






Wind-associated detours promote seasonal migratory connectivity in a flapping flying long-distance avian migrant

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Abstract

1. It is essential to gain knowledge about the causes and extent of migratory connectivity between stationary periods of migrants to further the understanding of processes affecting populations, and to allow efficient implementation of conservation efforts throughout the annual cycle. Avian migrants likely use optimal routes with respect to mode of locomotion, orientation and migration strategy, influenced by external factors such as wind and topography. In self-powered flapping flying birds, any increases in fuel loads are associated with added flight costs. Energy-minimizing migrants are therefore predicted to trade-off extended detours against reduced travel across ecological barriers with no or limited foraging opportunities.
2. Here, we quantify the extent of detours taken by different populations of European nightjars *Caprimulgus europaeus*, to test our predictions that they used routes beneficial according to energetic principles and evaluate the effect of route shape on seasonal migratory connectivity.
3. We combined data on birds tracked from breeding sites along a longitudinal gradient from England to Sweden. We analysed the migratory connectivity between breeding and main non-breeding sites, and en route stopover sites just south of the Sahara desert. We quantified each track's route extension relative to the direct route between breeding and wintering sites, respectively, and contrasted it to the potential detour derived from the barrier reduction along the track while accounting for potential wind effects.
4. Nightjars extended their tracks from the direct route between breeding and main non-breeding sites as they crossed the Mediterranean Sea–Sahara desert, the major ecological barrier in the Palaearctic–African migration system. These clockwise detours were small for birds from eastern sites but increased from east to west breeding longitude. Routes of the tracked birds were associated with partial reduction in the barrier crossing resulting in a trade-off between route extension and barrier reduction, as expected in an energy-minimizing migrant.

5. This study demonstrates how the costs of barrier crossings in prevailing winds can disrupt migratory routes towards slightly different goals, and thereby promote migratory connectivity. This is an important link between individual migration strategies in association with an ecological barrier, and both spatially and demographic population patterns.

KEYWORDS

barrier crossing, detour, flapping flight, migration strategy, migratory connectivity, tailwind

1 | INTRODUCTION

The degree to which individuals from breeding populations disperse and mix during the non-breeding season is commonly referred to as migratory connectivity (Finch, Butler, Franco, & Cresswell, 2017; Webster, Marra, Haig, Bensch, & Holmes, 2002). Knowledge of its extent and causes is essential to understand processes affecting populations of migrants throughout the annual cycle (Boulet & Norris, 2006; Hewson, Thorup, Pearce-Higgins, & Atkinson, 2016; Webster & Marra, 2005), and to implement effective conservation efforts (Cresswell, 2014; Marra, Norris, Haig, Webster, & Royle, 2006; Vickery et al., 2014). Acknowledging that events outside the breeding season may affect individual fitness and thereby limit or regulate population numbers, studies on migratory connectivity focus on describing the spatial relationship between wintering and breeding locations (Finch et al., 2017, but see Cohen et al., 2019; Delmore, Fox, & Irwin, 2012; Knight et al., 2018; Trierweiler et al., 2014). However, also decisions made during the migration period could influence fitness by affecting survival (Klaassen et al., 2014; Sillett & Holmes, 2002) and arrival timing to breeding sites (Tøttrup et al., 2012). Environmental factors, such as vast inhospitable areas (Moreau, 1961, 1972) and prevailing wind patterns (Erni, Liechti, & Bruderer, 2005; Kranstauber, Weinzierl, Wikelski, & Safi, 2015), can have profound effects in shaping general patterns of migration on both continental and regional scales (Aurbach, Schmid, Liechti, Chokani, & Abhari, 2018; La Sorte, Fink, Hochachka, & Kelling, 2016). Winds can determine longitudes at which juveniles settle for stop-over and non-breeding sites during the first migration (Vansteelant, Kekkonen, & Byholm, 2017), sites that they may continue to use for the rest of their lives (cf Cresswell, 2014). Environmental factors could thus influence the degree of migratory connectivity between important parts of the annual cycle in many migrant species, depending on innate migratory direction in juvenile birds, locomotion mode and migratory strategy (Åkesson & Hedenström, 2007; Alerstam & Hedenström, 1998; Berthold & Helbig, 1992; Marra et al., 2006).

In migrating birds using self-powered flapping flight, the movement is fuelled by energy stored prior to the flight. According to flight mechanics, a mass gain increases the cost of transport resulting in a negatively accelerated relationship between added fuel load and potential flight range (Alerstam & Lindström, 1990; Pennycuik, 2008). Hence, if food was evenly distributed in the landscape, the most economical strategy in terms of energy expenditure during

migration would be by performing short flights with minimal fuel loads interrupted with short fuelling events (Alerstam, 2001). Barrier crossings, however, are usually preceded by periods of extensive preparations when fuel is stored. Birds whose objective is to minimize energy, or time, spent on migration could therefore benefit from flying along a route alternative to the direct (orthodromic) path, if it allows for shorter flight steps with smaller fuel loads (Alerstam, 2001; Alerstam & Lindström, 1990; Hedenström & Alerstam, 1997). As avian migrants move through a moving medium while flying, the distances (including the barrier) experienced by the birds could also be reduced if flights are in the same direction as the prevailing winds (Bruderer & Bolt, 2001; Erni et al., 2005; Liechti, 2006; Liechti & Bruderer, 1998; Figure 1). Hence, wind conditions along alternative routes need to be considered when calculating the birds' flight distances. Due to the large-scale circulation of air over the Sahara desert, supportive wind may be found both during autumn (at lower altitudes) and spring (at higher altitudes; Schmaljohann, Liechti, & Bruderer, 2009; Figure S1). As the preferred migration direction likely differs depending on the individuals' goal location, different routes across the barrier may become optimal for different individuals depending on their breeding origin, also in a wind field uniform in direction (Figure 1). Hence, migration strategies common between populations could still result in site-specific migration routes with strong migratory connectivity between breeding sites and barrier-related stopovers as a result.

We combined tracking data of European nightjar *Caprimulgus europaeus* (henceforth nightjar) from breeding sites across Western and Northern Europe to investigate their route characteristics and the degree of seasonal migratory connectivity in their annual migrations to and from southern Africa (Evens et al., 2017; Jacobsen et al., 2017; Norevik, Åkesson, & Hedenström, 2017). Focusing on the barrier dominating the Palaearctic–African migration system, Mediterranean Sea–Sahara desert (Moreau, 1961, 1972), we aimed to quantify the degree of migratory connectivity between different important stationary sites within the annual cycle (i.e. the breeding and main non-breeding sites, and the en route stop-over sites just south of the Sahara desert). We also aimed to evaluate potential benefits of the recorded track in relation to direct route between the breeding and main non-breeding site, and vice versa. Under the prediction that nightjars strive to minimize the energy cost of transport of migration, we tested if the reduction in energy expenditure in association with the barrier outweighed

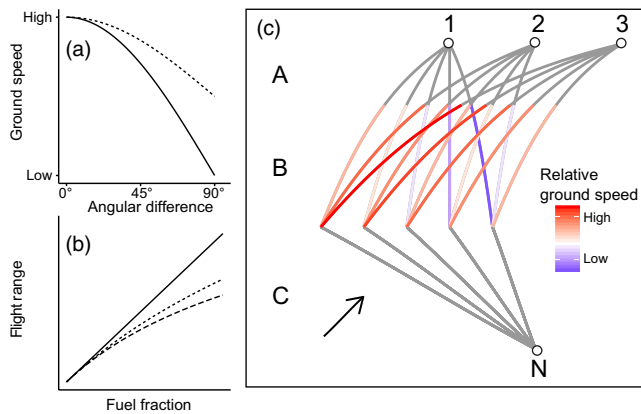


FIGURE 1 Illustration of the relationship between wind-induced ground speed along different routes across an ecological barrier and the potential energy saving via apparent migratory detours. (a) In a situation where the speed of the airflow equals the airspeed of the migrant (the horizontal dashed line), the ground speed decreases with increasing angular difference between the bird's preferred migratory direction and airflow. When accounting for the cost of compensating for side winds, the ground speed will drop to 0 as the angular difference approach 90° (solid line), while when only taking the tailwind component into account, the derived ground speed will be reduced to the migrant's airspeed. (b) Adapted from Figure 1 in Alerstam (2001). Due to the penalty of carrying extra mass, the fuel used for a single flight step will translate into a shorter flight distance in relation to the maximum range covered by multiple short steps with negligible fuel transport costs (solid line). The penalty will differ depending on whether the added fuel load increases both lift-related drag and parasite drag due to a larger body frontal area (dashed line) or only the former (dotted line). Presumably, the real cost is intermediate to the two. (c) Considering three populations (1–3) along a longitudinal gradient using a common non-breeding area (N), resulting in a weak migratory connectivity, migrating through two benign areas (A and C) and across an ecological barrier (B). Under a condition of constant airflow towards north-east (arrow) across the barrier, equal to the airspeed of the migrant, the ground speed (and inversely the air distance) across the barrier will vary with the relative migratory direction in spring. When accounting for the penalty of carrying large fuel loads across the barrier, an energy-minimizing migrant may use a route other than the shortest, given that the energy savings across the barrier (B) balance the cost of extra distances in the benign areas (A and C). Note that this simplified figure shows tracks following the same route over both in area B and in area A although migrants could adjust direction after the barrier crossing if it allows for a more economical route (c.f. Figure 5)

the cost of the added distance along the detoured routes, while accounting for potential wind effects. This approach enabled us to compare the relative benefits of the observed tracks in relation to the direct route from an energy perspective. Finally, to explore how well the observed tracks corresponded to population specific routes across the barrier associated with the lowest energy cost of transport of migration, we simulated migration tracks between the mean wintering site and a number of north European breeding sites via stopovers south and north of the Sahara desert and the Mediterranean Sea.

2 | MATERIALS AND METHODS

2.1 | Tracking data

In this study, we combined data from three tracking studies (Evens et al., 2017; Jacobsen et al., 2017; Norevik et al., 2017), on night-jars trapped at breeding sites along a longitudinal gradient from England (2.17°W) to Sweden (16.45°E). The tracking data collected between 2008 and 2015 consist of a mixture of light-level geolocation (GLS; $n = 25$) and GPS loggers ($n = 3$) from eight sites in five countries (Table 1 and Table S1). We defined the barrier crossing as any track segment that included the Mediterranean Sea–Sahara desert crossing, which resulted in a few cases (four in autumn and eight in spring) of barrier crossings starting or ending at the breeding sites. If the latitude component of the site in the southern end of the barrier was missing due to influences of the equinoxes (GLS), we used the mean latitude of all available individuals for the region in spring (6.38°N) and autumn (11.29°N), respectively. The amount of data for each part of the annual cycle varies due to sampling rate, shadowing effects (in the GLS data) and battery failure (Table 1). See each individual study for more information regarding trapping and logger retrieval (Evens et al., 2017; Jacobsen et al., 2017; Norevik et al., 2017).

2.2 | Migratory connectivity

We analysed the migratory connectivity by investigating where birds originating from different sites crossed the Sahara desert and spent their winter, for both autumn and spring migration. This was achieved by estimating the linear relationship between the longitude of the breeding sites, sites just south of the Sahara desert, and for the first and last wintering site for autumn and spring migrations, respectively. Additionally, we performed a Mantel test (Ambrosini, Møller, & Saino, 2009) to quantify the strength of migratory connectivity using the function *Mantel.rtest* in the R package *ADE4* (Dray & Dufour, 2007), in which the statistical significance of the Mantel correlation coefficient was determined by 9,999 random permutations. A Mantel test evaluates the similarity of two matrices, which in this case consist of distances between individuals at the respective sites. We also calculated the fraction of overlap of longitudes between the western and eastern birds by dividing the number of longitudes where both groups were represented by the total range of longitudes corresponding to stops for spring and autumn migrations, respectively.

2.3 | Workflow to calculate air distances and detour ratios

The shortest ground distance between the breeding and wintering ground is along the direct (orthodromic) route between the locations, but it is not necessarily the least costly route for flapping flying avian migrants. Provided that the route includes a crossing of a barrier, a detour (over benign areas) may reduce the total cost of

Site	Long.	Lat.	Location	n. aut.	n. wint.	n. spr.
				GPS/GLS	GPS/GLS	GPS/GLS
1	2.17°W	50.73°N	Wareham Forest, England	0/1	0/3	0/1
2	0.65°E	52.45°N	Thetford Forest, England	0/2	0/2	0/2
3	2.50°E	48.42°N	Forêt de Fontainebleau, France	0/1	0/1	0/1
4	5.30°E	51.04°N	Meeuwen-Gruitrode, Belgium	2/0	2/0	0/0
5	5.34°E	51.17°N	Bosland, Belgium	1/1	1/1	1/1
6	9.13°E	57.06°N	Northern Jutland, Denmark	0/6	0/6	0/6
7	16.43°E	57.11°N	Mönsterås, Sweden	0/11	0/11	0/11
8	16.45°E	56.24°N	Southern Öland, Sweden	0/1	0/1	0/1
Total				3/23	3/25	1/23

TABLE 1 Site locations and number of GPS and geolocator (GLS)-derived tracks available for autumn, winter and spring locations, respectively

migration if the barrier distance is reduced. Importantly, as winds move the air (in relation to the ground) within which the bird is flying, prevailing wind conditions along alternative routes may affect the air distance the bird has to fly to cover a certain ground distance, hence potentially affecting both barrier distance and the total cost of migration.

2.3.1 | Calculating ground distances and defining barrier segments

All route distances were quantified along the orthodrome, resulting in the shortest possible route between consecutive positions. We calculated the length along each route as the sum of distances between consecutive stationary sites, using the *distVincentyEllipsoid* function in the R package GEOSPHERE (Hijmans, 2015). We calculated the distance along the orthodrome between breeding and wintering sites to quantify the corresponding direct route (shortest ground distance). Length of the track segment that included the Sahara desert defined the observed barrier distance, while the corresponding distance along the direct route was calculated using the latitudes corresponding to the barrier-associated stationary sites.

2.3.2 | Sampling wind conditions

We sampled wind data from the period of movement at 30 linearly interpolated positions and timestamps between stationary sites along the routes using the function *gclIntermediate* in GEOSPHERE (Hijmans, 2015). We used the *NCEP.interp* function in RNCEP (Kemp, van Loon, Shamoun-Baranes, & Bouten, 2012) to obtain wind data for each location from the NCEP/NCAR Reanalysis project, as provided by the NOAA/OAR/ESRL PSD, Boulder, CO, USA (www.cdc.noaa.gov). We analysed winds at five of the available pressure levels (i.e. 1,000,

925, 800, 700 and 600 hPa), corresponding to approximate altitudes 100 m, 750 m, 1,500 m, 3,000 m and 4,300 m above sea level documented to commonly be used by migratory birds (Liechti & Bruderer, 1998; Schmaljohann et al., 2009). The data, consisting of west-east and south-north wind components, were combined into single wind vectors of strength and direction of the wind.

2.3.3 | Calculating air distance

We used the function *NCEP.Airspeed* in RNCEP (Kemp, Loon, et al., 2012) to calculate the wind profit, assuming that the nightjars had a fixed airspeed and adjusting the heading (and therefore the ground speed along the routes; Figure 1a,b) to maintain a preferred direction of migration (here defined as the direction to the next location along the track) for each pressure level (Kemp, Shamoun-Baranes, et al., 2012; Piersma & Jukema, 1990). Airspeed was set to 10 ms⁻¹, which is a radar measurement on the closely related red-necked nightjar *C. ruficollis* (Bruderer & Bolt, 2001). Based on the observations that migratory birds generally fly at altitudes associated with beneficial winds (Liechti & Bruderer, 1998; Schmaljohann et al., 2009), we extracted the maximal wind profit for each location and calculated the harmonic mean for each route segment. We derived the air distance along each segment by multiplying the ground distance with the ratio between the bird's airspeed and ground speed (Gill et al., 2014).

2.3.4 | Calculating expected detour ratios

To evaluate whether the detoured tracks could be energetically beneficial relative to the direct routes, we used the sum of derived air distances along the realized tracks and corresponding direct routes, respectively. This could be the case if the migrant experienced a shorter air distance across the barrier along the track relative to the derived barrier distance along the direct route, and that this reduction in barrier distance

outweighed the costs of the added distance of the detour. The derived air distances were used to calculate detours according to Alerstam (2001), who uses two versions of range equations. These are based on flight mechanics assuming that fuel load increases the drag corresponding to extra lift due to elevated mass as well as drag related to a larger body frontal area, or only the former. Presumably the real relationship is intermediate between the two equations (Alerstam & Hedenström, 1998; Figure 1b). Hence, the detour ratios were calculated as

$$\frac{D}{Y_b} = \frac{(f-f_a)}{2(1-1/\sqrt{1+f})} + a - 1, \quad (1)$$

or

$$\frac{D}{Y_b} = \frac{(f-f_a)}{\ln(1+f)} + a - 1. \quad (2)$$

where Y_b is the barrier distance along the direct route, D is the added distance along the detour, a is the fraction of barrier included in the detour, f is the fuel load required to cross the barrier, and f_a is the fuel load required to cross the reduced barrier along the detour. For a certain route with a defined barrier distance, these equations provide estimates of the potential added distance a bird may fly given a reduction in barrier distance relative to the given barrier for a break-even energy cost (Alerstam, 2001).

2.4 | Route simulation

The comparison between the direct route and the realized track provides an estimate of the energetic benefits of performing the observed detour, but it does not show if the birds follow the most beneficial route. To explore this, we simulated migration tracks between nine hypothetical breeding locations at latitude 55°N (longitudes 10°W to 30°E, with 5° increments) to the average wintering location of all the birds (22.54°E, 11.53°S). We used the average latitude component of the positions south of the Sahara desert (6.38°N), while shifting the longitudinal component with 5° increments from 10°W to 45°E to cover the whole range of Africa, and we added ten stops at latitude 40°N between longitudes 10°W to 35°E. This resulted in 1,080 possible routes between the wintering site and the breeding locations in autumn and spring, respectively. We sampled wind data at 50 intermediate positions along each segment at time points randomly drawn from the main migratory periods (1 March–30 April, and 1 August–30 October) in the years 2008–2017 for spring and autumn migrations, respectively.

2.5 | Statistical analysis

All analyses were performed in R 3.4.1 (R Core Team, 2017). Extent of detour was square root transformed and modelled using linear models with breeding longitude and season as fixed effects. The differences between the observed tracks and direct routes were modelled using linear mixed models (LMM) with breeding longitude as fixed effect and individual as random effect using the *lmer* function in the R package *LME4* (Bates, Mächler, Bolker, & Walker, 2015).

3 | RESULTS

3.1 | Migratory connectivity

Strong correlations were found between the longitudes of breeding site and barrier-related stops in both autumn ($\beta = 1.18$, $\pm 95\% = 0.75$ – 1.61) and spring ($\beta = 1.55$, $\pm 95\% = 1.13$ – 1.96), while neither breeding ($\beta_{\text{autumn}} = -0.02$, $\pm 95\% = -0.31$ to 0.27 , $\beta_{\text{spring}} = -0.05$, $\pm 95\% = -0.35$ to 0.25) nor barrier-related stops ($\beta_{\text{autumn}} = 0.07$, $\pm 95\% = -0.17$ to 0.31 , $\beta_{\text{spring}} = 0.06$, $\pm 95\% = -0.17$ to 0.31) correlated with the wintering area longitude (Figure 2a–f). This was also illustrated in the extent of longitudinal overlap of the western (England, France and Belgium) and eastern (Denmark and Sweden) breeding sites in the barrier-related stops and wintering locations. The longitudinal overlap in the stops related to the barrier was 11% and 24% of the total range in autumn and spring, respectively, while the overlap was 90% between wintering sites. The Mantel correlation coefficient (r_M) between breeding sites and barrier-related stops was 0.63 ($n = 26$, $p < .001$), and 0.69 ($n = 24$, $p < .001$) for autumn and spring stops, respectively. The Mantel correlation between breeding and wintering sites was lower, but still significant ($r_M = 0.25$, $n = 28$, $p = .002$).

3.2 | Realized routes and added ground distance relative to direct track

The length of detour in relation to the direct route varied with breeding longitude ($\beta = -0.011$, $SE = 0.0032$, $p < .001$; Figure 3a–d) and season ($\beta_{\text{spring}} = 0.2590$, $SE = 0.0570$, $p < .001$; Figure 3a–d), and the change across longitudes was larger in spring relative to autumn ($\beta = -0.0147$, $SE = 0.0047$, $p = .003$; Figure 3a–d).

3.3 | Air distances across barrier and evaluation of realized detour ratios

When accounting for wind conditions along the routes, the barrier distances along the tracks were significantly shorter than along the corresponding direct route in spring ($\beta = -529.1$ km, $SE = 177.5$, $p = .007$; Figure 4a), while no difference was distinguished in autumn ($\beta = -53.1$ km, $SE = 76.4$, $p = .49$; Figure 4b). The realized detour ratio in spring was significantly smaller than the calculated detour ratio according to Equation (1) ($\beta = -0.250$, $SE = 0.091$, $p = .009$; Figure 4e), and for Equation (2) ($\beta = -0.157$, $SE = 0.048$, $p = .002$; Figure 4c) indicating that the tracks, according to our estimations, were energetically more beneficial in comparison with the direct route. As we were not able to detect a post-barrier for eight of the birds, we per our definition extended the barrier to the breeding site. This results in an overestimation of the barrier distance that may affect the results. We therefore also run our analyses after including a hypothetical stopover site on the route at latitude 40°N just after the birds have crossed the barrier. The barrier distances along the tracks were still significantly shorter than along the corresponding direct route ($\beta = -425.8$ km,

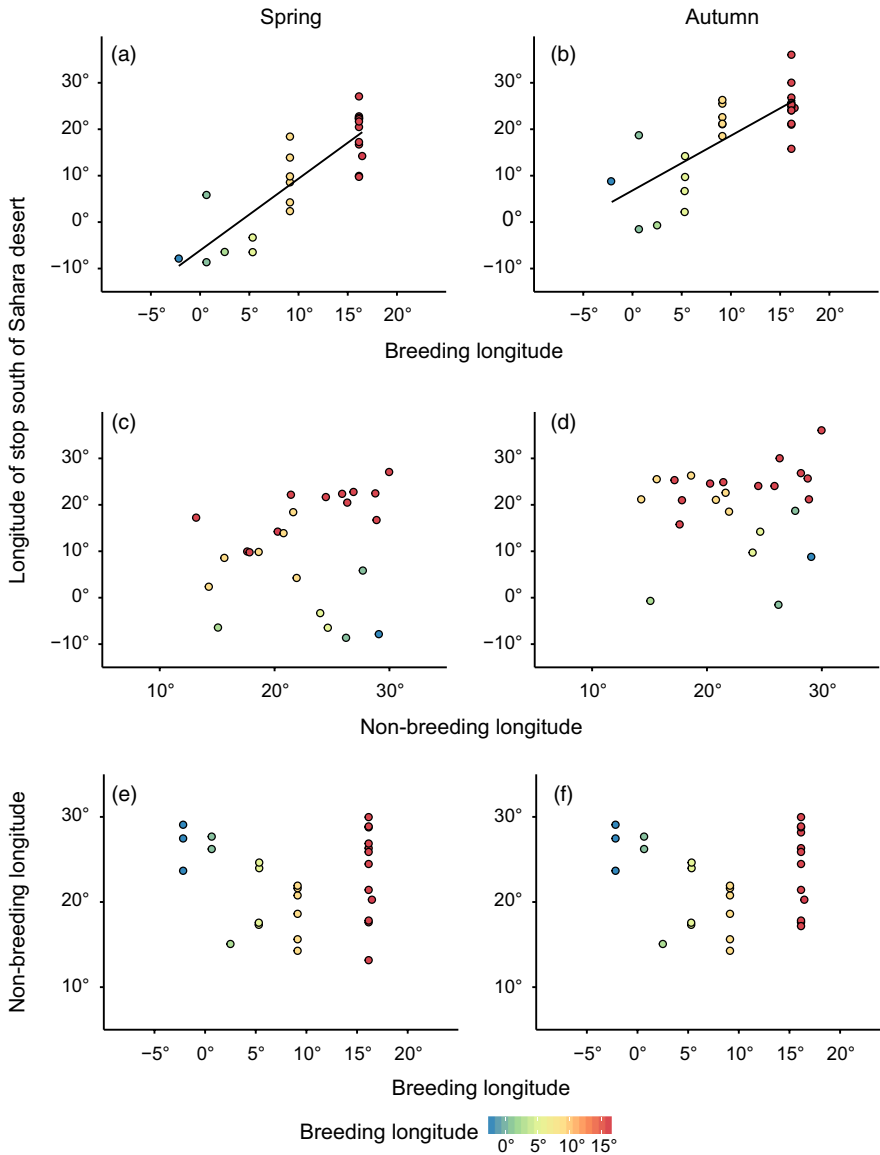


FIGURE 2 Correlations of longitude components between different parts of the annual cycle shown for spring (a, c, e) and autumn (b, d, f), respectively: a and b; longitudes for breeding sites and stopovers just south of the barrier; c and d; non-breeding and barrier-related stopover longitudes, and, e and f; breeding and non-breeding longitudes. Lines represent statistically significant relationships

$SE = 145.3$, $p = .008$), and the realized detour ratio in spring was significantly smaller than the calculated detour ratio according to Equation (1) ($\beta = -0.181$, $SE = 0.078$, $p = .025$), and for Equation (2) ($\beta = -0.143$, $SE = 0.045$, $p = .003$). We could not detect any significant differences between measured and predicted route extension according to Equation (1) in autumn ($\beta = 0.125$, $SE = 0.072$, $p = .089$; Figure 4e), or according to Equation (2) ($\beta = 0.111$, $SE = 0.067$, $p = .11$; Figure 4d).

3.4 | Route simulation

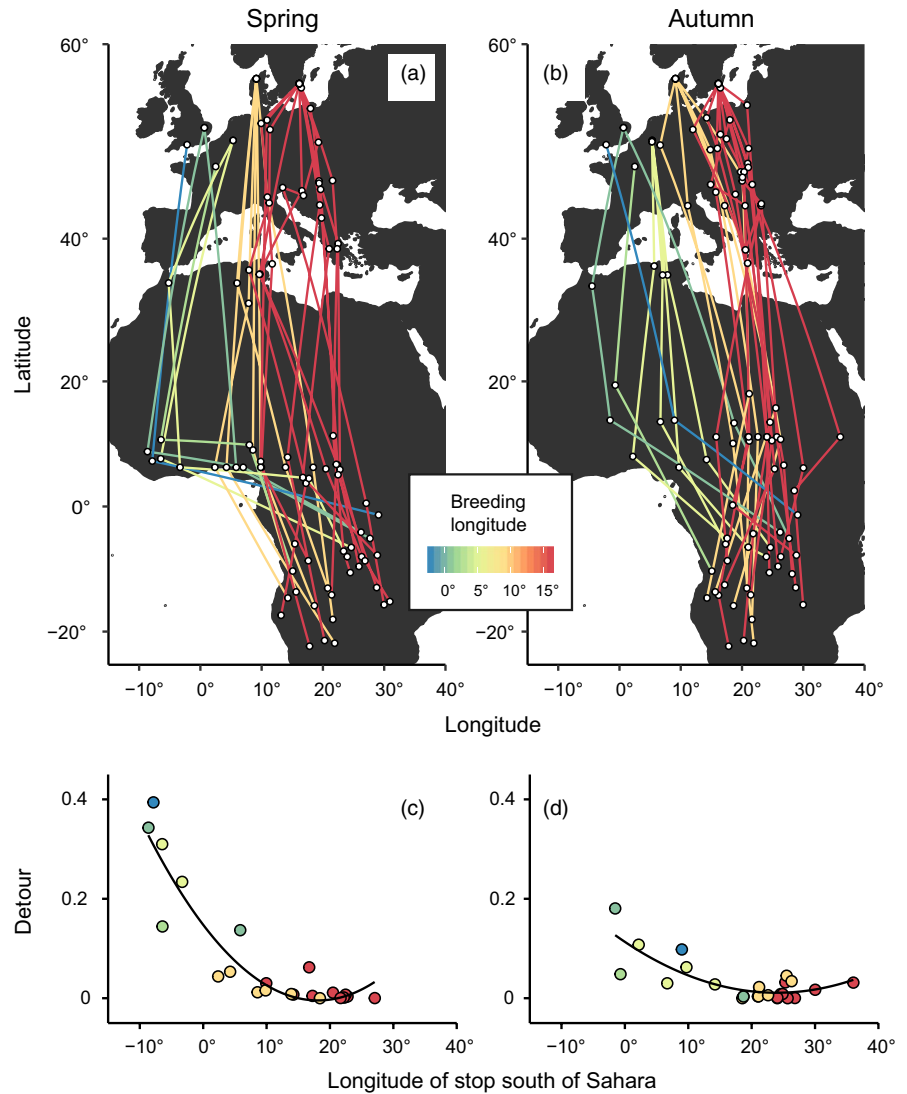
To explore how the nightjar tracks corresponded with the least costly routes, we simulated tracks between nine hypothetical breeding locations and the average position of the birds' wintering positions, which resulted in 1,080 routes for spring and autumn, respectively (Figure 5). The average routes of the 10% most beneficial routes from each breeding location depicted a clockwise loop migration broadly resembling the migration pattern of the tracked birds. Notably

however is the rather large spread of longitudes at which the more western populations cross the Sahara desert in spring (Figure 5a), and the rather well-defined eastern detour of autumn tracks in Europe (Figure 5b), which differs from the realized migration tracks. When plotting the twelve tracks for each breeding location associated with the shortest barrier crossing (safest route), without accounting for the cost of the extra travel distance, two apparent differences were noted (Figure S2). First, tracks from all breeding locations used the same point of barrier crossing resulting in a funnelling of all simulated routes prior the barrier, and secondly, simulated routes crossed the barrier along the westernmost or easternmost parts were clearly separated from the realized tracks of the nightjars.

4 | DISCUSSION

As a result of the miniaturizing of tracking technology, migration routes of individuals and populations are now being described at

FIGURE 3 Maps illustrating the distributions of stationary locations as estimated from the tracking devices for spring (a) and autumn (b), respectively. Lines illustrate the direct (orthodromic) routes between locations and colour corresponds to breeding site longitude. The detour, measured as the extended fraction of the track in relation to the direct routes between breeding and wintering sites for each bird for spring (c) and autumn (d), respectively. The fitted lines show the relationship between the longitude component of the location just south of Sahara and the extent of detour expressed as: $y = 0.08 - 0.48x + 0.23x^2$, $\text{Adj.}R^2 = 0.86$, and, $y = 0.03 - 0.15x + 0.09x^2$, $\text{Adj.}R^2 = 0.63^2$ for spring and autumn, respectively



an unprecedented rate. The empirical data sometimes reveal rather puzzling patterns involving large detours that, for example, have been proposed to be due to distribution of important fuelling sites (e.g. Lindström et al., 2011) or historical range expansions (Ruegg & Smith, 2002; Sutherland, 1998; Tøttrup, Pedersen, Onrubia, Klaassen, & Thorup, 2017). In this study, we explore how energy-minimizing migrants could perform detours to reduce the costs associated with barrier crossings by analysing migratory routes of nightjars within the Palaearctic–African migration system.

We demonstrate that optimal detours vary with breeding longitude, resulting in relatively strong migratory connectivity between barrier-related stopovers and breeding sites. Notably, the tracked nightjars exhibit a broad front parallel migration pattern across Europe and the Mediterranean Sea–Sahara desert and retain the spatial structure of the breeding sites through approximately half of both autumn and spring migrations, respectively (Salomonsen, 1955; Webster et al., 2002). The relatively low migratory connectivity between breeding and main non-breeding sites is commonly observed in avian long-distance migrants and may in this case be related to the geography of the African continent (Finch et al., 2017).

The opposite pattern of migratory connectivity across seasons was recently described in a group of Nearctic–Neotropical species migrating through the Gulf of Mexico region (Cohen et al., 2019), where the geographical structure between barrier-associated sites and breeding distribution estimated from isotope signature was generally weak, consistently weaker than earlier estimates of migratory connectivity between breeding and wintering sites (Cohen et al., 2019). The contrast to this study can likely be attributed to the general difference in distribution of land masses differs between the Old and New World migratory systems, as inter-population mixing generally decreases with increased land availability (Finch et al., 2017). Finer-scale studies using individual-based tracking techniques may further disentangle the contrasting patterns of seasonal migratory connectivity between the Old and New World migratory systems. Route selection under influence of varying weather patterns within the Gulf of Mexico region by individuals with known wintering and breeding sites (Deppe et al., 2015; Stanley et al., 2015) could be informative to further explore both how and why different populations may use different barrier-associated routes. The inherent shortcomings of geolocators in terms of spatiotemporal resolution

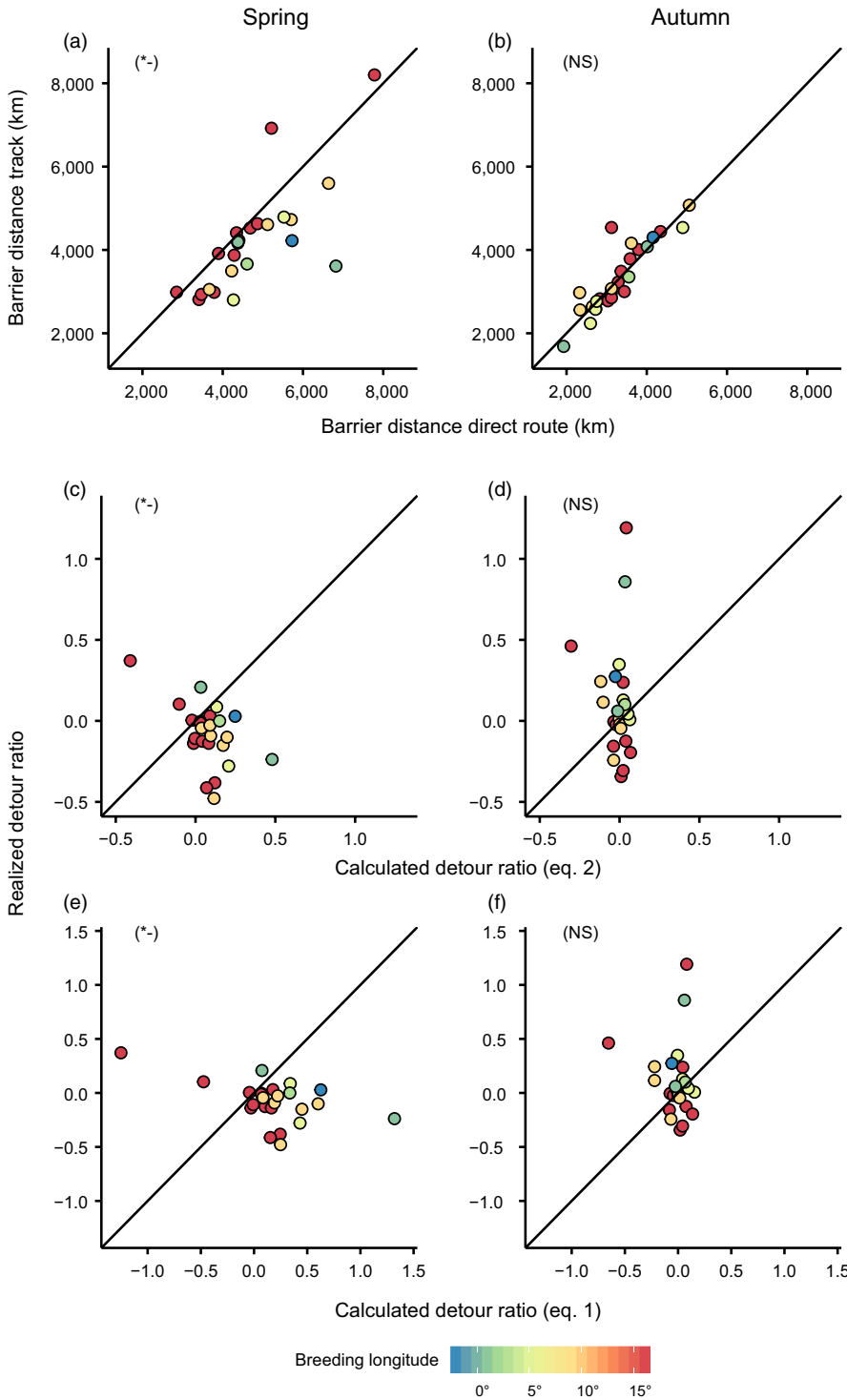


FIGURE 4 Linear relationships in spring (a, c, e) and autumn (b, d, f) for barrier distance along the direct route and track (a and b); and calculated values corresponding to the direct (orthodromic) route and the track according to Equation (2) (c and d) or Equation (1) (e and f). The lines represent $x = y$ and dots falling below the lines correspond to occasions when tracks resulted in a shorter barrier crossing (a and b), or lower calculated transport costs (c-f) than the direct route. Significant differences ($p < .01$) are denoted with a '*' and '-' indicates that observed values were lower than those predicted. Colours correspond to the breeding site longitude

limited the wind-sampling en route and may influence our results. Future studies should preferably use tags equipped with for example Global Positioning System sensors providing more detailed tracks that allow more sophisticated sampling of track-specific wind data.

We show that nightjars undertake spring migrations via West and Central Africa with clockwise detours varying in extent related to their breeding longitude, resulting in a relatively strong migratory connectivity between barrier-related stops and breeding sites. Similar detours via West Africa have been described in

other species (e.g. Åkesson, Bianco, & Hedenström, 2016; Åkesson, Klaassen, Holmgren, Fox, & Hedenström, 2012; Trierweiler et al., 2014; Vansteelant, Shamoun-Baranes, van Manen, van Diermen, & Bouten, 2016). Prevailing wind pattern over northern Africa is likely influencing the routes of individual migrants and the convergent evolution into flyways (Kranstauber et al., 2015; La Sorte et al., 2016). In the specific case of the nightjar, we demonstrate that spring routes are associated with the balancing of savings (i.e. wind-influenced reduced barrier crossing) and detour costs (i.e. added total migratory

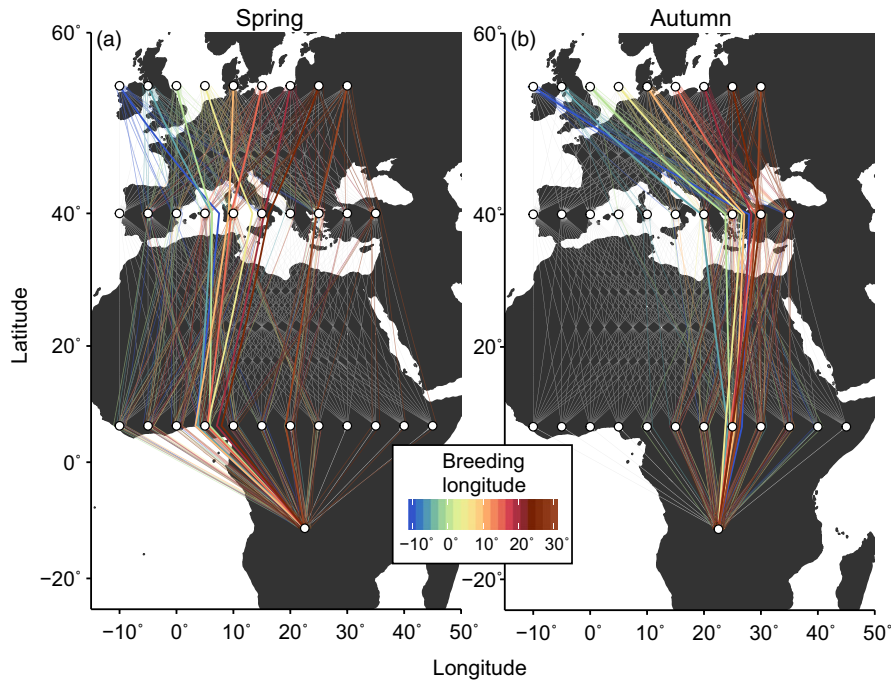


FIGURE 5 Simulated spring (a) and autumn (b) routes, respectively, between the average wintering position of the tracked birds in southern Africa and a series of breeding locations in northern Europe (white dots). Routes connect positions south and north of the main Palaearctic–African barrier, the Mediterranean Sea and the Sahara desert resulting in 1,080 unique routes, 120 for each breeding location. Wind data were sampled along all possible routes (grey lines), and air distances were calculated. Narrow lines represent the twelve (10%) least costly routes for each breeding location, colour-coded according to the breeding longitudes. Broad lines correspond to the average route per breeding location. The distribution of the average routes results in a clockwise route pattern seen in the nightjars and broadly corresponds to the distribution of documented tracks presented in Figure 3

distance). The extended availability of land south of the Sahara desert allows the birds to select routes and stops in front of the barrier that optimize barrier crossing and the overall cost of spring migration. Although we cannot exclude that the longitudinal distribution of spring routes across the barrier is influenced by a genetic component (Berthold & Helbig, 1992), we show that it corresponds well with the predicted optimal detours based on energy minimizing (Alerstam, 2001). Our results demonstrate that prevailing winds in association with an ecological barrier can promote geographical structure between the breeding sites and distant stopovers, and not only reducing migratory connectivity by funnelling migratory birds of different origins and destinations, as have been described earlier (Horton et al., 2016; Moreau, 1961, 1972). This is an important link between individual migration strategies and route choice, and spatial (and potential demographic) patterns on a population level.

The calculated wind profit resulted in shorter barrier crossings along the more western detoured tracks. As a shorter barrier crossing presumably reduces the mortality risk during migration (Klaassen et al., 2014), it is likely preferred by migrants that strive to maximize safety (Alerstam & Lindström, 1990). However, our simulated tracks resulted in relatively poor matches between the tracked birds and the longitudes associated with the shortest (safest) barrier crossing, indicating that the nightjars did not primarily strive to maximize safety during migration. Instead, the energy saved by the partial reduction in barrier distance outweighed the added costs of the detoured track, as expected if the birds strive to minimize the energy cost of transport

of migration. As an alternative to wind-influenced reductions in flight paths, the detoured routes may be explained by geographical variations in fuelling conditions in front of the barrier (Alerstam, 2001). Total energy expenditure during migration can be reduced by flying in wind conditions that reduce the cost of transport over ground. In the same line of thinking, relatively high fuelling rates will limit the time and energy spent at stopovers resulting in similar benefits of detoured routes in front of barriers where large fuel loads are required (Lindström et al., 2011). We note that some northbound nightjars stop for several weeks just before reaching the Sahara in spring, presumably to fuel for the subsequent barrier crossing (Evens et al., 2017; Jacobsen et al., 2017; Norevik et al., 2017). Like nightjars within the Palaearctic–African migration system, common swifts *Apus apus* undertake large detours via West Africa that, combined with favourable winds for north migration, coincide well with the spring rains in Liberia and the associated massive emergence of aerial insect prey (Åkesson et al., 2016, 2012). In contrast, and contrary to what would be expected if regional variability in feeding opportunity was the main driver of the detoured routes (Hahn et al., 2014), the pre-barrier stops of the nightjars appear evenly distributed across longitudes. In addition, in Swedish breeding nightjars that still undertake looped migrations there is a significant overlap between individuals between seasons that is difficult to explain whether longitudinal variation in habitat quality differs between seasons.

In conclusion, avian migrants are predicted to respond differently to topography and atmospheric circulation patterns

depending on internal factors such as flight mode, migratory strategy and behavioural responses to winds (Alerstam, 2001; Alerstam & Lindström, 1990; Liechti & Bruderer, 1998). Large ecological barriers have the potential of shaping the spatial and temporal set-up of migratory pathways by influencing the decisions by migrants in early life (Cresswell, 2014; Gill et al., 2014; Kranstauber et al., 2015; La Sorte et al., 2016; Moreau, 1961, 1972; Vansteelandt et al., 2017), resulting in links between important stationary sites in the annual cycle (Henningsson & Alerstam, 2005; Salomonsen, 1955; Webster et al., 2002) in vast numbers of avian species (Deppe et al., 2015; Hahn, Bauer, & Liechti, 2009). Alternatively, the variation in route shape and migratory connectivity could be due to differences in available land use, historical range expansions, navigational principles, innate migratory directions or a combination of these factors (Åkesson & Bianco, 2016; Alerstam, Hedenström, & Åkesson, 2003; Delmore et al., 2012; Finch et al., 2017; Ruegg & Smith, 2002; Sutherland, 1998). The nightjars studied here showed strong migratory connectivity in association with the Sahara desert–Mediterranean Sea crossing. We demonstrate that routes associated with these spring stops could be energetically more beneficial alternatives to the direct routes after accounting for potential wind effects (Alerstam, 2001). We conclude that the interaction between topography, winds and migration strategies may largely influence route shape, simply by a variation in the location of the goal area, and that an optimality approach is an informative starting point when evaluating complex migrations with superficially very different spatial patterns.

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AUTHORS' CONTRIBUTION

G.N., S.Å., G.C., R.E., I.H. and A.H. conceived the ideas; G.N. analysed the data and drafted the manuscript with input from S.Å. and A.H.; all authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

Individual positioning data are provided in the original tracking studies (Evens et al., 2017; Jacobsen et al., 2017; Norevik et al., 2017). Location data and raw data for the simulations are available at the Dryad Digital Respository <https://doi.org/10.5061/dryad.ms1fm8p> (Norevik et al., 2019).

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