



Diverse migration strategies in hoopoes (*Upupa epops*) lead to weak spatial but strong temporal connectivity

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Abstract

The annual cycle of migrating birds is shaped by their seasonal movements between breeding and non-breeding sites. Studying how migratory populations are linked throughout the annual cycle—migratory connectivity, is crucial to understanding the population dynamics of migrating bird species. This requires the consideration not only of spatial scales as has been the main focus to date but also of temporal scales: only when both aspects are taken into account, the degree of migratory connectivity can be properly defined. We investigated the migration behaviour of hoopoes (*Upupa epops*) from four breeding populations across Europe and characterised migration routes to and from the breeding grounds, location of non-breeding sites and the timing of key migration events. Migration behaviour was found to vary both within and amongst populations, and even though the spatial migratory connectivity amongst the populations was weak, temporal connectivity was strong with differences in timing amongst populations, but consistent timing within populations. The combination of diverse migration routes within populations and co-occurrence on the non-breeding grounds between populations might promote exchange between breeding populations. As a result, it might make hoopoes and other migrating bird species with similar strategies more resilient to future habitat or climatic changes and stabilise population trends.

Keywords Geolocator · Wintering · Autumn migration · Spring migration · Partial migration

Introduction

The annual cycle of migrating birds is shaped by their migration between breeding and non-breeding sites, often separated by thousands of kilometres. The linking of populations across

sites visited in the annual cycle is termed migratory connectivity. If all individuals of a breeding site migrate to the same non-breeding region, breeding and non-breeding grounds are tightly linked and migratory connectivity is strong; whereas if individuals spread out over vast areas during the non-breeding

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season and mix with individuals of other populations, breeding and non-breeding grounds are only loosely linked and migratory connectivity is weak (Webster and Marra 2005). Migratory connectivity is likely a consequence of how migration behaviour has evolved. For instance, it might have evolved through post-glacial range expansions and recolonisations, in combination with isolation by geographical barriers and species-specific habitat requirements (Ruegg and Smith 2002; Webster and Marra 2005). Migratory connectivity can affect populations in various ways. For instance, populations with strong migratory connectivity appear to decline more severely (Gilroy et al. 2016) as negative conditions experienced at either the breeding or non-breeding grounds affect an important part of the population (Iwamura et al. 2013). In contrast, low migratory connectivity might make populations more resilient to changes in habitat conditions (Finch et al. 2017). The degree of migratory connectivity can also affect the transmission of parasites which has consequences on parasite diversity and prevalence (Durrant et al. 2008; Pagenkopp et al. 2008; von Rönn et al. 2015).

Migratory connectivity has traditionally been investigated with non-invasive methods such as stable isotopes (Reichlin et al. 2013), genetic markers (Harrison et al. 2010; Rodríguez et al. 2011) or ringing data (Ambrosini et al. 2009; Korner-Nievergelt et al. 2012), but more and more studies now use direct tracking methods, such as satellite tracking and geolocation, and also increasingly cover multiple breeding populations (Hahn et al. 2013; Trierweiler et al. 2014; Hallworth et al. 2015; Procházka et al. 2017). Current studies show a broad spectrum of migratory connectivity—from strongly connected populations such as the pied flycatcher (*Ficedula hypoleuca*) or the Neotropical ovenbird (*Seiurus aurocapilla*) (Hallworth et al. 2015; Ouwehand et al. 2016) to weakly connected populations such as Montagu's harriers (*Circus pygargus*, Trierweiler et al. 2014) or purple martins (*Progne subis*, Fraser et al. 2012). Such differences in the degree of migratory connectivity can probably not solely be explained by population specific migration routes. For instance, pied flycatchers from different breeding sites still migrated to distinct non-breeding regions despite a strong overlap in migration routes (Ouwehand et al. 2016). In contrast, purple martins showed distinct migration routes but different populations nevertheless mixed on the non-breeding grounds, resulting in weak migratory connectivity (Fraser et al. 2012).

One aspect that has not been made explicit in most studies of migratory connectivity is the temporal component of migration behaviour. To understand migratory connectivity in a broader sense, an approach should be adopted that explicitly considers the spatial aspects, e.g. migration routes and location of non-breeding sites, and temporal aspects, e.g. timing of migration, breeding or moulting (Bauer et al. 2016). Thus, to understand migratory connectivity properly, both spatial as well as temporal migration behaviour should be included.

We investigated the migration behaviour of a long-distance Palearctic-African migrant, the hoopoe (*Upupa epops*). Hoopoes have a broad distribution (Cramp et al. 1985), but several populations have declined recently and consequently have been listed as a species of conservation concern (BirdLife International 2017). The degree of migratory connectivity was determined amongst four European breeding populations in Spain, Switzerland, Germany and the Czech Republic. Using geolocators, information was obtained on migration timing, routes and location of non-breeding sites of individual birds. Previous work in one breeding population from Switzerland has shown that hoopoes use a variety of migration routes and non-breeding sites in sub-Saharan Africa (Bächler et al. 2010) and show low fidelity to specific non-breeding sites (van Wijk et al. 2016a). Hoopoes also varied considerably in timing of migration with the latest individuals leaving the European breeding grounds when others had already arrived at the African non-breeding grounds (van Wijk et al. 2017).

If hoopoes from the other European populations show similarly variable migration behaviour, weak spatial and temporal migratory connectivity can be expected. However, the existence of a division in migration directions at 10–12°E, i.e. roughly from Denmark to Sardinia (Reichlin et al. 2009), could lead to different migration routes in populations breeding east and west of this divide and thus, potentially, to separated non-breeding sites. Furthermore, ring recoveries suggest that individuals from central Europe can overwinter in Southern Europe (Bernis 1970; Reichlin et al. 2013), implying that a part of the European hoopoes may not share non-breeding sites with hoopoes that cross the Sahara.

Material and methods

Study sites and data collection

We studied migration behaviour of hoopoes from breeding populations in eastern Germany (Saxony 51° 25'N, 14° 29' E), the south-eastern Czech Republic (South Moravia 48° 50' N, 16° 41' E), southern Switzerland (Valais 46° 14'N, 7° 22'E), and southern Spain (Granada 37° 20'N, 3° 3'E), from 2010 to 2015 (see Table 1 for details). The studied populations mainly breed in nestboxes, except for the Czech population that breeds in natural cavities. Adult birds were equipped with geolocators of type SOI-GDL1 and recaptured in subsequent years to retrieve geolocators. Comprising a relative mass of < 2% of the bird's body mass, geolocators were found not to affect body condition, physiological state, breeding success nor annual apparent survival in hoopoes breeding in Switzerland (van Wijk et al. 2016b) and assume that this is true for the other breeding populations in this study as well (see Table 1 for detailed information on recapture rates in this

Table 1 Overview of number of birds in the different populations that were used for analysis

	Number equipped				Number used				Recapture rates				
	2010	2011	2013	2014	2011	2012	2014	2015	2011	2012	2014	2015	Overall
Spain			30				6 (6)				20%		20%
Switzerland	59		110		7 (10 & 10)		11 (19 & 8)		20%		19%		19%
Germany	25	15	40	50	4 (4)	2 (3)	4 (4)	1 (1)	16%	20%	10%	2%	9%
Czech Republic			29				4 (5)				17%		17%

Number equipped refers to the number of individuals that were equipped with a geolocator. Number used to the number of geolocators that could be used for analysis with in parentheses the number of geolocators that were retrieved in bold and lost in italic. Several geolocators could not be used for data analysis, because they had (several) gaps in the data of recording of up to 6 months

study). The data presented here is novel, but part of the data on hoopoes from Switzerland were used in a publication on the dependencies in the timing of the annual cycle (van Wijk et al. 2017). In total, 358 hoopoes were equipped with geolocators; 53 of which could be retrieved and 39 of those contained usable data (Table 1). None of the individuals were tracked for more than 1 year.

Migration data

Geolocator data were analysed using the *TrendLight* function in R (version 3.1; R Core Team 2014) with a threshold method to define sun events and stationary periods following van Wijk et al. (2016a). To correct for bad light transitions, non-distinctive sun events were excluded using the *loessFilter* function with a threshold of five interquartile ranges. Positions were calculated using site-specific sun elevation angles for each non-breeding site (varying between -3 and -6) using the HillEkstrom method within the R-package *GeoLight* (Lisovski and Hahn 2012). From the final positions, the individual non-breeding site was defined as the site where a bird stayed for at least 6 weeks after leaving the breeding grounds. To depict the error, the modi, first and third quartile of latitude and longitude positions were calculated.

Spatial differences in migration behaviour

Since hoopoes migrate during equinox during which latitudinal estimates are unreliable, longitude data was used to characterise migration routes. In particular, longitude data after departure from the breeding grounds for post-breeding migration directions and longitude data after leaving the non-breeding grounds for pre-breeding migration directions. Five major routes between Europe and Africa were classified: (I) the Iberian Peninsula, (II) the Balearic Islands, (III) Corsica/Sardinia, (IV) the Apennine Peninsula and (V) the Balkan Peninsula.

To investigate the differences between populations in routes and non-breeding sites, a suite of statistical models was used. Routes were analysed using a multinomial logistic

regression with population and sex as predictor variables; for routes during post-breeding migration, additionally, the date of departure from the breeding grounds was included. The location of non-breeding sites was analysed using a general linear model with the longitude as response variable and population, migration route, sex and departure date from the breeding grounds as explanatory variables assuming a Gaussian error distribution. All possible models were fitted that included the various combinations of these variables (without interactions) and were ranked based on the Akaike information criterion (AIC).

To elucidate potential year effects, the models were ran considering data for the period 2013–2014, for which data from all populations are available, and compared their outcomes with models considering data of all years pooled together.

Temporal differences in migration behaviour

The timing of the departure date from the breeding grounds, arrival date at the non-breeding grounds, departure date from the non-breeding grounds and arrival date at the breeding grounds were analysed using general linear models that included population and sex as explanatory variables and had a Gaussian error distribution. For the arrival in the non-breeding grounds, migration route was also included. Again, all possible models were fitted using different combinations of these variables and the models were ranked according to their AIC scores.

Quantification of migratory connectivity

The strength of migratory connectivity for the spatial and temporal component was quantified using Mantel correlations (r_M) (Ambrosini et al. 2009), which calculates the correlation between two matrices. Other methods exist, but Mantel correlations have been shown to perform well across data types (Cohen et al. 2018). For testing the spatial component of migratory connectivity, the two matrices contained the pairwise orthodromic distances between the locations of all hoopoes in breeding and non-

breeding quarters, respectively. Only migrating individuals were included in this analysis. A high Mantel correlation value indicates that individuals, which are close in the breeding grounds, are also close in the non-breeding grounds, and thus, their migratory connectivity is strong. For the temporal component of migratory connectivity, it was evaluated whether birds that breed close together also have similar timing of migration with respect to four key events—departure from breeding grounds, arrival in the non-breeding grounds, departure from non-breeding grounds and arrival in the breeding grounds. A high Mantel correlation value indicates that individuals which are close in the breeding grounds had a more similar timing compared to the timing of other breeding populations and thus strong temporal migratory connectivity. To test whether the Mantel correlations were significantly different from zero, permutation tests were ran (9999 permutations). These analyses were done in R using package *ade4* (Dray and Dufour 2007).

Results

All birds from Switzerland ($n = 18$), Germany ($n = 11$) and Czech Republic ($n = 4$) were migratory, whereas half of the birds from Spain were resident ($n = 3$) and half were migratory ($n = 3$).

Spatial differences in migration behaviour

During post-breeding migration, migratory birds from Spain chose the route across the Iberian Peninsula, whereas birds from Switzerland and the Czech Republic used several routes, and birds from Germany almost exclusively used the route via the Balkan Peninsula (Fig. 1 and Fig. S1). The best-ranking of the eight models for the selection of the autumn migration route included departure date and breeding population (Table S1); i.e. the autumn migration route depended on where birds had reproduced and when they departed. For instance, birds from the Czech Republic and Switzerland more likely migrated via the Iberian Peninsula when departing early: late departing individuals from Czech Republic more likely followed a route via the Apennine Peninsula and late departing Swiss individuals more likely choose a route via the Balearic Islands (Fig. S2). Thus, the later hoopoes from Czech Republic and Switzerland departed from their breeding grounds, the more they followed a southerly direction.

All migrating birds spent the non-breeding season in the (Sudano-)Sahelian region across West-Africa (Fig. 1c). None of the birds had multiple non-breeding sites, but instead, they stayed in the same location throughout the non-breeding period. The non-breeding sites of all

populations largely overlapped with no apparent segregation (Fig. 1c). Model selection indicated that the longitude of the non-breeding location was related to the autumn migration route, but not to population, sex or departure time from the breeding grounds (Table S2). For instance, hoopoes that migrated across the Iberian Peninsula used more westerly non-breeding locations than hoopoes that migrated via other autumn migration routes (Fig. 2).

For pre-breeding migration, none of the birds used the route via the Balkan Peninsula, and the route via the Iberian Peninsula was the most frequently chosen route followed by the routes across Corsica/Sardinia, the Balearic Islands and the Apennine Peninsula (Fig. 1b). The choice of route did not depend on sex or population (Table S3).

Temporal differences in migration behaviour

The timing of the four key events during migration differed between populations, whilst sex and autumn migration route had no detectable effect (Table 2). In general, the timing of migration was more similar amongst birds from the central European populations than that of birds from Spain (Fig. 3). Specifically, individuals from the population in Spain left the breeding grounds on average on July 24 ± 12 days (mean \pm SE), similar to birds from Germany (July 29 ± 13 days) and the Czech Republic (July 26 ± 6 days), whereas individuals from the Swiss population left later than all other populations (August 11 ± 11 days). Arrival in the non-breeding grounds was much earlier for birds from Spain (August 21 ± 4 days) compared to the birds from Switzerland (October 1 ± 16 days), Germany (October 5 ± 15 days) and Czech Republic (October 13 ± 5 days). Birds from Switzerland departed on average on March 6 ± 7 days, on February 23 ± 22 days for birds from Germany and on February 18 ± 8 days for birds from Czech Republic. Unfortunately, no data could be obtained on the departure from the non-breeding grounds for any birds from Spain, but the only bird from Spain with information on the date of arrival in the breeding grounds, arrived almost 2 months earlier (on February 23) compared to the other populations. Birds from Switzerland were back in the breeding grounds on April 11 ± 6 days, birds from Germany on average on April 15 ± 6 days and birds from Czech Republic on April 13 ± 2 days (Fig. 3).

Migratory connectivity

The Mantel correlation for the spatial component of migratory connectivity was low ($r_M = 0.062$, $n = 34$), and the permutation test indicated that it was not significantly different from zero ($P = 0.19$). In contrast, the Mantel correlations for the temporal components of migratory

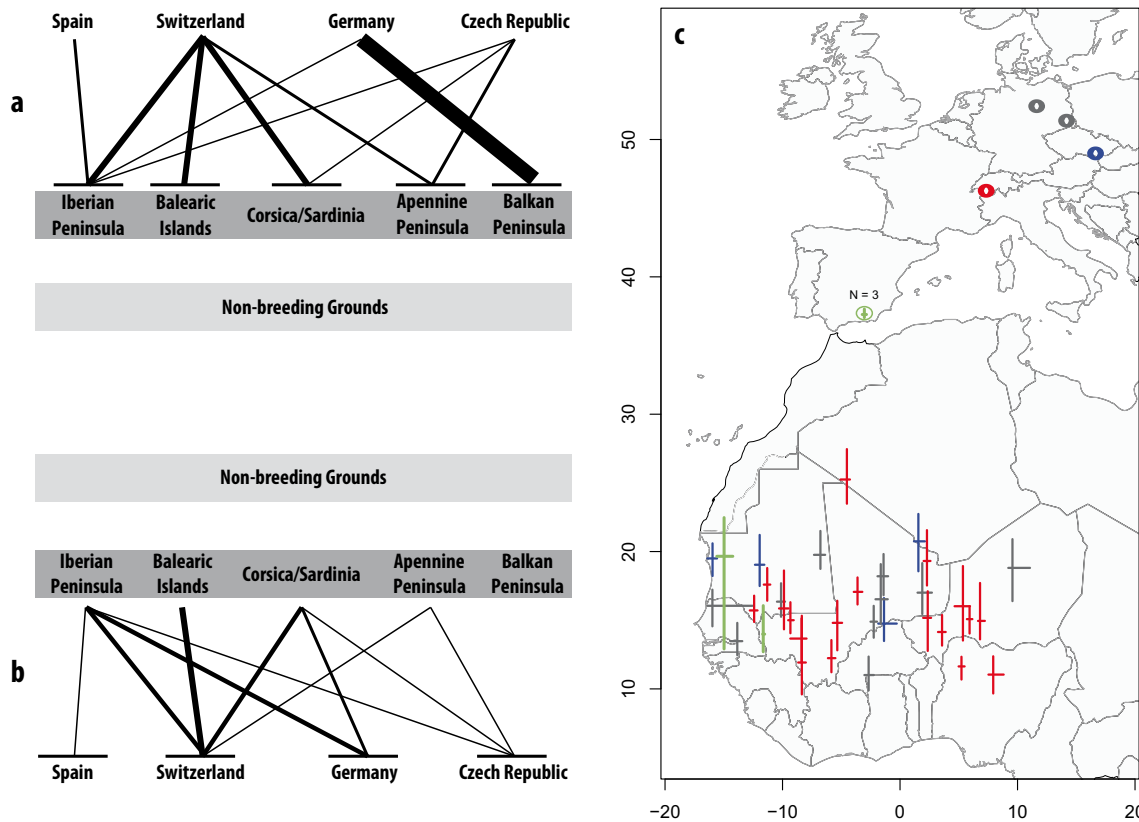


Fig. 1 The proportional use of **a** post-breeding and **b** pre-breeding migration routes via either the Iberian Peninsula, the Balearic Islands, Corsica/Sardinia, the Apennine Peninsula or the Balkan Peninsula for the different breeding populations (thickness of the lines corresponds with the number of individuals) and **c** non-breeding sites of individual

hoopoes from different breeding populations (coloured dots). Individual non-breeding sites are depicted with the modus and first to third quartiles; for the Spanish population, three birds were resident (presented in a similar fashion at the green circle)

connectivity were significantly larger than zero for the timing of arrival at the non-breeding grounds ($r_M = 0.436$, $P < 0.01$, $n = 30$), for the departure from the non-breeding grounds ($r_M = 0.200$, $P = 0.01$, $n = 23$) and the arrival at the breeding grounds ($r_M = 0.609$, $P = 0.02$, $n = 27$), but not for the departure from the breeding grounds ($r_M = 0.078$, $P = 0.16$, $n = 34$).

Discussion

The migration behaviour of hoopoes in terms of routes taken, timing of migration steps and location of non-breeding sites was very diverse both within and amongst our European breeding populations. Individuals from all populations used a range of migration routes both from and to the breeding grounds, largely overlapped on the non-breeding grounds, but their timing of migration differed between populations. Consequently, the spatial aspect of migratory connectivity was weak whilst its temporal aspect was strong.

Interestingly, birds from eastern Germany migrated to their non-breeding grounds almost exclusively via the

Balkan Peninsula, whereas all other populations used more westerly routes. This finding supports the existence of a division in migration directions, and is in line with earlier findings based on ring recoveries (Reichlin et al. 2009). However, birds from eastern breeding populations did not continue their migration in south-easterly direction to end up in Eastern Africa. This distinct population-specific migration route could have evolved, e.g. genetically (Helbig 1991; Bearhop et al. 2005), by prevailing wind directions (Morganti et al. 2011; Sjöberg et al. 2015), through landscape topography (Kuyt 1992; Gudmundsson 1994), social interactions (Mellone et al. 2011) or post-glacial range expansions established routes (Ruegg and Smith 2002; Alvarado et al. 2014). Hoopoes show a panmixia throughout Europe, meaning that breeding populations across the range have been in continuous contact in recent times and cannot be distinguished genetically (Wang et al. 2017). Wind is unlikely to play a major role in the migration directions of hoopoes, and topography does not seem to influence population-specific migration routes either. For instance, the breeding populations from both Germany and Czech Republic are located North of the Alps, but they have very different ways of passing the Alps, i.e. either

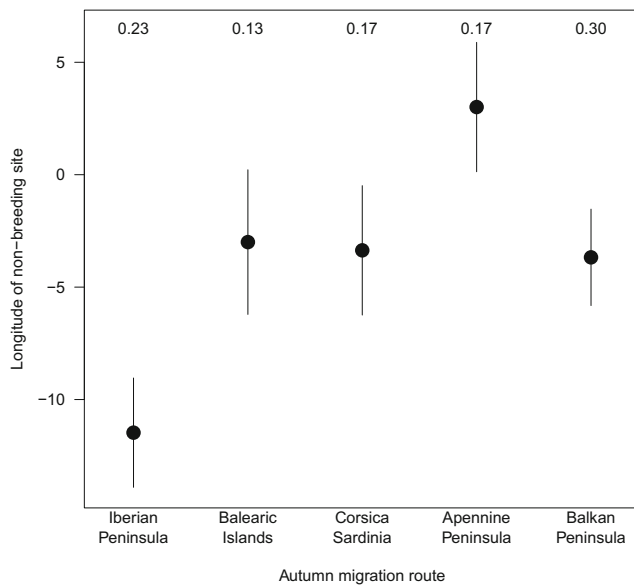


Fig. 2 Longitude of the non-breeding location depending on the chosen autumn migration route. Shown are the predictions (mean \pm SE) from the best model (Table S2). The numbers show the proportion of hoopoes that have used the corresponding autumn migration route

crossing them directly or circumventing them on either their western (breeding population from Czech Republic) or eastern fringes (breeding population from Germany). Social interactions on migration are more commonly found in birds migrating diurnally in flocks, such as geese (Harrison et al. 2010), and it is generally assumed that (near)passerines like hoopoes migrate alone during the night. They might encounter conspecifics on stopover sites, but it seems unlikely that this will greatly affect their migration direction. Possibly, the specific migration route of hoopoes from the population in Germany could be a relic of recolonisation patterns following post-glacial range expansions as has been shown in bird migration systems in the Americas (Ruegg and Smith 2002).

On the non-breeding grounds, as hypothesised by Reichlin et al. (2009, 2013), a fraction of birds from Spain were resident, whereas the remaining individuals from Spain and the other populations spread out over vast areas in Western Africa. It would be interesting to see if vice versa, hoopoes caught within a small non-breeding range would also spread over a large breeding shown as has for instance been shown in Whinchats (*Saxicola rubetra*, Blackburn et al. 2017).

For birds that migrated to sub-Saharan Africa, there were no clear segregations amongst populations. Rather, the locations of non-breeding sites seem to be, at least partially, a consequence of the specific migration routes used; e.g. birds that migrated via the Iberian Peninsula spend the non-breeding season more westwards compared to birds that took any other route. That routes can affect where birds overwinter has also been shown in other species (e.g. in Swainson's thrushes (*Catharus ustulatus*), Delmore et al. (2012) or in Ospreys (*Pandion haliaetus*), Martell et al. (2001)).

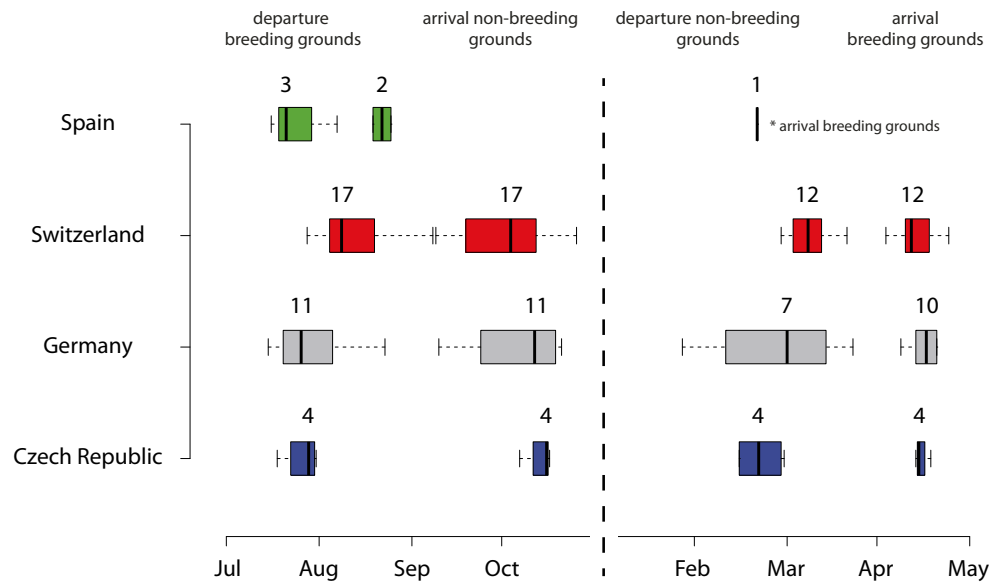
When comparing the migration timing across populations, the most notable difference was that birds from Spain started migration earlier and returned earlier to the breeding grounds. This difference probably relates to the length of the breeding season: whilst the breeding season in southern Spain already starts in late February, the earliest birds in eastern Germany start breeding mid-April. Likewise, the breeding season is finished much earlier in Spain (usually late June) compared to Germany (mostly end of July, but up to late August). The timing may differ for the central European populations since they might “wait out” the onset of spring in the Mediterranean region before continuing northwards, as has been shown in Collared flycatchers—*Ficedula albicollis* (Briedis et al. 2016). Timing also seems to influence migration more directly in terms of which migration route birds take in autumn post-breeding. Most notably, it seemed that birds from Switzerland and

Table 2 Model selection results for four timing of key events with respect to population (origin), sex and sometimes autumn migration route as assessed by linear regression models

Model	Np	Departure breeding		Arrival non-breeding		non-breeding Departure		Arrival breeding	
		Deviance	Δ AIC	Deviance	Δ AIC	Deviance	Δ AIC	Deviance	Δ AIC
Population + sex	6	3476.69	1.33	7199.40	9.99	3681.91	1.60	748.96	1.16
Population	5	3550.15	0.00	5355.00	0.00	3746.67	0.00	773.64	0.00
Sex	3	5267.87	8.63	9155.18	10.48	4789.43	3.65	3643.78	36.29
Intercept only	2	5533.88	8.20	9464.96	9.38	4802.96	1.71	3689.12	34.61
Population + sex + route	10	–	–	3920.87	1.58	–	–	–	–
Population + route	9	–	–	4078.90	0.65	–	–	–	–
Sex + route	7	–	–	6797.79	10.44	–	–	–	–
Route	6	–	–	5074.50	0.55	–	–	–	–

Given are the model deviance, the number of estimated parameters (np) and the difference between the AIC value of the current and the best model (Δ AIC)

Fig. 3 Timing of key events for the different European breeding populations of hoopoes. Boxes show median dates per population and their quartiles, whiskers the 95% confidence interval and numbers indicate sample sizes



Czech Republic adopted a more direct, southern route, when they left the breeding grounds (very) late.

As a consequence of the diversity between and within populations in routes and the large overlap in non-breeding regions, it can be concluded that there is only weak spatial connectivity in hoopoes. Thus, in principle, individuals from different breeding populations could meet on migration, stopover sites or on the non-breeding grounds. If pair formation starts before they arrive in the breeding grounds, individuals could pair on non-breeding or stopover sites and then move together to one of their natal breeding grounds. Juvenile hoopoes are known to overlap on their non-breeding grounds with adults (van Wijk et al. 2016a); they generally show strong dispersal between natal and later breeding sites (Bötsch et al. 2012) and show up as immigrants in specific breeding populations (Schaub et al. 2012). Low genetic differentiation between hoopoe populations supports the frequent dispersal between breeding populations (Wang et al. 2017) as do ring recoveries of immigrants into local breeding populations (Reichlin et al. 2009).

It thus seems that hoopoes show variable migration behaviour across populations, high migratory dispersion (they occupy large non-breeding ranges compared to their breeding origin) and thus a low spatial migratory connectivity. Such low spatial migratory connectivity is possibly rather common across migrant landbird populations (Finch et al. 2017), and as a consequence, environmental changes on specific non-breeding sites might lead to a diffuse but widespread effects on many breeding sites. Yet, because only a small fraction of individuals is affected, the low spatial migratory connectivity renders individual breeding populations more resilient to such changes (Webster et al. 2002; Gilroy et al. 2016; Rushing et al. 2016). By contrast,

if environmental changes on non-breeding grounds occur over large scales, such as climate change, it will affect many breeding populations and not just specific ones.

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Compliance with ethical standards

Informed consent Informed consent was obtained from all individual participants included in the study.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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