M. G. R., Pearce-Higgins, J. W., Atkinson, P. W. and Hewson, C. M. 2023. Spring arrival of the common cuckoo at breeding grounds is strongly determined by environmental conditions in tropical Africa. – *Proc. R. Soc. B* 290: 20230580.
- Figueira, L., Martins, P., Ralph, C. J., Stephens, J. L., Alexander, J. D. and Wolfe, J. D. 2020. Effects of breeding and molt activity on songbird site fidelity. – *Auk Ornithol. Adv.* 137: 1–15.
- Gibbs, H. L., Sorenson, M. D., Marchetti, K., Brooke, M. D., Davies, N. B. and Nakamura, H. 2000. Genetic evidence for female host-specific races of the common cuckoo. – *Nature* 407: 183–186.
- Hedenström, A. and Alerstam, T. 1997. Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. – *J. Theor. Biol.* 189: 227–234.
- Hewson, C. M., Thorup, K., Pearce-Higgins, J. W. and Atkinson, P. W. 2016. Population decline is linked to migration route in the common cuckoo. – *Nat. Commun.* 7: 12296.
- Holland, R. A. 2014. True navigation in birds: from quantum physics to global migration. – *J. Zool.* 293: 1–15.
- Holmes, R. T. and Sherry, T. W. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: implications for population dynamics, habitat selection, and conservation. – In: Hagan, J. M. and Johnston, D. W. (eds), *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, pp. 563–575.
- Honza, M., Taborsky, B., Taborsky, M., Teuschl, Y., Vogl, W., Moksnes, A. and Røskaft, E. 2002. Behaviour of female common cuckoos, *Cuculus canorus*, in the vicinity of host nests before and during egg laying: a radiotelemetry study. – *Anim. Behav.* 64: 861–868.
- Kitorov, P., Tsey, A. and Mukhin, A. 2010. The good and the bad stopover: behaviours of migrant reed warblers at two contrasting sites. – *Behav. Ecol. Sociobiol.* 64: 1135–1143.
- Lindholm, A. K. 1999. Brood parasitism by the cuckoo on patchy reed warbler populations in Britain. – *J. Anim. Ecol.* 68: 293–309.
- Linscott, J. A. and Senner, N. R. 2021. Beyond refueling: investigating the diversity of functions of migratory stopover events. – *Ornithol. Appl.* 123: 1–14.
- Lopez-Ricaurte, L., Vansteelant, W. M. G., Hernández-Pliago, J., García-Silveira, D., Casado, S., Garcés-Toledano, F., Martínez-Dalmau, J., Ortega, A., Rodríguez-Moreno, B. and Bustamante, J. 2023. Itinerant lifestyle and congregation of lesser kestrels in West Africa. – *J. Avian Biol.* 2024: e03063.
- Merkle, J. A., Abrahms, B., Armstrong, J. B., Sawyer, H., Costa, D. P. and Chalfoun, A. D. 2022. Site fidelity as a maladaptive behavior in the Anthropocene. – *Front. Ecol. Environ.* 20: 187–194.
- Mettke-Hofmann, C. 2014. Cognitive ecology – ecological factors, life-styles and cognition. – *Wiley Interdiscip. Rev. Cogn. Sci.* 5: 345–360.
- Monroy-Ojeda, A., Grosselet, M., Ruiz, G. and Valle, E. D. 2013. Winter site fidelity and winter residency of six migratory Neotropical species in Mexico. – *Wilson J. Ornithol.* 125: 192–196.
- Nakamura, H. and Miyazawa, Y. 1997. Movements, space use and social organization of radio-tracked common cuckoos during the breeding season in Japan. – *Jpn. J. Ornithol.* 46: 23–54.
- Nakamura, H., Miyazawa, Y. and Kashiwagi, K. 2005. Behavior of radio-tracked common cuckoo females during the breeding season in Japan. – *Ornithol. Sci.* 4: 31–41.
- Newton, I. 2008. The migration ecology of birds. – Academic Press.
- Newton, I. 2012. Obligate and facultative migration in birds: ecological aspects. – *J. Ornithol.* 153: 171–180.
- Newton, I., McGrady, M. J. and Oli, M. K. 2016. A review of survival estimates for raptors and owls. – *Ibis* 158: 227–248.
- Nilsson, C., Klaassen, R. H. G. and Alerstam, T. 2013. Differences in speed and duration of bird migration between spring and autumn. – *Am. Nat.* 181: 837–845.
- Picardi, S., Abrahms, B., Gelzer, E., Morrison, T. A., Verzuh, T. and Merkle, J. A. 2023. Defining null expectations for animal site fidelity. – *Ecol. Lett.* 26: 157–169.
- Rappole, J. H., Ramos, M. A. and Winker, K. 1989. Wintering wood thrush movements and mortality in Southern Veracruz. – *Auk* 106: 402–410.
- Ruthrauff, D. R., Harwood, C. M., Tibbitts, T. L., Warnock, N. and Gill, R. E. Jr 2021. Diverse patterns of migratory timing, site use, and site fidelity by Alaska-breeding whimbrels. – *J. Field Ornithol.* 92: 156–172.
- Salewski, V., Bairlein, F. and Leisler, B. 2002. Different wintering strategies of two Palearctic migrants in West Africa – a consequence of foraging strategies? – *Ibis* 144: 85–93.
- Stoddard, M. C. and Kilner, R. M. 2013. The past, present and future of ‘cuckoos versus reed warblers’. – *Anim. Behav.* 85: 693–699.
- Strandberg, R., Klaassen, R. H. G., Hake, M., Olofsson, P., Thorup, K. and Alerstam, T. 2008. Complex timing of marsh harrier *Circus aeruginosus* migration due to pre- and post-migratory movements. – *Ardea* 96: 159–171.
- Thorup, K., Tøttrup, A. P., Willemoes, M., Klaassen, R. H. G., Strandberg, R., Vega, M. L., Dasari, H. P., Araújo, M. B., Wikelski, M. and Rahbek, C. 2017. Resource tracking within and across continents in long-distance bird migrants. – *Sci. Adv.* 3: e1601360.
- Trierweiler, C., Mullié, W. C., Drent, R. H., Exo, K. M., Komdeur, J., Bairlein, F., Harouna, A., de Bakker, M. and Koks, B. J. 2013. A Palaearctic migratory raptor species tracks shifting prey availability within its wintering range in the Sahel. – *J. Anim. Ecol.* 82: 107–120.
- Van Donk, S., Shamoun-Baranes, J., Bouten, W., van Der Meer, J. and Camphuysen, K. C. J. 2020. Individual differences in foraging site fidelity are not related to time-activity budgets in herring gulls. – *Ibis* 162: 429–445.
- van Wijk, R. E., Bauer, S. and Schaub, M. 2016. Repeatability of individual migration routes, wintering sites, and timing in a long-distance migrant bird. – *Ecol. Evol.* 6: 8679–8685.
- Verhoeven, M. A., Loonstra, A. H. J., McBride, A. D., Both, C., Senner, N. R. and Piersma, T. 2021. Migration route, stopping sites, and non-breeding destinations of adult black-tailed godwits breeding in southwest Fryslân, the Netherlands. – *J. Ornithol.* 162: 61–76.
- Warnock, N. 2010. Stopping vs. staging: the difference between a hop and a jump. – *J. Avian Biol.* 41: 621–626.
- Wikelski, M., Tarlow, E. M., Raim, A., Diehl, R. H., Larkin, R. P. and Visser, G. H. 2003. Costs of migration in free-flying songbirds. – *Nature* 423: 704.

- Willemoes, M., Strandberg, R., Klaassen, R. H. G., Tøttrup, A. P., Vardanis, Y., Howey, P. W., Thorup, K., Wikelski, M. and Alerstam, T. 2014. Narrow-front loop migration in a population of the common cuckoo (*Cuculus canorus*) as revealed by satellite telemetry. – PLoS One 9: e83515.
- Williams, H. M., Willemoes, M., Klaassen, R. H. G., Strandberg, R. and Thorup, K. 2016. Common cuckoo home ranges are larger in the breeding season than in the non-breeding season and in regions of sparse forest cover. – J. Ornithol. 157: 461–469.
- Wunderle, J. M. and Latta, S. C. 2000. Winter site fidelity of Nearctic migrants in shade coffee plantations of different sizes in the Dominican Republic. – Auk 117: 596–614.