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BEHAVIORAL ECOLOGY - ORIGINAL RESEARCH

Strong migratory connectivity and seasonally shifting isotopic niches in geographically separated populations of a long-distance migrating songbird

**Steffen Hahn · Valentin Amrhein · Pavel Zehtindijev ·
Felix Liechti**

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Abstract Whether migratory animals use similar resources during continental-scale movements that characterize their annual cycles is highly relevant to both individual performances and population dynamics. Direct knowledge of the locations and resources used by migrants during non-breeding is generally scarce. Our goal was to estimate migratory connectivity of a small Palaearctic long-distance migrant, the common nightingale *Luscinia megarhynchos*, and to compare resources used in non-breeding areas with resources used at the breeding grounds. We tracked individuals of three geographically separated populations and characterised their stable isotope niches during breeding and non-breeding over 2 years. Individuals spent the non-breeding period in population-specific clusters from west to central Africa, indicating strong migratory connectivity at the population level. Irrespective of origin, their isotopic niches were surprisingly similar within a particular period, although sites of residence were distant. However, niche characteristics differed markedly between breeding and non-breeding periods, indicating a consistent seasonal isotopic niche shift in the sampled populations. Although nightingales of distinct breeding populations migrated to different non-breeding areas, they chose similar foraging conditions within specific periods. However, nightingales clearly changed resource use between breeding and non-breeding periods, indicating adaptations to changes in food availability.

Keywords Ecological niche · Annual cycle · Non-breeding period · Geolocator · Stable isotopes

Introduction

The extent to which migratory animals exploit similar habitats and resources throughout their annual cycles is important with regard to population dynamics (Sherry and Holmes 1996; Norris and Taylor 2006; Taylor and Norris 2010) as well as other processes such as disease transmission (e.g. Hoye et al. 2011). Until recently, tracking small migrants like songbirds and identifying their areas of residence have been insurmountable challenges (Bridge et al. 2011). The development and application of miniature geolocation data loggers has now partly solved this problem (e.g. Stutchbury et al. 2009; Baechler et al. 2010; Tottrup et al. 2012). Although the use of miniature geolocation data loggers is becoming more and more widespread, we are still at the beginning of comprehending the complexities of bird migration, especially with regard to larger-scale patterns as inferred from many studied individuals and/or several populations over longer periods of time.

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S. Hahn (✉) · F. Liechti
Department of Bird Migration, Swiss Ornithological Institute,
Seerose 1, 6204 Sempach, Switzerland
e-mail: Steffen.Hahn@vogelwarte.ch

V. Amrhein
Zoological Institute, University of Basel, Vesalgasse 1,
4051 Basel, Switzerland

V. Amrhein
Research Station Petite Camargue Alsacienne,
68300 Saint-Louis, France

P. Zehtindijev
Institute of Biodiversity and Ecosystem Research, Bulgarian
Academy of Sciences, 2 Gagarin Street, 1113 Sofia, Bulgaria

One case in point is our understanding of resource and habitat use throughout the annual cycle. The various places visited by a migratory animal likely differ in climate, vegetation, and other biotic and abiotic conditions. Migrants could in principle employ a niche-follower strategy and seek out similar resources throughout the annual cycle, or alternatively they could adopt a niche-shifter strategy, wherein the migrant adjusts to different habitats and resources available at different locations (Nakazawa et al. 2004). In both cases, it is likely that experiences associated with a particular location or time period affect an animal's performance in subsequent periods (Harrison et al. 2011; Hoye et al. 2012; Rockwell et al. 2012). Such carry-over effects operate at the individual level, but if most individuals of a population are influenced by similar conditions, e.g. under strong migratory connectivity, carry-over effects can have population-level consequences (Norris and Taylor 2006).

To identify the evolved niche-following/shifting strategies requires both a determination of population-specific migratory connectivity and the quantification of niches during different periods of the annual cycle. Stable isotope analyses offer a quantitative approach for the characterization of ecological niches (Layman et al. 2007; Newsome et al. 2007). Because proportions of stable isotopes in consumer tissues reflect the isotopic values of ingested food, one can regard changes in certain isotope ratios of an animal's tissues as an indication of a change in diets, which is often related to transitions among isotopically distinct habitats (del Rio et al. 2009). The stable N isotope ratio [the relative ratio of 15 N/14 N, expressed as δ^{15}N (Bond and Hobson 2012)] and the stable C isotope ratio (13C/12C, expressed as δ^{13}C) can be regarded as axes in a parametric space defining an isotopic niche (Newsome et al. 2007). δ^{15}N is typically enriched along trophic levels within an ecosystem; it reflects the position within the food chain. In contrast, δ^{13}C in terrestrial habitats gives information about the consumers' reliance on primary producers with different photosynthetic pathways (C3, C4 or CAM) (Cerling et al. 1997). C4 plants are mainly monocotyledons, which grow in the herbaceous layer of open xeric habitats (Sage and Monson 1999; West et al. 2010). In Europe less than 1 % of native plant species are C4 plants (Collins and Jones 1985). However, C4 plants are common in Africa's natural grasslands, savannahs, and agricultural landscapes (Sage and Monson 1999), but most African shrub and tree species and the associated understory are C3 plants (Sanchez-Zapata et al. 2007; Symes and Woodborne 2009). The distinct local distribution pattern of C3/C4 plants in Africa allows for quantification of C sources and can therefore be used as a proxy for habitat use of ground feeders (Ferger et al. 2013).

We here aimed to identify migratory connectivity of birds from distant breeding populations and determine whether birds of these populations are conservative with regard to habitat use, as indicated by their isotopic niches during subsequent phases of their annual cycle. Addressing this question requires: (1) identification of areas used during the non-breeding season, and (2) determination of resource use on the different sites. To this end, we used geolocators to track individual common nightingales *Luscinia megarhynchos megarhynchos* from three geographically separated European populations. Nightingales are long-distance migrants with a breeding distribution ranging from western Europe to Turkey. During the breeding season, they preferably inhabit broad-leaved/deciduous woodlands, edges of forests, clear cuts and shrubby habitats, and they usually forage under dense canopy, feeding mainly on ground-dwelling arthropods during the reproduction period (Cramp 1988). Sparse observations suggest a similar foraging behaviour during winter (Serle 1957). Additionally, nightingales are highly territorial during the breeding (e.g. Amrhein et al. 2007) and non-breeding period (Wink 1976; King and Hutchinson 2001), indicating long periods of local residence in both seasons.

We estimated migratory connectivity of three distant populations across the species' breeding range and quantified for each population the isotopic niches occupied during two subsequent annual cycles. If nightingales generally use similar habitats for foraging (see above), we expected similar isotopic niches during breeding and non-breeding residence periods, especially for C sources, as well as similar isotopic niches among populations within a particular period. However, if habitat conditions vary across the species' distributional range, we expected isotopic niches to be more similar between neighbouring populations compared to distant populations.

Materials and methods

Our three study populations of common nightingales comprised a western European population in France (47.6°N, 7.5°E; north of the Alps), a southern European population in Italy (44.6°N, 11.8°E; south of the Alps), and an eastern European population in Bulgaria (with two sub-sites: 42.1°N, 27.9°E and 43.4°N, 28.3°E). Breeding habitats at all three study sites were composed of similar mosaics of wet broad-leaved deciduous forests with dense understory along rivers and channels, and partially shrubby habitats. The western and southern breeding populations were 470 km apart and geographically separated by the Alps, the eastern population was about 1,300 km distant from the nearest (southern) population. These populations are representative of birds using the western, central and eastern flyways for crossing the Mediterranean and the Sahara (Korner-Nievergelt et al. 2012).

Determination of non-breeding residence

During the breeding season in 2009, we captured 100 adult individuals at each site using mist-nets (62–65 % males, sex determined by shape of the cloaca, brood patch, behaviour and wing length). Birds were ringed and equipped with geolocators SOI-GDL1.0 (Swiss Ornithological Institute; mean mass: 1.12 g including harness = 4.8 % of average adult body mass). The geolocator was attached to the bird's back using a leg-loop harness (Rappole and Tipton 1991) made from VMQ silicone O-rings (Johannsen, Switzerland). To retrieve geolocators in 2010, we recaptured birds in their previous breeding territories, and if accessible, in surrounding areas. Recapture rate varied between sexes and study sites, with an average of 26 % for males (range 19–31 %), and 8 % for females (range 5–11 %), and was similar to data from long-term studies of northern populations [males 12–19 %, females 7–10 % (Hilprecht 1965); unisex 21 % (Becker 1995)]. After loss or failure of some geolocators, we obtained data on the non-breeding areas of residence from 28 individuals (11 from the western, six from the southern, and 11 from the eastern population). We used the threshold method to derive positions by defining sunrise and sunset times from the light intensity pattern for each recorded day (Hill 1994). Sun set and sun rise were determined using GeoLocator software (Swiss Ornithological Institute).

Geographic positions of residence areas for the 2009/2010 non-breeding season were calculated with the R package GeoLight1.02 (Lisovski and Hahn 2012 run as R version 2.15, www.r-project.org). Generally, residency during the non-breeding period lasted from October/November to March (S. Hahn et al., unpublished data). Here, we focus on a core non-breeding period from 15 November 2009 to 15 February 2010. Each geolocator was calibrated during the stationary non-breeding period using the Hill-Ekstrom calibration method, i.e. variance minimisation of latitudinal positions (Lisovski et al. 2012). Resulting sun elevation angles ranged between −6° and −1.3° (mean −4.5°).

To get an estimate of the position accuracy we used data from a 20- to 30-day period in the breeding habitat. Here, shading by the environment and the behaviour of the bird caused on average a 33 min shorter day length, and sunrise and sunset were affected by +16 min and −17 min. Consequently, the accuracy for these positions averaged at 117 km and 146 km for longitude and latitude, respectively (accuracy in geolocation by light varies with time of the year and latitude; Lisovski et al. 2012).

We applied kernel density analyses to separately identify non-breeding areas of residence for each population [Environmental Systems Research Institute (Esri) ArcGIS 9.3, search radius 300 km]. We accounted for the varying numbers of positions per bird by multiplying each individual dataset to the least common multiple of positions within each population. Hence, all individuals within a population account equally for kernel density analysis. Additionally, we estimated the strength of migratory connectivity of each population by calculating the average distance between birds during the non-breeding period using nearest-neighbour distances of centroid points from individual kernel density plots.

Isotopic niche

We sampled multiple tissues that record resource use at different time scales from the same individuals to determine the population-specific isotopic niches. We clipped about 5 mm from the tip of the second primary feather and 1–2 mm from the tip of the back toe claw for analysis of stable isotopes. Sampling included birds with geolocators as well as a random sample of males and females without geolocators, which resulted in sample sizes ranging from 47 to 59 birds per period and population [details in electronic supplementary material (ESM) Table 1]. All birds were caught between 13 April and 9 June.

Nightingales undergo a complete post-breeding moult between July and August, immediately after the breeding season, but before migration (Schönfeld 1996). Thus, the keratin of primary feathers would have been synthesized in the region of breeding. In contrast, claws grow continuously, with an average growth rate of 0.04 mm per day in passerine species (Bearhop et al. 2003; S. Hahn, unpublished data). The back toe claw of an adult nightingale was 7.2 ± 0.7 mm long (SD, $n = 661$), and its inner conical bone including the *stratum germinativum* is about 4 mm long (S. Hahn, unpublished data). Hence, the keratinous material of a claw tip sample of 1.5 mm length was formed between 40 and 180 days before the sample had been collected, i.e. during the non-breeding periods of residence between November and the beginning of March.

We checked for a potential effect of date of feather and claw sampling on isotopic patterns by including sampling date as a covariate in the statistical analysis (see below). Because we collected samples in two breeding seasons (2009 and 2010), we obtained information about stable isotopes from two breeding periods (feathers grown in 2008 and 2009) and from two non-breeding periods (claw material grown in boreal winters of 2008/2009 and 2009/2010).

Feather and claw samples were cleaned with hexane to remove contaminations, and were air-dried under a fume hood. For each tissue, sub-samples of about 200 μg were analysed for δ^{15}N (‰ difference from the 15 N/14 N ratio in atmospheric N_2) and for δ^{13}C (‰ difference from the 13C/12C ratio in Vienna Pee Dee limestone) in a HEKAtech EuroEA elemental analyser coupled on-line through a Finnigan con-flo interface to a Finnigan Delta S isotope ratio mass spectrometer. Reproducibility based on replicate measurements of standards (USGS40 and atmospheric N, $n = 49$) during the period of measurements was 0.11 ‰ (= SD) for both N and C. Because the discrimination factor from food to claws is lower than that from food to feathers, we adjusted the raw data of feather isotope data to claw data using conversions for δ^{13}C and δ^{15}N given in Bearhop et al. (2003). The isotopic niche for each population was determined as two-dimensional spaces of δ^{15}N and δ^{13}C. We used standard ellipse area as a measure of niche extent, with major axes representing population and period specific range of the focal isotopes (Jackson et al. 2011). Finally, we calculated the proportional overlap between niches (as percentage of the smaller niche) to specify similarities of niche extents and niche position. Calculations were done with SIBER in the R package SIAR version 4.1.1 (Jackson et al. 2011).

C sources during breeding and non-breeding periods

We determined the proportion of food originating from C4 plants as a proxy for minimum feeding in open habitats by using Bayesian isotope mixing models (R package SIAR version 4.1.1 run with R 2.13.1). As C source data, we used averages δ^{13}C from C3 and C4 grass species of −26.7 ± 2.3 (SD) ‰ and −12.5 ± 1.1 (SD) ‰ (Cerling et al. 1997), respectively. We accounted for isotopic discrimination in δ^{13}C from plants to insects to bird feathers/claws by summing discrimination factors from plants to insects [+0.21 ± 2.00 (SD) ‰, $n = 57$; Caut et al. 2009] and from insects to feathers [+3.50 ± 0.80 (SD) ‰] for insectivorous birds (Hobson and Bairlein 2003; Pearson et al. 2003; for adjusting δ^{13}C of feathers to claws, see above).

Results

Migratory connectivity and non-breeding areas of residence

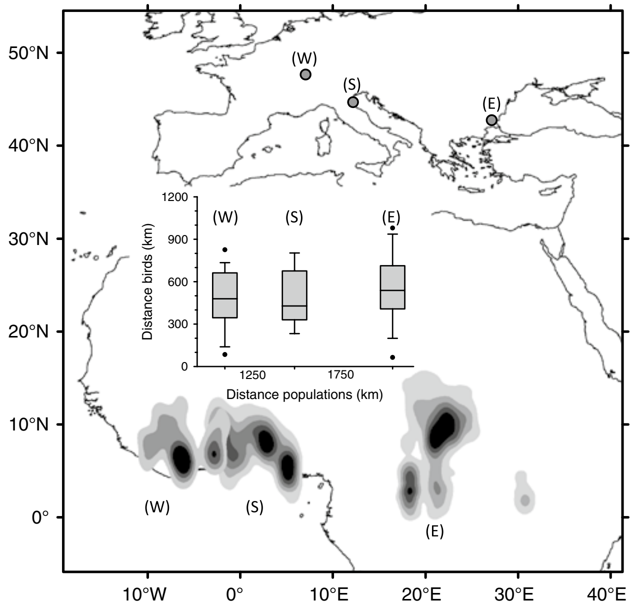

Fig. 1 Population-specific areas of residence during the non-breeding period of western (*W*), southern (*S*) and eastern (*E*) breeding populations of common nightingales. Residence areas are calculated as 30/45/60/75/90 % contour volume plots converted from Kernel density analysis for the periods from mid-November 2009 until mid-February 2010. The *inset* gives centroid distances between populations (in km) and distances between individuals within a particular population (*box plots* with *quartiles*, in km) for each non-breeding population (for eastern population, the easternmost outlier was excluded). Distances were calculated as loxodromic distances

All birds from all populations spent their stationary non-breeding period in sub-Saharan Africa. The longitudinal distribution of the three breeding populations was reflected in the distribution pattern during the stationary non-breeding period: birds from the western breeding population formed a cluster in West Africa in the region of the Côte d'Ivoire (centroid point of kernel density) to southern Mali and Liberia (Fig. 1). The southern breeding population clustered from Côte d'Ivoire to Nigeria with the centroid point about 1,250 km east of the western population (Fig. 1). Birds from the more distant eastern breeding population spent the winter in central Africa, i.e. in southern Chad, Central African Republic (centre point) and Congo, with one outlying individual resident in southern Sudan/Uganda (Fig. 1). The areas of residence during the non-breeding period of the western and southern breeding populations overlapped to some extent, whereas the non-breeding range of the eastern breeding population was geographically separated from the others. If the outlying individual of the eastern population was excluded, mean density of birds, measured as nearest-neighbour distance of individual kernel centroid points within populations, did not significantly differ among study populations ($F_{2,114} = 1.05$, $p = 0.35$; Fig. 1, inset) and averaged at 510 ± 22 km (mean ± SE) over all populations. This indicates a similar degree of migratory connectivity among populations. When including the outlier, nearest-neighbour distances within populations increased significantly from the western (483 ± 29 km) over the southern (490 ± 52 km) to the eastern population (697 ± 55 km; Kruskal-Wallis $H_{2,125} = 8.84$, $p = 0.01$).

Isotopic niches during periods of residence

In birds with known breeding and non-breeding areas, δ^{13}C of primary feathers (grown during the breeding/moulting period) and δ^{13}C of claws (grown during the stationary non-breeding period) differed significantly (paired *t*-test: $t = -7.72$, $p = 0.001$, $n = 23$), but δ^{15}N of feathers and claws were similar (paired *t*-test: $t = -1.29$, $p = 0.21$, $n = 23$). Moreover, there was no significant difference between birds of known (with geolocator) and unknown (without geolocator) non-breeding area in δ^{13}C and δ^{15}N of feathers or of claws (for feathers—δ^{13}C, $Z = -0.96$, $p = 0.34$; δ^{15}N, $t = -0.46$, $p = 0.65$; for claws—δ^{13}C, $Z = -0.76$, $p = 0.45$; δ^{15}N, $t = -1.82$, $p = 0.08$; ESM Fig. 1). We therefore pooled the data of birds with known and unknown non-breeding sites for each tissue.

For the breeding period (i.e. feathers), the western population had more negative δ^{13}C than southern and eastern populations ($F_{2,331} = 7.35$, $p = 0.001$; Tamhane's T2 post hoc test: west vs. south/east, $p = 0.01$; south vs. east, $p = 0.71$). There was also a difference in δ^{13}C between years with enriched ^{13}C in 2009 ($F_{1,331} = 15.1$, $p = 0.001$), but the interaction year × population was not significant ($p = 0.18$). δ^{15}N of feathers did not significantly differ between populations ($F_{2,331} = 0.02$, $p = 0.98$) or years ($F_{2,331} = 0.38$, $p = 0.54$).

Regarding the stationary non-breeding period, δ^{13}C of claws did not significantly differ among populations ($F_{2,302} = 3.03$, $p = 0.06$) and years ($F_{1,302} = 0.11$, $p = 0.75$; interaction year × population $p = 0.54$). However, δ^{15}N values were population-specific ($F_{2,302} = 15.35$, $p = 0.001$), with higher δ^{15}N values in the western and southern than in the eastern population (Tamhane's T2 post hoc test: western vs. southern $p = 0.58$; southern vs. eastern $p = 0.001$). Sampling date did not significantly affect δ^{13}C or δ^{15}N (C—$F_{1,302} = 0.68$, $p = 0.41$; N—$F_{1,302} = 0.28$, $p = 0.60$).

The shapes of isotopic niches were similar across populations but differed between periods: during the breeding period, the isotopic niche of all populations was rather narrow for δ^{13}C (range 0.95–2.14 ‰) but broad for δ^{15}N (range 3.35–4.44 ‰). In contrast, for the stationary non-breeding period the isotopic niche was broad for δ^{13}C (range 2.14–4.29 ‰) as well as for δ^{15}N (range 1.78–2.90 ‰), indicating a larger variation in δ^{13}C in the diet metabolized in the non-breeding areas than in the breeding areas (Fig. 2). The extent of the isotopic niche varied between the breeding and non-breeding periods (Fig. 2). In the western and southern populations, the isotopic niches were consistently smaller during breeding (on average 30 %) compared to the isotopic niches during non-breeding in both annual cycles (ESM Fig. 2). In contrast, this pattern was reversed for the eastern population, which showed a 36 % smaller non-breeding than breeding isotope niche.

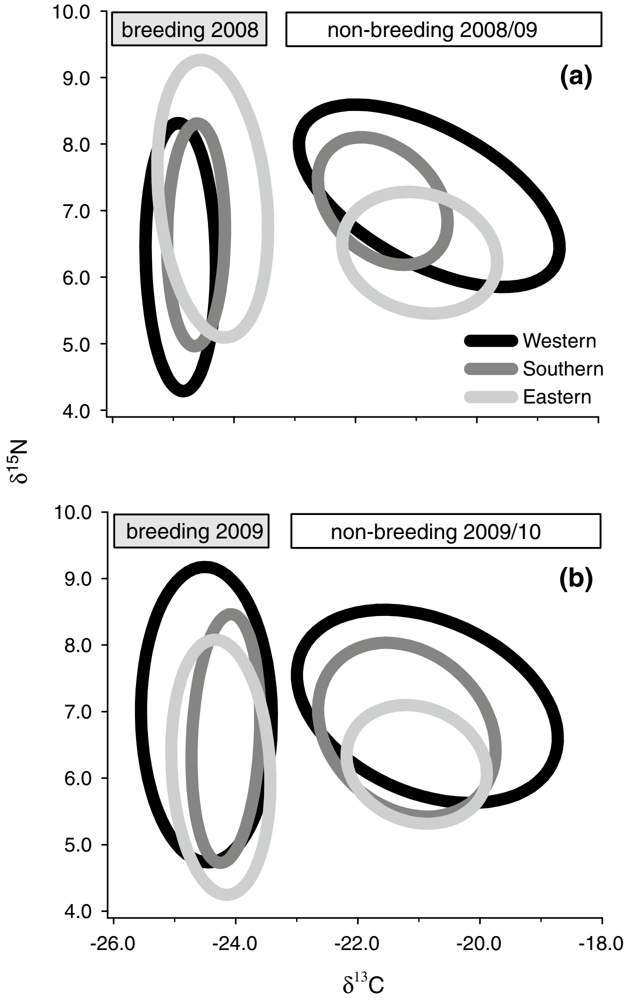

Fig. 2 Isotopic niches of three nightingale populations occupied during the breeding and the non-breeding period in two annual cycles from **a** 2008 to 2008/2009 and **b** 2009 to 2009/2010. Isotopic niches are calculated as standard ellipses

There was a clear shift in location and extent of isotopic niches during the breeding and the non-breeding period, respectively: the isotopic niches of breeding and non-breeding periods were separated in all three populations and in both annual cycles (Fig. 2). However, the isotopic niches largely overlapped for all populations within each period in all years (breeding period 83 % overlap, non-breeding period 77 % overlap). Moreover, the between-population overlap slightly decreased with increasing distance between populations, with 18 % decrease for a centroid distance of 1,700 km during breeding and with 20 % decrease over 3,000 km distance during the non-breeding period (Fig. 3). The between-years overlap in niche extents was higher for the non-breeding (on average 94 % based on the smaller niche) than for the breeding period (average 71 %), with the lowest overlap for the southern populations (Fig. 3).

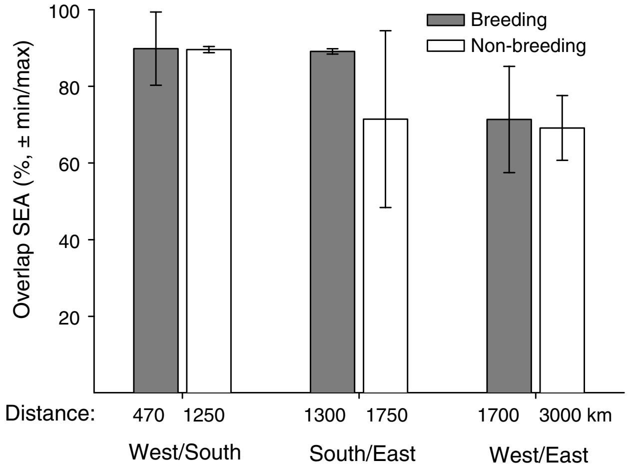

Fig. 3 Mean overlap of isotopic niches of three populations within breeding periods 2008 and 2009 and non-breeding periods of 2008/2009 and 2009/2010. The overlap of isotopic niches (standard ellipsis areas; *SEA*) is calculated between western, southern and eastern populations as the percentage overlap based on the smaller standard ellipsis. *Error bars* indicate minimum and maximum overlap within the two annual cycles. Between-population distances (centroid point of kernel density, see Materials and methods) are given in km (loxodromic distance)

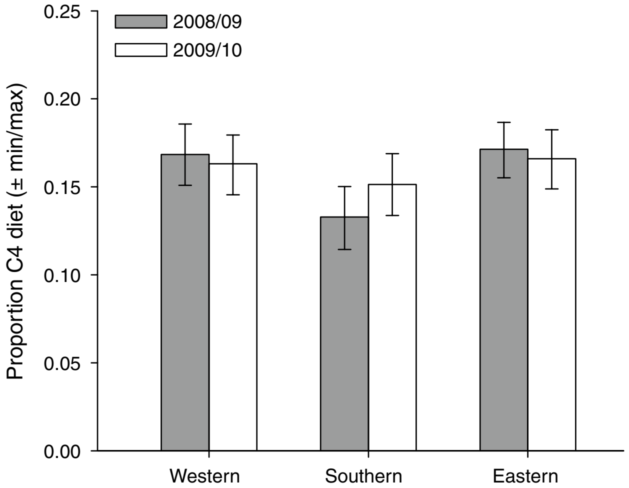

Fig. 4 Proportion of food based on C4 photosynthetic pathway in the diet of nightingales from western, southern and eastern populations, during the non-breeding residence periods in 2008/2009 and 2009/2010. Because C4 plants grow only in open habitats, the proportion of C4 diet can be used as a proxy for minimum proportion of foraging in open habitats. Data are given as medians (± minimum/maximum) calculated from δ^{13}C of claws

C sources during breeding and non-breeding periods

During the breeding period, all populations relied almost exclusively on C from C3 plants (100 % for western and southern population, 99 % for eastern population; mode values in both years). In the non-breeding period, diet composition changed towards a higher proportion of C4-based C sources with a median of 16 % of a C4-based diet (Fig. 4).

Discussion

The combined approach of inferring non-breeding regions by geolocation and quantifying isotopic niches yielded these major findings:

1. All three populations showed similar degrees of migratory connectivity, as they spent the non-breeding period in geographically separated clusters with a similar mean density of birds.
2. Isotopic niches of the studied populations were similar within a particular breeding or non-breeding period, respectively, but differed markedly between periods.
3. Period-specific isotopic niches overlapped considerably even in distant populations.
4. Niche size was mainly determined by large ranges of δ^{15}N during the breeding period (i.e. trophic level) and by large ranges of both δ^{15}N and δ^{13}C (i.e. habitat association) during the non-breeding period.

Species with large breeding distributions often inhabit large areas during the non-breeding season (e.g. Wisz et al. 2007). Thus, individuals from a local breeding population could either mix with individuals from other populations across the entire non-breeding range or also migrate to a single, separated non-breeding site, resulting in different degrees of migratory connectivity (Salomonsen 1955; Webster et al. 2002).

Previous studies of terrestrial long-distance migrating birds provided examples for both strong (e.g. Boulet and Norris 2006; Stutchbury et al. 2009; Tottrup et al. 2012) and weak migratory connectivity (e.g. Baechler et al. 2010; Fraser et al. 2012). However, former studies inferred migratory connectivity by indirect approaches like genetic or chemical markers (Boulet and Norris 2006) or by tracking individuals from only one study population (e.g. Tottrup et al. 2012; Delmore et al. 2012; but Fraser et al. 2012 used a multiple population approach).

Unfortunately, the strength of migratory connectivity is often expressed in non-numerical terms (i.e. Fraser et al. 2012), because a quantitative measure is still not established for global positioning system and geolocator data (for ring recovery data on continental scale see Ambrosini et al. 2009). We here provided the first quantitative evidence for strong migratory connectivity in geographically separated breeding populations of a long-distance migrant, as indicated by the separate locations of population-specific non-breeding clusters and by the similar within-cluster densities in all populations. However, neighbouring clusters of the western and southern populations did overlap to some extent, and therefore local populations may stay in contact during the non-breeding residence period [partial allohiemy (Salomonsen 1955)]. The strength of migratory connectivity could have implications for population dynamics (Norris and Taylor 2006), host-parasite interactions (Moller and Szep 2011) and conservation (Marra et al. 2006). For instance, under high migratory connectivity, individuals from the same breeding population spend a substantial amount of time in the same non-breeding area. Thus, unfavourable local or regional conditions like climate alterations at non-breeding sites can affect local breeding population size (Jones et al. 2008; Wilson et al. 2011). Such effects are assumed to be responsible for the decline of many Palaearctic long-distance migrants spending the non-breeding season in western Africa (Zwarts et al. 2009).

We found a consistent shift in isotopic niches from the breeding to the non-breeding period in all studied populations. This was mainly caused by seasonally increasing stable C isotopes from diet components based on the C4 photosynthetic pathway. Because C4 plants in Africa are almost exclusively distributed in the herbaceous layer of grasslands and savannahs (Sage and Monson 1999), the niche shift towards C4 patterns is likely related to the use of a broad diversity of habitats for foraging in farmland (Ferger et al. 2013). A flexible foraging behaviour generally allows the exploitation of different resources according to their availability, and thus is especially beneficial for territorial individuals. Indeed, African nightingale habitat may often border small-scale patches of extensively used farmland (V. Amrhein, personal observations), but quantitative data on habitat selection, foraging behaviour or diet composition of nightingales or other related species during the non-breeding period and comparisons to the breeding grounds are still not available.

Niche shapes and their seasonal shifts were surprisingly similar across geographically separated populations. δ^{15}N typically increases by a factor of 2.5–3 between subsequent trophic levels within the food chain (Caut et al. 2009). However, baseline values in plants can vary greatly on a local scale, e.g. due to fertilization and nitrification (West et al. 2010). A wide δ^{15}N range in the consumers' tissues typically results from diet components originating from different trophic levels, e.g. fruits, herbivorous insects and carnivorous insects (Herrera et al. 2003). Thus, the large δ^{15}N ranges in all nightingale populations during the breeding period indicate either particularly variable δ^{15}N baseline values at all localities and/or an omnivorous diet containing insects and berries (Cramp 1988).

In contrast, δ^{15}N in the isotopic niches of the non-breeding period was remarkably narrow given the large areas occupied during the non-breeding period and the distances between the populations. Due to large natural variation in δ^{15}N in African habitats (Symes and Woodborne 2009), we expected a similar ecological niche for all three populations with respect to the trophic level of individuals (based on δ^{15}N) as well as for habitat use for foraging (based on δ^{13}C). However, the small isotopic niche of the eastern population in Central Africa is striking. While habitat use, as indicated by δ^{13}C, was similar to that of the western populations, δ^{15}N ranges were consistently small. Such a pattern can result from either a restricted or superabundant (insect outbreak) food availability at a single trophic level (see above). Additionally, a uniform diet selection from the same trophic level by many individuals can also lead to a narrow δ^{15}N range in the isotopic niche.

A broad isotopic niche that is associated with flexible foraging behaviour during the non-breeding period might explain why many European nightingale breeding populations have apparently not been strongly affected by the changing conditions in their non-breeding areas and have remained remarkably stable during the last decades (Sanderson et al. 2006).

However, there are also potential disadvantages of niche shifting between periods and years. If individuals forage truly opportunistically and local food availability requires shifting habitats, they might have to pay a cost of becoming familiar with new sites, as site use becomes less predictable and repeatable for an individual. More importantly, a major advantage of strong site fidelity could be an adaptation to the local parasite fauna (Moller and Szep 2011), whereas (irregular) habitat shifting would expose an animal to a diverse parasite fauna. Consequently, we would predict higher parasite prevalence in birds shifting habitats (as indicated by a variable δ^{13}C pattern) than in birds with uniform C signatures, which, however, remains to be tested.

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