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Migratory connectivity and population-specific migration routes in a long-distance migratory bird

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Knowledge about migratory connectivity, the degree to which individuals from the same breeding site migrate to the same wintering site, is essential to understand processes affecting populations of migrants throughout the annual cycle. Here, we study the migration system of a long-distance migratory bird, the Montagu's harrier *Circus pygargus*, by tracking individuals from different breeding populations throughout northern Europe. We identified three main migration routes towards wintering areas in sub-Saharan Africa. Wintering areas and migration routes of different breeding populations overlapped, a pattern best described by 'weak (diffuse) connectivity'. Migratory performance, i.e. timing, duration, distance and speed of migration, was surprisingly similar for the three routes despite differences in habitat characteristics. This study provides, to our knowledge, a first comprehensive overview of the migration system of a Palaearctic-African long-distance migrant. We emphasize the importance of spatial scale (e.g. distances between breeding populations) in defining patterns of connectivity and suggest that knowledge about fundamental aspects determining distribution patterns, such as the among-individual variation in mean migration directions, is required to ultimately understand migratory connectivity. Furthermore, we stress that for conservation purposes it is pivotal to consider wintering areas as well as migration routes and in particular stopover sites.

1. Introduction

In migratory birds, factors outside the breeding range, e.g. hazards encountered during migration and environmental conditions on the wintering grounds, are crucial for understanding population processes as they may affect breeding populations through effects on survival and reproduction [1–5]. Consequently, it is crucial knowing where birds travel and winter and to what degree individuals from a certain population are using the same migration route or migrate to the same wintering site, i.e. how and to what extent breeding and non-breeding populations are connected [1,6]. When this connectivity is strong, individuals from one breeding site migrate mainly to one wintering site [1]. When connectivity is weak, individuals from one breeding population spread across the whole wintering range or various wintering sites. Thus, under strong connectivity, birds at a certain wintering site probably have a common origin (breeding site) whereas under weak connectivity, birds at a certain wintering site have very different, widely spaced origins, and individuals may even be flexible in their choice of breeding sites, migration routes and wintering sites between years [7].

While past studies focused on connections between breeding and wintering areas, the migratory travels themselves have rarely been considered despite knowing that birds spend relatively much time of their annual cycle on migration (e.g. [8–10]), and ecological circumstances *en route* (e.g. food availability and
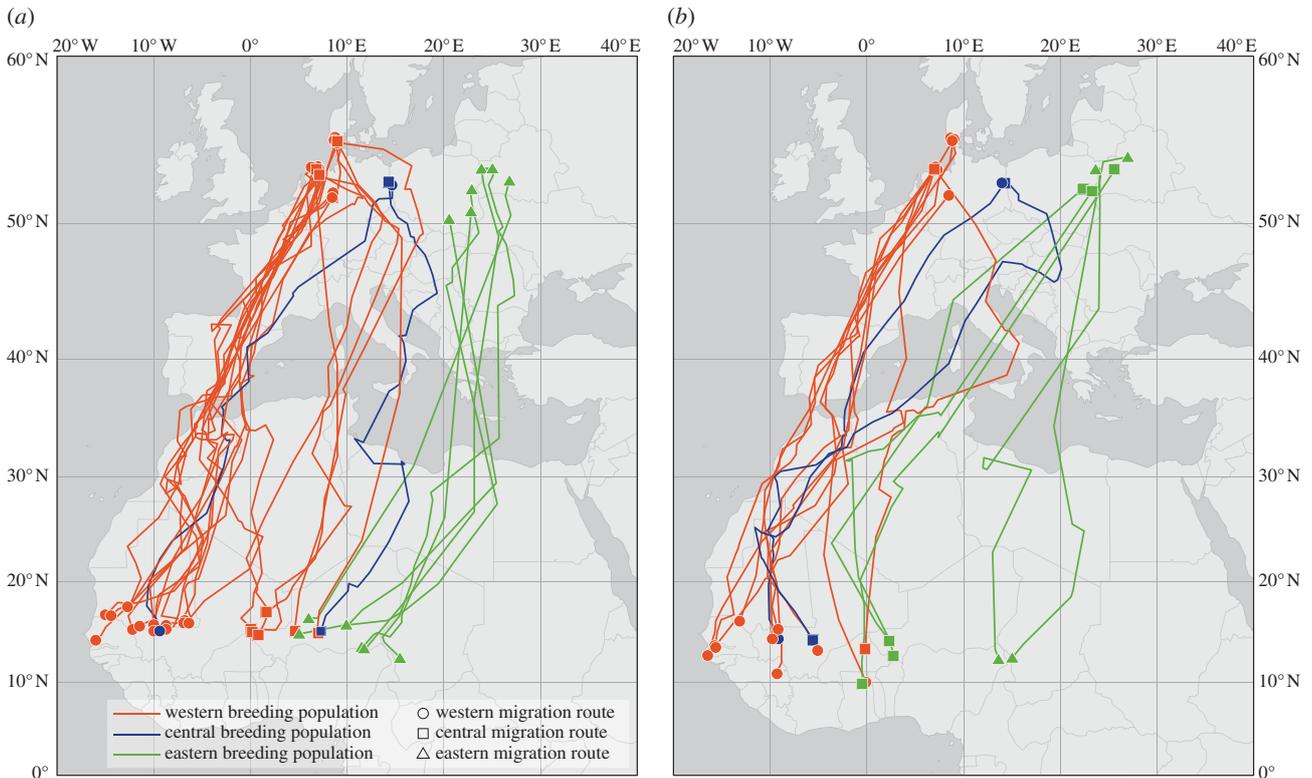
Figure 1. Migration routes of adult Montagu's harriers for (a) autumn ($n = 27$) and (b) spring ($n = 17$). Colours indicate different breeding populations (orange, western; blue, central; green, eastern). Symbols refer to migration routes (circle, western; square, central; triangle, eastern). For individuals tracked during several years, only one representative track is shown per season. Maps are in Mercator projection. Differences between autumn endpoints and spring starting points result from midwinter movements [27].

predation pressure at stopover sites) are known to have an important effect on migratory schedules, affecting for example spring arrival dates [11–14]. Furthermore, a considerable proportion of the annual mortality seems to occur during migration periods [15–17]. Different routes may vary in habitat and landscape, which in turn might have an important effect on migratory behaviour (e.g. [18]). For a more complete understanding of a migration system, including possible population-specific bottlenecks, an evaluation of migratory performance (i.e. timing, duration, distance and migration speed) for different migratory routes is required.

Satellite telemetry is an excellent method to track migratory birds throughout their annual cycle [19]. We used this method to study population-specific migration routes and wintering areas in the Montagu's harrier *Circus pygargus*, a long-distance migratory Palaearctic-African raptor with a sub-Saharan African non-breeding distribution. Before recent tracking studies [20–22], the species was believed to have a nomadic lifestyle in winter, tracking migratory locust outbreaks [23], suggesting low migratory connectivity. On the basis of recoveries of ringed Montagu's harriers and field observations, it was speculated that northwestern European birds make an anti-clockwise loop migration, with the southbound travel via Iberia, and the northward journey via Italy [24–26], whereas eastern European birds would travel via the Bosporus into eastern Africa [23], indicating the possibility of population-specific migration routes.

With this study, we aim to: (i) map wintering areas and migration routes of Montagu's harriers breeding throughout northern Europe, (ii) investigate the extent of migratory connectivity, including population-specific migration routes, and (iii) characterize different migration routes in terms of migratory performance. To address these aims, we satellite-tagged 34 adult Montagu's harriers in three breeding populations 1200 km apart,

and tracked them, some of them repeatedly up to six times, during their migrations to and from Africa between 2005 and 2011. This is the first time, to our knowledge, that the migration system of a Palaearctic-African long-distance migrant is described in such detail, providing novel insights for population dynamics and conservation issues. Based on our results, we discuss the concept of connectivity, especially the importance of spatial scale.

2. Material and methods

(a) Satellite tracking

From 2005 to 2011, 34 adult Montagu's harriers were fitted with satellite transmitters in three different subpopulations in northern Europe. We distinguished between western (The Netherlands, $n = 13$ individuals; western Germany, $n = 6$; Denmark, $n = 6$), central (eastern Germany, $n = 2$) and eastern (eastern Poland, $n = 3$; western Belarus, $n = 4$) breeding populations (cf. figure 1). (Colour)-ring and wing-tag recoveries indicate that these three populations are widely spaced subpopulations of the same metapopulation (B. J. Koks, Dutch Montagu's Harrier Foundation & www.busards.com 2007–2012, unpublished data).

All individuals were captured near the nest using a pole trap or a mistnet in combination with a stuffed raptor. The birds were released within 40 min after capture and we never observed nest desertion in relation to tagging. Transmitters were attached using a 6 mm-Teflon ribbon harness. We used 9.5 and 12 g solar satellite transmitters (PTT-100 series, Microwave Telemetry Inc., Columbia, MD, USA). Transmitters were programmed on a 10 : 48 or 6 : 16 h on : off cycle, respectively. Data were received via the ARGOS system (CLS, Toulouse, France [28]).

The total tracking dataset (2005–2011) contained about 47 000 fixes. For every track, the best signal (based on 'location class', [28]) was selected for every transmission period ('best of

duty cycle positions', cf. [29,30]). We checked for outliers by plotting data on a map, and removed locations that implied unrealistic travel speeds (more than 18 m s^{-1}). Starting point of the autumn track was the last fix from the breeding area or pre-migratory stopover area (see below). Montagu's harriers typically have several wintering areas, see [27], thus the endpoint of the autumn track was the first point from the first respective wintering area, and the start point of the spring track was the last fix from the last respective wintering area. The endpoint of the spring track was the first fix from the breeding area. In total, we obtained 104 tracks, of which 17 were incomplete as the bird died or the transmitter failed during migration.

(b) Migratory performance

As soon as a bird moved further than 40 km from its breeding or (last) wintering site, it was assumed that migration had started. Similarly, as soon as a bird approached its (first) wintering or breeding site within 40 km, it was assumed that migration had ended. Forty kilometres is a conservative threshold, as radio-tracking studies and GPS-logger data indicate that Montagu's harriers rarely venture further than 25 km from the nest during the breeding season ([31,32], www.uva-bits.nl). Total duration of migration was the time between departure (last position at breeding/pre-migratory or wintering site) and arrival date (first position at wintering or breeding site).

Distances between positions were calculated as loxodromes [30,33]. Migration distance was calculated as the sum of loxodrome distances between consecutive best of duty cycle positions [29,30,34]. In these calculations, we only included points when the distance to the previous point was more than 100 km, in order to exclude local movements at stopover sites (see below).

Overall migration speed (in kilometres per day) was calculated as the total migration distance divided by total duration. We also determined, for every track, the point where the Mediterranean Sea was crossed (point between 30 and 40° N), and we subsequently also calculated migration distance, duration of migration and regional migration speeds separately for Europe and Africa. Positions were not always obtained for every transmission period. Consequently, we could not always determine the exact start, mid and endpoint of a track, and hence sample sizes differ for the different parameters. Locations were particularly scarce for the central/eastern Mediterranean, which seemed to be caused by local radio signal disturbance [35], affecting all tracks running via Italy and Greece.

A complication in the analysis of migration patterns was the fact that harriers commonly make pre-migratory movements, especially failed breeders during summer [30]. As these movements occur well before regular migratory movements, we believe that these movements are not related to the process of migration itself, and hence we excluded these movements, including pre-migratory stopovers, from our analysis (cf. [30]). One female stopped for a long period in southern Europe after her spring migration (example of a post-migratory stopover in spring), and we excluded this track from all subsequent analysis.

We distinguished between periods of travel and periods of stopover. Daily segments based on 'best of duty cycle positions' shorter than 40 km were considered to be stopovers (note that the average daily travel distance is more than 160 km d^{-1}, cf. [22]). In this study, we only considered relatively long stopovers, i.e. stopovers that lasted at least 3 days, as shorter stops probably were missed in the case of missing locations because of radio signal disturbance, which was more common for the central and eastern migration route (see above). These 'longer' stopovers represent the main stopovers made by Montagu's harriers.

(c) Statistical analyses

Average values of migratory performance were calculated for individuals that were tracked several times, in order to avoid pseudo-replication. Differences between migration routes in timing of migration, duration of migration, migration distance and migration speed were tested by ANOVA, in which we conducted separate tests for all combinations of seasons (autumn and spring) and regions (Europe, Africa and total).

We analysed migratory connectivity by investigating where birds originating from different breeding populations: (i) crossed the Mediterranean Sea (route choice), and (ii) where they spent the winter (choice of wintering site), for both autumn and spring migration. This was achieved by correlating breeding site longitude, longitude of the crossing point of the Mediterranean Sea, and wintering site longitude, in which we used the longitude of the first and last wintering site for autumn and spring migration correlations, respectively (cf. above). In addition, we quantified the strength of migratory connectivity using a Mantel test, following the procedure described by Ambrosini et al. [36]. The Mantel test was conducted using the R package 'ade4', in which the statistical significance of the Mantel correlation coefficient was determined by 9999 random permutations [37].

# 3. Results

(a) Migration routes

For the autumn, three main routes could be distinguished for Montagu's harriers breeding in northern Europe: a western route via Spain, a central route via Italy and an eastern route via Greece (figure 1a). From the western breeding population ($n = 23$ birds), 78% migrated via the western route, 22% via the central route and no bird travelled via the eastern route. Of the two birds from the central breeding population, one male migrated via the western route and one female via the central route. All individuals from the eastern breeding population ($n = 8$ birds) travelled via the eastern route.

In spring, the picture was less straightforward as more variation and thus overlap in main routes existed (figure 1b). Most birds from the western breeding population returned via the western route (15 birds, 83%) and only a few via the central route (three birds, 17%). None of the western birds switched routes between seasons. The two birds from the central breeding population also returned via their western and central route, respectively. Four birds from the eastern population returned via the central route. Another bird followed a route in between Italy and Greece, but as this route lay much more to the east than for the birds returning via Italy (figure 1b), we considered that this individual returned via the eastern route. Yet another individual travelled via the central route in spring 2008, but followed the eastern route in spring 2009 and 2010. In summary, 72% of the spring tracks of the eastern birds ran via the central route and 28% ran via the eastern route.

Birds that were tracked for several years generally were faithful to their routes, both in autumn and in spring (with one exception, see above). Generally, spring routes tended to lay westwards of autumn routes, as was especially obvious for the eastern birds.

(b) Migratory connectivity

Strong correlations existed between breeding site, sea crossing and wintering area longitude (figure 2), even though the different breeding populations partly overlapped in their sea crossing points (i.e. their routes) and wintering ranges. For example, overlap between the wintering ranges of western and eastern breeding birds was 5.6 longitudinal degrees, which is about
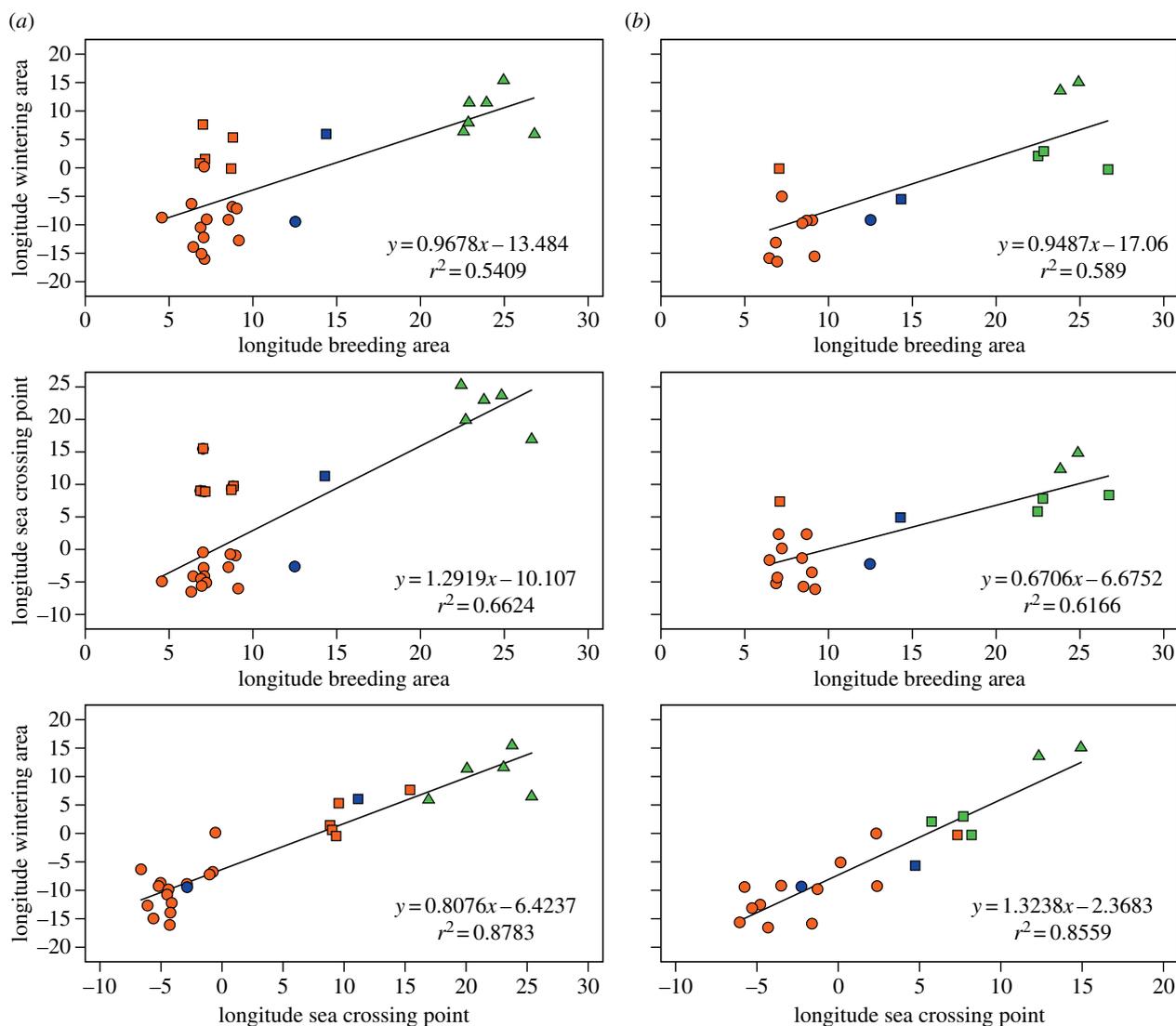
Figure 2. Correlations of breeding, sea crossing and wintering longitudes. (*a*) Autumn and (*b*) spring migration. Colours and symbols indicate breeding populations (Spain, Italy, Greece) and migration routes (western, central, eastern Europe), and correspond to figure 1. Equations and *p*-values refer to linear regressions.

18% of the total longitudinal range covered by these populations (similar comparisons with the central breeding population are impossible owing to a too small sample size). The Mantel correlation coefficient (rM) was 0.56 ($n = 27$ individuals, $p < 0.001$) and 0.60 ($n = 20$ individuals, $p < 0.001$), for autumn and spring migration, respectively.

Distances between individuals originating from the same breeding population increased with distance from the breeding site. For example, for the western population the standard deviation in longitudinal distance was 103 km at the breeding site, which increased to 573 and 771 km for the Mediterranean Sea crossing and wintering area, respectively. Similarly, standard deviation was 110, 431 and 611 km for the breeding area, Mediterranean Sea crossing and wintering area, respectively, for the eastern population. The two individuals from the central breeding population were captured within 200 km from each other, and these individuals were wintering 1200 km apart.

(c) Migratory performance and stopovers

The timing of migration was very similar between routes, and no significant differences were detected between routes for autumn or spring (table 1). However, routes did differ significantly in duration of migration and migration speed, at least for the spring travel through Africa. In spring, individuals

travelling via Spain took more time to cross Africa, which was also reflected in slower migration speeds, in comparison to individuals travelling via Italy/Greece (table 1). Such differences between routes were not found for the spring travel through Europe or for autumn in general. Differences in migration distances in Europe were the result of variation in breeding latitudes between populations.

In autumn, Montagu's harriers made stopovers in Europe and in northern Africa. In spring, a large number of lengthy stopovers were made in northwest Africa (northeastern Morocco and northern Algeria, figure 3). In autumn, 25% of all stopovers were located in northern Africa, whereas in spring 45% of all stopovers were located in this region. Furthermore, in autumn 46% of all individuals made a stopover, whereas in spring 88% of the birds stopped in this region.

4. Discussion

(a) Do Montagu's harriers have population-specific wintering sites?

For all three populations, the (longitudinal) scatter between individuals increased with an increasing distance from the breeding site, creating typical 'smoke plume patterns' of

Table 1. Timing, duration of migration, migration distance and migration speed for migrating Montagu's harriers, for different seasons, migration routes (see main text), and regions. (Average values and s.d. are provided. p-values refer to ANOVA's to test for differences between routes. See also the electronic supplementary material, figure S1.)

	autumn migration				spring migration		
	Spain	Italy	Greece	p-value	Spain	Italy/Greece	p-value
timing of migration							
departure date	29 Aug ± 7 (17)	25 Aug ± 10 (6)	27 Aug ± 9 (5)	0.54	30 Mar ± 8 (15)	5 Apr ± 9 (8)	0.12
passage Mediterranean Sea	15 Sep ± 7 (18)	10 Sep ± 6 (6)	12 Sep ± 10 (5)	0.33	24 Apr ± 5 (11)	23 Apr ± 12 (8)	0.93
arrival date	30 Sep ± 9 (15)	28 Sep ± 9 (6)	23 Sep ± 9 (6)	0.27	5 May ± 5 (10)	7 May ± 7 (7)	0.54
duration of migration (d)							
Europe	16 ± 5 (17)	15 ± 7 (6)	12 ± 8 (3)	0.5	11 ± 3 (10)	12 ± 4 (7)	0.32
Africa	16 ± 5 (15)	18 ± 6 (6)	10 ± 3 (5)	0.05	26 ± 6 (11)	19 ± 7 (8)	0.03
total	32 ± 9 (14)	33 ± 6 (6)	24 ± 6 (5)	0.17	37 ± 7 (10)	32 ± 10 (7)	0.26
migration distance (km)							
Europe	2301 ± 155 (17)	1911 ± 413 (6)	2075 ± 665 (3)	0.04	2248 ± 192 (10)	2557 ± 237 (7)	0.009
Africa	2669 ± 236 (15)	2813 ± 386 (6)	2421 ± 501 (5)	0.17	2863 ± 351 (11)	2899 ± 416 (8)	0.84
total	4953 ± 311 (14)	4724 ± 604 (6)	4596 ± 147 (5)	0.17	5159 ± 364 (10)	5516 ± 465 (7)	0.1
migration speed (km d^{-1})							
Europe	168 ± 61 (17)	154 ± 50 (6)	278 ± 262 (3)	0.17	233 ± 51 (10)	225 ± 65 (7)	0.8
Africa	183 ± 61 (15)	171 ± 44 (6)	261 ± 124 (5)	0.1	117 ± 33 (11)	186 ± 82 (8)	0.02
total	172 ± 47 (14)	153 ± 23 (6)	200 ± 55 (5)	0.24	145 ± 30 (10)	186 ± 59 (7)	0.08

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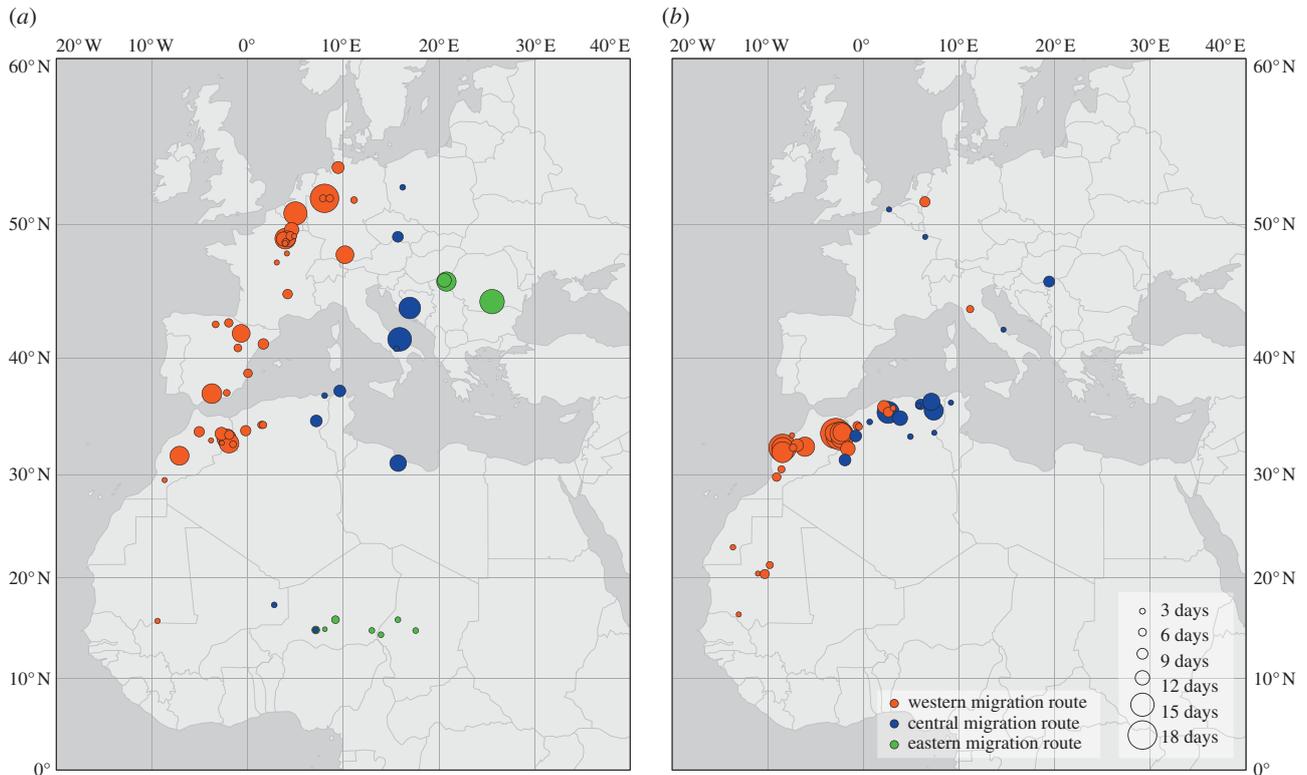
Figure 3. Main stopover sites for Montagu's harriers, for (*a*) autumn and (*b*) spring migration. Colours indicate different migration routes (orange, Spain; blue, Italy; green, Greece). Symbol size reflects the duration of stopovers. Note that satellite transmitter performance in the eastern Mediterranean is relatively poor (cf. [35]), thus (short) stopovers might have been missed in this region.

migration routes (e.g. [38]; figure 1). Consequently, wintering ranges for different breeding populations partly overlapped. For example, a Montagu's harrier wintering in Nigeria could breed in The Netherlands as well as in Belarus, i.e. potential breeding sites are 1200 km apart. Still, the overlap in wintering ranges was not complete, and our results show that Montagu's harriers are not randomly distributed throughout their wintering range but rather a clear spatial structure exists (figure 2). These results exactly match the description of 'weak (diffuse) connectivity' [1]. Accordingly, the Mantel correlation coefficient, a measure for the strength of migratory connectivity, was about 20% lower for the Montagu's harrier compared with the California Swainson's thrush *Catharus ustulatus*, a species for which strong connectivity was reported [39].

Species differ remarkably in the strength of migratory connectivity. Several examples of patterns of strong connectivity exist, and recent examples include the Asian houbara bustard *Chlamydotis macqueenii* [40] and Swainson's thrush [39,41]. Equally abundant seem examples of no or very weak connectivity, as found in for example, bobolink *Dolichonyx oryzivorus* [42] and purple martin *Progne subis* [43]. The latter example is particularly intriguing as no connectivity was found for the eastern subspecies *P. s. subis*, whereas the wintering range of a population of the western subspecies *P. s. arbicola* did not overlap at all with the wintering range of the eastern subspecies, suggesting strong connectivity at the species level [43]. This example emphasizes the importance of spatial scale in defining patterns of connectivity.

An important factor determining the degree of overlap in wintering ranges, and hence the strength of connectivity, is how much individuals spread out during migration, i.e. the degree of variation among individuals in mean migration direction (cf. [44]). If this spread is large, connectivity will

be weak. Second, the degree of overlap will also be affected by the distance between the source populations. Thus, whether the winter distribution resembles weak or strong connectivity is also very much a matter of scale, and the strength of connectivity cannot be considered without accounting for the distances between the breeding populations. For example, a comparison between two widely separated populations might generate different conclusions about connectivity than a comparison between two nearby populations, despite the fact that population-specific distribution patterns arise from the same biological principles. Clearly, we need to rethink the concept of migratory connectivity, and a different approach integrating aspects like the variation in individual mean migration directions and distances between source populations is required.

We generally have a poor understanding about the degree of variation in migration directions. For example, do species or populations differ in the degree of variation in migration directions? Also, what is the relative contribution of endogenous factors (variation in endogenous migration directions [44]) compared to ecological factors (e.g. wind patterns) and landscape (e.g. high mountains, sea crossing possibilities, barriers) [45]? Clearly, explaining the spread in individual mean migration directions is an important challenge for future research in this field. Moreover, it is important to include the first year birds, as the first year travel could set the migration routine that is repeated by the adult, and it is known that the migration of juveniles often differs from adults in several fundamental aspects [46,47]. Knowledge about how individual migrants from a certain breeding population spread out during migration might also help to understand the hitherto unexplained interspecific variation in connectivity (see above).

(b) Do Montagu's harriers have population-specific migration routes?

Although Montagu's harriers, with their high aspect ratio pointed wings, are not restricted to narrow sea crossings like typical soaring migrants [48], they appear to cross the Mediterranean Sea non-randomly, but use specific migration routes, related to relatively narrow sea crossings. We identified three such routes for northern European harriers, running via Spain (western route), Italy (central route) and Greece (eastern route) (figure 1). The eastern route had hitherto not been generally recognized, but we can now reject the idea that all eastern European birds travel via the Bosporus into Eastern Africa [23,24].

Route choice depended on the breeding population in which there is a gradual change in the use of different migration routes when moving from west to east. Individuals were faithful to their routes, but different individuals from the same breeding population could use different routes. Such 'dual pathways' indicate that individuals from the same breeding population separate during migration. Thus, just as for the wintering sites, the probability that an individual uses a certain route is related to breeding origin, but this 'connectivity' is rather weak as routes of different breeding populations overlap.

Patterns for spring migration are less straightforward owing to a larger variation in individual routes. However, also in spring, the pattern is observed that western birds tend to travel via more western routes and eastern birds tend to travel via more eastern routes. Interestingly, in spring, the whole migration system shifts slightly to the west, presumably caused by different wind conditions [49] and westwards movements during winter in Africa [27], corroborating the idea of loop migration in harriers [50]. The fact that eastern breeding birds pass the Mediterranean via Italy in spring implies that Montagu's harriers should be much more common in spring than in autumn in this region. Indeed, many more harriers are observed at Italian watchpoints during spring migration compared to autumn [25,26], but we can reject the idea that this is caused by an anti-clockwise loop migration pattern of western breeding birds [23–26], instead it seems related to the clockwise loop migration pattern of eastern birds.

Route choice was also related to breeding population in the purple martin [51]. Interestingly, in that example, migratory connectivity between breeding and wintering sites was very weak to absent [43], indicating that population-specific migration routes does not always imply connectivity. Hence, routes alone cannot explain patterns in migratory connectivity.

(c) Migratory performance for different routes

The performance of the harriers was very similar for the three different routes. The only possible difference we found was the travel through Africa in spring, where individuals migrating via the western route (Spain) needed more time to cross Africa, which was also reflected in lower regional migration speeds, in comparison with individuals travelling via the central route (Italy/Greece). Indeed, we discovered a previously unknown major stopover area in Morocco/Algeria [52], and this area is used extensively both in autumn and spring, predominantly by birds travelling via the western route. Field surveys in Morocco revealed high prey abundance in both autumn and spring, and the most abundant prey species were passerines such as larks (which were breeding in spring when eggs/nestlings formed an important part of the harriers' diet; [53,54], B. J. Koks, Dutch Montagu's Harrier Foundation 2010–2011, own unpublished data). North-western Africa receives some rainfall during early winter—more than central and eastern northern Africa [55], suggesting that conditions in northern Africa are less favourable for migratory stopovers along the central and eastern migration route.

The very similar migratory performance along the different routes is somehow surprising with respect to differences in landscape, topography and habitat composition. In order to characterize landscape features along the flyways, we extracted land-use data [56] for a 300 km buffer around dogleg-shaped routes that mimic the observed migration routes, using ArcGIS v. 9.3. Hypothetical routes were allowed to bend between 30–40° North (Mediterranean Sea passage), in which the bending point corresponded to the average observed crossing point. This analysis revealed differences in landscape between the three flyways (see the electronic supplementary material, figure S2), though these differences were not significant ($\chi_4^2 = 5.8$, $p = 0.21$). Nevertheless, the western route had a smaller proportion of water (11% versus 19% and 18% for the central and eastern route, respectively). For the western route, the shortest possible sea crossing distance is 25 km for the birds travelling via Gibraltar and 180 km for birds travelling via southeast Spain. This is shorter than the minimum sea crossing distances for the central (150 km from Sicily to Tunisia, 350 km from Sardinia to Tunisia/Algeria) and eastern (450 km via Crete) route. It should be noted that intermediate routes would require even longer sea crossings, for example, from France to Algeria (670 km), or from Greece to Libya (900 km). Furthermore, compared with the other routes, the western route had a slightly lower proportion of unfavourable habitats (bare soil, desert, forest, snow, urban: 50% versus 55% and 54% for the central and eastern route, respectively), whereas it had a larger amount of potential foraging habitat (farmland, herbaceous, shrubs: 39% versus 26% and 28% for the central and eastern route, respectively). Two recent studies on migration patterns of Swaison's thrushes [41] and purple martins [51], respectively, also report surprisingly little differences in the migratory performance between very different routes. These similarities in performance might suggest that the behaviour of migrants is to some extent 'hard-wired', which may reflect a rather strong endogenous (genetic) control of migration [57], and that subtle differences in landscape do not play an important role.

(d) Implications for conservation

In order to conserve a certain population of a migratory bird, one could argue that it is sufficient to map the routes the individuals from this particular population take, where they have their crucial stopover sites and where they spend the winter, in order to efficiently direct conservation efforts [58–60]. Although mapping population-specific migration patterns possibly is the most important first step, information about connectivity is also relevant, as it reveals the connections between different breeding, stopover and wintering sites. For example, it would be relevant to know to what extent individuals from the focal population mix with individuals from other populations at the wintering ground, to understand how the effects of a certain conservation measure dilutes over a number of breeding populations.

In the study of carry-over effects, there has hitherto been a focus of effects of conditions at the wintering grounds [3], presumably as it has been notoriously difficult to track sufficient samples of individual birds from different breeding populations. Hence, processes during migration have hitherto been seldom considered, despite the fact that processes during migration can have equally large impacts on timing, survival and reproduction (e.g. [4,13–17]). We emphasize that it is pivotal to not only focus on wintering sites, but to also map migration routes and in particular stopover sites. For example, in our case, based on the tracking results we could expect that population dynamics of the western breeding population depends on processes at western and central sub-Saharan wintering sites, and western and central migration routes. By contrast, population dynamics of the eastern breeding population probably depend on processes at the central and eastern wintering sites and migration routes. Thus, environmental change in northeastern Morocco, a region that turned out to be a major stopover site for birds using the western route [52,54], the breeding population in western but not in eastern Europe would be affected. Mapping routes and wintering sites also highlight the practical difficulties of conserving migration systems, as many different sites and countries are involved [58,60]. On the other hand, we can still identify 'key sites', such as the stopover area in northeastern Morocco/northern Algeria, which are used by many different individuals and thus imply a large conservation relevance.

Ethical permissions were granted by the Institutional Animal Care and Use Committee of the University of Groningen (licence nos. D4382B, D4748B) and by the Niedersächsisches Landesamt für Verbraucherschutz und Lebensmittelsicherheit, Oldenburg (licence nos. 33-42502-06/1139).

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