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Consistency in long-distance bird migration: contrasting patterns in time and space for two raptors

Yannis Vardanis^{a,*}, Jan-Åke Nilsson^a, Raymond H. G. Klaassen^{b, c, d, e}, Roine Strandberg^a, Thomas Alerstam^a

^a Evolutionary Ecology, Department of Biology, Lund University, Sweden

^b Dutch Montagu's Harrier Foundation, Scheemda, The Netherlands

^c Animal Ecology Group, Centre for Evolutionary and Ecological Studies (CEES), University of Groningen, The Netherlands

^d Dutch Centre for Avian Migration and Demography, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

^e Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

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As the evolutionary responses to environmental change depend on selection acting on individual differences, disentangling within- and between-individual variation becomes imperative. In animal migration research, multiyear tracks are thus needed to estimate the individual consistency of phenotypic traits. Avian telemetry studies have recently provided the first evidence of individuality across space and time in animal migration. Here, we compare repeatability patterns of routes and timing between two migratory birds, the marsh harrier, *Circus aeruginosus*, and the osprey, *Pandion haliaetus*, as recorded by satellite tracking. We found interspecific contrasts with low repeatability in timing and duration and a high repeatability in routes for ospreys, but the reverse pattern for marsh harriers. This was mainly caused by (1) larger between-individual variation in routes for ospreys (broad-front migration) than for marsh harriers (corridor migration) and a higher degree of repeated use of the same stopover sites among ospreys, and (2) higher within-individual consistency of timing and duration among marsh harriers, while individual ospreys were more flexible. Our findings suggest that individuality in space and time is not a shared trait complex among migrants, but may show adaptive variation depending on the species' life history and ecology.

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The potential among migratory animals to respond to environmental change is a topic that so far has mostly been studied at the population level for logistical reasons (Knudsen et al., 2011; Sutherland, 1998). However, as the evolutionary responses of a population depend on selection pressures acting on the phenotypic and genetic variation among individuals (Lynch & Walsh, 1998), disentangling individual variation will be necessary for predicting how a changing environment might affect migration patterns (Conklin, Battley, & Potter, 2013). To this end, multiyear tracking of individual migratory histories are needed (Alerstam, 2006; Baker, 1978; Pulido, 2007a), allowing us to quantify the consistency of phenotypes.

The individual consistency of animal behaviours (Bell, Hankison, & Laskowski, 2009) has typically been estimated by the

repeatability index r , the part of phenotypic variation in a population that can be attributed to differences between individuals (Nakagawa & Schielzeth, 2010). The degree of route fidelity of long-distance migration has mainly been assessed for avian migrants, although estimates exist also for marine turtles (Broderick, Coyne, Fuller, Glen, & Godley, 2007; Schofield et al., 2010). Nevertheless, the study of consistency in migratory behaviour is still critically defined by the difficulty of tracking individual migratory organisms over long periods. Thus, most studies have focused on calculating repeatability for time-related traits in one or a few annual stages (Table 4 in Thorup, Vardanis, Tøttrup, Kristensen, & Alerstam, 2013).

Recently it has become possible to evaluate the repeatability in both space and time for long-distance migration across the entire annual cycle by tracking individual birds during several years using satellite telemetry (spanning 2–7 years: Lopez-Lopez, Garcia-Ripolles, & Urios, 2014; Vardanis, Klaassen, Strandberg, & Alerstam, 2011) and light level-based geolocation (spanning 2–3 years: Dias, Granadeiro, & Catry, 2013; Stanley, MacPherson, Fraser,

* Correspondence: Y. Vardanis, Department of Biology, Lund University, Ecology Building, SE-223 62 Lund, Sweden.

E-mail address: yannis.vardanis@gmail.com (Y. Vardanis).

McKinnon, & Stutchbury, 2012). In this context, comparing repeatabilities among species can be particularly informative, as the repeatability for a trait may vary among species, and these differences can provide insights into the ecological conditions shaping consistency in migratory traits (van Noordwijk et al., 2006).

Here, we use long-term tracking data to compare the spatial and temporal patterns of repeatability in migratory routes and timing between two long-distance migrants, the marsh harrier, *Circus aeruginosus*, and the osprey, *Pandion haliaetus*. Both species migrate between Sweden and sub-Saharan West Africa within the same flyway, in which adults are highly faithful to individual breeding and wintering sites (Cramp & Simmons, 2004). They both migrate using a combination of flapping and soaring flight and have similar resulting total migration speeds and moult strategies (Alerstam, Hake, & Kjellén, 2006; Strandberg et al., 2008). At the same time, they show ecological differences in their migratory strategies, such that ospreys migrate on a broad front (Fransson et al., 2001; Poole, 1989), consistently revisit individual-specific intermediate goal areas (Alerstam et al., 2006) and travel during a shorter time window of the day (Mellone et al., 2012). Furthermore, marsh harriers have a more complex migration schedule as they tend to make premigratory stopovers (Strandberg et al., 2008).

Our null hypothesis was that the two species would show the same pattern of high repeatability in migratory timing and low repeatability in migratory route found in some recent studies of long-distance terrestrial bird migrants (e.g. Lopez-Lopez et al., 2014; Stanley et al., 2012; Vardanis et al., 2011). Studies of repeatability in migratory animals are still very few, making it important to consider the alternative hypothesis that repeatability patterns may differ between species, which would suggest that individual flexibility in migratory timing and routes are traits that show adaptive variation depending on the species' life history and ecology. Thus, our aim was to test this hypothesis by comparing the degree of individual consistency in migratory timing and routes between two raptor species with similar breeding and wintering areas. We consider possible ecological reasons related to stopover behaviour and broad- versus narrow-front migration for these interspecific differences in the individuality of bird migration.

METHODS

Tracking Data

We used tracking data from eight adult ospreys and six adult marsh harriers that made more than one migratory round trip (an autumn and a subsequent spring journey) between the breeding sites in Sweden and the wintering sites in West Africa and back to Sweden again during the years 1996–2012, as recorded by satellite telemetry. Part of this data set has been published (ospreys: Alerstam et al., 2006; marsh harriers: Vardanis et al., 2011), but we add more data for both species in this comparative study. The complete data set consisted of eight ospreys and 38 tracks (three individuals and 21 tracks added), with 21 autumn and 17 spring journeys, as well as six marsh harriers and 39 tracks (eight tracks added), with 21 autumn and 18 spring journeys (Table 1, Fig. 1). We used several types of satellite transmitters. The very first devices deployed in 1996 on ospreys lasted for a limited time period (normally only one annual cycle) and provided locations only every 3 or 6 days (Argos PTT-100, Microwave Telemetry Inc., Columbia, MD, U.S.A.). In 1997–2006, we used solar-powered transmitters to track ospreys and marsh harriers (Solar Argos PTT-100, Microwave Telemetry Inc.), which provided locations on a (near-) daily basis (for details, see: Hake, Kjellén, & Alerstam, 2001; Strandberg et al., 2008). From 2006 we also used GPS-based satellite transmitters (Solar Argos/GPS PTT-100, Microwave Telemetry Inc.), which

Table 1

Tracking records obtained by satellite telemetry during 1996–2012 of repeated migratory journeys made by eight adult ospreys and six adult marsh harriers between breeding sites in Sweden and wintering sites in West Africa

Species	Individual	Number of complete tracks		Tracking period			
		Autumn	Spring	1st		2nd	
				Start	End	Start	End
Osprey	OM1	5	5	A06	S11		
	OM2	3	3	A98	S01		
	OF1	3	3	A07	S10		
	OF2	3	2	A06	A07	A08	S09
	OF3	2	1	A98	A98	A04	S05
	OM3	2	1	A96	S97	A00	A00
	OM4	2	1 (1) ^a	A98	S00		
	OF4	1 (1) ^b	1	A96	S97	A98	A98
	Total	21	17				
Harrier	MHM1	7	6	A06	A12		
	MHF1	5	5	A07	S12		
	MHF2	5	4	A05	A09		
	MHM2	2	1	A06	S97	A07	
	MHF3	1 (1) ^c	1	A04	A05		
	MHM3	1 (1) ^c	1	A07	A08		
	Total	21	18				

O: osprey; MH: marsh harrier; M: male; F: female; A: autumn; S: spring. In four cases where the transmitter failed, the bird was fitted with a new transmitter, providing a second tracking period. Incomplete tracks are in parentheses.

^a Sahara crossing only.

^b Sahara crossing included.

^c Europe crossing only.

provide bihourly GPS positions during the day. In four cases, the transmitter failed and the bird was fitted with a new transmitter (second tracking period; Table 1). All transmitters were tracked by the ARGOS system (CLS, Toulouse, France). For battery- and solar-powered transmitters, geographical positional fixes were calculated using Doppler shift, and individual positions differ in accuracy (location accuracy classes Z, B, A, 0–3; see www.argos-system.org/manual). We inspected the entire data set to exclude nonvalidated (Z) and low-accuracy locations (0, A, B) obviously off-track (single positions implying a combination of travel speed of >25 m/s and off-course direction deviating >45° off the route inferred by the high-quality positions before and after them). Positions were transformed to the Mercator map projection (Gudmundsson & Alerstam, 1998). Following the same approach as Vardanis et al. (2011), we used these coordinates to calculate the longitudes and dates that the birds' migratory routes crossed the latitudes 46°N, 36°N and 26°N. These three latitudes were selected to represent measures of timing and geography of the migratory routes for the crossing of different regions: Europe, the Mediterranean Sea and the Sahara Desert, respectively.

Analyses

We calculated the repeatability of the longitudes and dates using the ANOVA-based method (Lessells & Boag, 1987; Nakagawa & Schielzeth, 2010) for a maximum of eight ospreys and six marsh harriers for variables with at least two measurements (Table 1). This analysis served to test the degree of individual consistency in longitudes, timing and duration across years, for the two species. The duration of the migratory journey was calculated as the total time for the journey between breeding and winter sites excluding pre- and postmigratory movements within 2° latitude zones close to the breeding and wintering areas (Strandberg et al., 2008). We corrected durations for the small variation in latitudinal extent of the journeys (individuals had their breeding sites as well as winter sites at slightly different latitudes) by dividing by the number of latitude degrees crossed during the journey, and using this measure

Figure 1. Maps showing the routes of eight adult ospreys (first row) and six adult marsh harriers (second row) that completed at least one round trip between the breeding grounds in Sweden and the wintering quarters in West Africa during 1996–2012. Each panel highlights the three individuals with most repeated journeys of each species (a: OM1; b: OM2; c: OF1, d: MHM1; e: MHF1, f: MHF2; see Table 1 for details) in blue (autumn) and red (spring), as well as the trips of all other individuals of the species in grey.

as an index of duration in our analyses (this index thus corresponds to the inverse of mean latitudinal speed of migration).

Repeatability is an estimate of the fraction of total variance (sum of between- and within-individual variation) that refers to between-individual variation (Nakagawa & Schielzeth, 2010). This means that, when comparing two cases where the level of within-individual variation is the same, repeatability will be highest for the case with largest between-individual variation. Comparing cases with the same between-individual variation, repeatability will of course be highest for the case with lowest within-individual variation. To disentangle the relative contribution of the two sources of the variation between the species, we compared the within- and between-individual variances using Fisher's *F* ratios significance test (Sokal & Rohlf, 1995). Between-individual variance was calculated from the mean values of the *n* different individuals, with degrees of freedom equal to (*n* – 1). Within-individual variance was calculated as the mean of the variances of the *n* individuals, with degrees of freedom equal to (*n* – 1).

Finally, we identified and analysed apparent intermediate goal areas (i.e. geographically limited areas that were used for stopover or passed in transit during repeated journeys) of the four ospreys and the three harriers with at least two full round trips. These journeys were recorded with transmitters typically providing good-quality positional data on a daily basis, allowing us to delimit stopover sites. An area was considered to be a stopover site if a bird moved less than 50 km/day along the seasonally appropriate migratory course. An apparent goal area was subsequently defined as an area where an individual made at least (1) one stopover and one passage (defined as a position during active migratory flight) or (2) three passages, within a radius of 50 km. We considered these criteria as an indication that an area was not revisited just by chance but formed a key element of the individual's migration routine.

After identifying these areas for each individual (Tables A1, A2), we calculated the 'recurrence' (dimensionless) at each apparent goal area (the proportion of journeys when the given area had been visited by the relevant individual, including both stopover and passage visits) in total (seasons combined), in autumn only, and in spring only. We also determined the 'seasonal overlap' (dimensionless) in the use of a given area, by multiplying the autumn and spring recurrence estimates (i.e. the overlap corresponding to the average probability of visits to a given area during both seasons of the same annual migration cycle).

To use these proportions to test for possible differences between the two species, we first normalized our variables following the suggested methodology by Warton and Hui (2010). To do that, we used the logit of the raw values, $\log(p/(1 - p))$, where *p* is the untransformed recurrence, adding the minimum nonzero proportion of the sample to both the numerator and denominator of the logit function to solve the problem of sample proportions that were equal to 0 and 1. To explore whether recurrence and overlap differed between the species, we ran linear mixed models with the logit-transformed values of autumn, spring and total site use recurrence at apparent goal areas, as well as the seasonal overlap in site goal area visits as the dependent variable, and with species as a fixed factor and individual as a random factor. Tests were performed using the maximum likelihood ratio method. All analyses were performed in IBM SPSS Statistics, v. 21 (IBM, Armonk, NY, U.S.A.).

Ethical Note

We captured birds as adults at their nesting sites when their chicks were at least 3 weeks old (marsh harriers) or 5 weeks old (ospreys). Trapping methods are described by Alerstam et al. (2006) and Strandberg et al. (2008). We attached the transmitters as

backpack harnesses and released the birds near the nest within 1 h of capture. The devices weighed 30–35 g for ospreys (1.5–2.5% of the birds' body mass) and 18–22 g (2.7–3.3%) for marsh harriers (Microwave Telemetry, Inc.). The capture did not cause any increased nest failure beyond that expected in nests without intervention, as no osprey and two (out of six) marsh harriers of the study failed to breed during the year of tagging, which is lower (ospreys, 28%) or within (marsh harriers, 24–35%) the range of nest desertion known for nontagged birds (Cramp & Simmons, 2004; Sternalski, Blanc, Augiron, Rocheteau, & Bretagnolle, 2013). The temporal and spatial patterns of mortality throughout the annual cycle have recently been analysed for these species (Klaassen et al., 2014). The estimated mean annual survival of the satellite-tracked birds was somewhat lower (marsh harriers/ospreys: 0.5/0.6; $N = 17/18$) than the expected annual survival rate (0.7/0.8), indicating that the transmitters may possibly have had a small adverse effect on the long-term survival of the birds or that mortality was slightly overestimated because some cases of probable deaths may in fact have been due to transmitter failures (see more detailed discussion in Klaassen et al., 2014). The meta-analysis by Barron, Brawn, and Weatherhead (2010) also indicated the lack of a clear effect of capture and transmitter attachment on nest success and survival rate of birds. Captures of the raptors and the use of radiotransmitters were approved by the Ethical Committee in Malmö-Lund (permissions M204-06 and M27-10).

RESULTS

Differences Between Individuals

Individual osprey showed highly significant differences in their routes (longitude) during both autumn and spring migration (except at 26°N in spring; Table 2). In contrast, routes of individual marsh harriers did not differ significantly (except at 36°N in autumn). Individual marsh harriers, but not ospreys, showed highly significant differences in timing of migration (except at 36°N in spring). For duration of migration, we found highly significant differences between individual marsh harriers during both autumn and spring, and also for individual ospreys during autumn (although not as pronounced as for the marsh harrier) but not during spring (Table 2). These patterns suggest contrasting individual consistency in routes and timing of migration for these two species.

Individual Repeatability

A strong effect of individual will be reflected by a high repeatability estimate approaching unity, while a lack of an effect of individual will be associated with close to zero repeatability. Hence, repeatability in route was often high and approaching unity for

ospreys but close to zero for the marsh harrier, and vice versa for timing and duration (Table 3). However, the 95% confidence intervals (CIs) were often wide. Still, in all but one case (across the Sahara in spring), route repeatability was significant (exceeding zero) for ospreys, but in no case was it significant for the marsh harrier. Furthermore, in two cases there was no overlap in CIs for route repeatability in ospreys and marsh harriers, suggesting significant species differences. On the other hand, CIs for the repeatability in timing were generally overlapping zero in all but one case (marsh harrier crossing the Sahara in spring). Repeatability in duration was clearly significant for the marsh harrier during autumn migration (Table 3).

We also compared the variance at the within- and between-individual levels between species (Table A3). There were no significant species differences in migratory timing, while between-individual variance in duration was significantly larger for marsh harriers. The between-individual variance in route (longitude) was significantly larger for ospreys than for marsh harriers (except at 36°N in autumn). In Europe, ospreys also showed a significantly lower within-individual variance in route (Table A3).

Goal Area Fidelity

Four ospreys and three marsh harriers were tracked for at least two full annual migrations, and for these individuals we identified four to seven potential intermediate goal areas for each individual (Tables A1, A2). The importance of these areas can be inferred by the frequency of visits; however, there were consistent differences between the two raptor species (Fig. 2). There were proportionally many fewer instances of no visits (represented as white sections in Fig. 2) for these sites among ospreys than among marsh harriers. Also, remarkably, all four ospreys visited at least one site on all journeys (autumn and spring), whereas we found no such consistently visited sites among any of the marsh harriers, which in turn tended to use season-specific stopover sites. Ospreys also used fewer stopover sites (four or five) than marsh harriers (six or seven sites). However, marsh harriers used potential intermediate goal areas more facultatively and readily skipped a given area in a certain year or even alternated among them during different years of the study period (see all instances of 'no visit' in all possible intermediate goal areas in Fig. 2b).

The total recurrence of visits to apparent goal areas was on average almost twice as high for ospreys (mean $\pm$ SD = 0.69 ± 0.23) than for marsh harriers (0.37 ± 0.16). Furthermore, the seasonal overlap (corresponding to the probability of visiting these sites in both migratory seasons in a given year) was on average rather high for the osprey (0.46 ± 0.37) but low for the marsh harrier (0.09 ± 0.13 ; Fig. 3). Logit-transformed recurrence and overlap values showed significant differences between species in autumn ($F_{1,5,4} = 12.6$, $N = 2$, $P = 0.02$) and spring ($F_{1,3,4} = 4.8$, $N = 2$,

Table 2
ANOVA tests of the effect of individual on route, timing and duration of migration for ospreys and marsh harriers

Season	Latitude	Longitude		Date		Duration	
		Osprey	Harrier	Osprey	Harrier	Osprey	Harrier
Autumn	46°N	68.9*** (8,22)	1.6 _(6,23)	2.9* _(8,22)	5.9** _(6,23)	5.5** _(7,20)	82.6*** _(4,19)
	36°N	58.1*** (7,20)	5.8** _(4,19)	2.9 _(7,20)	9.4** _(4,19)		
	26°N	11.0*** (7,20)	1.7 _(4,19)	1.4 _(7,20)	11.1*** _(4,19)		
Spring	26°N	1.2 _(4,13)	0.3 _(3,15)	3.8 _(4,13)	22.1*** _(3,15)	2.7 _(4,13)	15.3** _(3,15)
	36°N	21.5*** (4,13)	0.5 _(3,15)	3.7 _(4,13)	3.3 _(3,15)		
	46°N	492.9*** (4,13)	0.7 _(3,15)	1.3 _(4,13)	9.5** _(3,15)		

We analysed variation between individuals in route (longitude) and timing (date) at three latitudes, corresponding to regions in Europe (46°N), the Mediterranean (36°N) and the Sahara (26°N), during autumn and spring migration. F values, sample sizes (number of individuals, total number of observations) and significance levels ($*P < 0.05$; $**P < 0.01$; $***P < 0.001$) are given for each one-way ANOVA test (numerator and denominator degrees of freedom for F values are the number of individuals – 1 and the number of observations – 1, respectively).

Table 3
Repeatability estimates (r) for routes, timing and duration of autumn and spring migration of ospreys and marsh harriers

Season	Latitude	Longitude		Date		Duration	
		Osprey	Harrier	Osprey	Harrier	Osprey	Harrier
Autumn	46°N	0.88 0.71–1.05	0.06 –0.22–0.34	0.17 –0.16–0.5	0.35 –0.16–0.86	0.35 –0.12–0.82	0.92 0.72–1.13
	36°N	0.87 0.68–1.07	0.41 –0.42–1.25	0.19 –0.21–0.58	0.55 –0.24–1.34		
	26°N	0.54 0.08–1.01	0.09 –0.49–0.67	0.04 –0.21–0.3	0.60 –0.16–1.35		
	26°N	0.04 –0.67–0.75	–0.15 –0.59–0.28	0.38 –0.58–1.33	0.81 0.06–1.56	0.26 –0.67–1.19	0.74 –0.21–1.69
Spring	36°N	0.81 0.34–1.29	–0.11 –0.71–0.50	0.37 –0.58–1.32	0.32 –1.13–1.77		
	46°N	0.99 0.96–1.02	–0.13 –0.81–0.67	0.07 –0.68–0.81	0.63 –0.57–1.84		

We calculated repeatability in route (longitude) and timing (date) at three latitudes, corresponding to regions in Europe (46°N), the Mediterranean (36°N) and the Sahara (26°N). Sample sizes for each estimate are given in Table 2. The 95% confidence intervals (calculated from F ratios according to Nakagawa & Schielzeth, 2010) are given below each estimate. Intervals that did not overlap with zero are shown in bold.

$P = 0.04$). Also, total recurrence ($F_{1,36} = 25.2$, $N = 2$, $P < 0.001$) and seasonal overlap ($F_{1,36} = 16.9$, $N = 2$, $P < 0.001$) differed significantly between species.

DISCUSSION

We found a consistent pattern in individual route repeatability (as reflected by longitude values) of high and clearly significant estimates for ospreys but low and statistically nonsignificant estimates for marsh harriers (see also Vardanis et al., 2011, for marsh harriers). Similarly, we found the opposite species-specific pattern for timing and duration of migration, but this effect was estimated with higher uncertainty (CIs in Table 3). Our aim in the present study was to determine whether the repeatability patterns in migratory space and time across the entire annual cycle differ between ospreys and marsh harriers. We evaluated, for the first time, the long-term, individual-based migration patterns of these two species using high-resolution satellite-tracking data. However, we are well aware that our sample sizes are rather limited for precise

repeatability estimates (cf. Wolak, Fairbairn, & Paulsen, 2012), as the often wide 95% CIs of Table 3 suggest. Thus, our specific repeatability estimates need to be interpreted with caution.

The Geographical Dimension: Repeatability in Route and Stopover Site Use

We suggest that the difference in route repeatability between the two species is mainly explained by two factors: (1) larger between-individual variation in routes in ospreys compared to marsh harriers (Fig. 1) and (2) a higher degree of recurrently used stopover sites by individual ospreys compared to marsh harriers (Fig. 3).

The within-individual variation in routes was indeed rather similar in the two raptor species (for example, average within-individual standard deviation at 36°N was 314 km for the marsh harrier and 182 km for the osprey) compared to the standard deviation in routes between individuals, which was clearly larger for ospreys (730 km) than marsh harriers (253 km; Table A3, Fig. 1),

Figure 2. Repeated site use in (a) four ospreys and (b) three marsh harriers that were tracked for at least 2 complete years. The seven individuals are arranged along the X axis, each with four to six bars representing the apparent goal areas identified for that individual (see also Table 1 for details of trips and Tables A1, A2 for details of the goal areas). Hence, for osprey OM1, there were four apparent goal areas, and for osprey OM2, there were five apparent goal areas (Tables A1, A2), and so on. The Y axis shows the number of migratory journeys, with data for spring migration (S) in grey and autumn migration (A) in black. Filled parts of bars indicate journeys when the area was used for stopover, hatched parts of bars indicate when the area was briefly visited (passage) while open parts of bars denote journeys when the site was not visited by the bird.

Figure 3. Mean $\pm$ SD rates of autumn, spring and total recurrence at apparent goal areas, as well as the seasonal overlap in goal area visits, for the four ospreys ($N = 19$ goal areas used) and the three marsh harriers ($N = 19$ goal areas used) that were tracked for at least 2 complete years (based on the data of repeated goal area use shown in Fig. 2).

reflecting broad-front migration in ospreys and a narrow migration corridor in marsh harriers. As a consequence, route repeatability should be high for ospreys because the route of one individual osprey is unlikely to be similar to the route of another osprey. In contrast, the routes of individual marsh harriers were all in a rather narrow migration corridor, with between-individual variation small compared with the within-individual variation in route, and repeatability was thus closer to zero. In addition, the ospreys' habit of revisiting individual-specific goal areas (often used for stopover; already described by Alerstam et al., 2006) meant that routes of the same osprey in different years converged towards these apparent goal areas and this contributed to the overall degree of repeatability in routes for this species.

Why is there a broad geographical migration front of ospreys (i.e. large variation in routes between individuals and between siblings from the same broods; cf. Österlöv, 1977) and a high degree of fidelity to individual-specific stopover areas? One possibility may be related to ospreys' reliance on fish for food. High-quality foraging sites are probably relatively scarce, but widespread throughout Europe, which could promote broad-front migration. Furthermore, hunting efficiency is possibly reduced with increasing densities of foraging ospreys, promoting thinning among individuals and thus wider variation in routes (cf. Alerstam, 1990). Hunting efficiency may improve with increasing local knowledge about the area, and thus, would explain high fidelity to specific stopover sites. Another reason for high stopover site fidelity could be that the quality of these sites, as reflected by the availability of a largely renewable food source, may show little fluctuation between seasons and years.

Among solitary migrants, the marsh harrier and various small songbirds seem to show a lower degree of route repeatability and nonbreeding site fidelity (Catry et al., 2004; Drost, 1941; Stanley et al., 2012; Vardanis et al., 2011) than the osprey. Although marsh harriers and songbirds differ in many aspects (e.g. size and flight mode), they are similar in that their potential feeding habitat

is much more widespread and prey availability may be spatially more variable compared to a feeding specialist like the osprey. Marsh harriers probably have more to gain from being flexible in their choice of stopover sites, meaning that the relative role of other factors potentially affecting route choice, such as seasonal variation in the distribution of favourable foraging areas and seasonal variation in wind, becomes more important.

The Temporal Dimension: Repeatability in Timing and Duration

Even though repeatability in timing and duration of migration was consistently larger for the marsh harrier than the osprey, the confidence intervals (Table 3) indicate that this tendency is more suggestive rather than conclusive compared to the geographical dimension discussed above. The timing of migration is presumably determined by an interaction between (1) endogenous factors and developmental processes associated with the individuals' annual cycles of migration, breeding and moult and (2) environmental factors associated with variability of resources and travel conditions. However, it remains unclear why ospreys tend to have a larger individual plasticity in timing and duration of migration than marsh harriers. One interesting possibility is that the potential foraging constraints that make ospreys more repeatable with respect to their routes and use of individual-specific stopover sites may influence migratory timing in the opposite way, for example if stopover duration is related to the foraging conditions at a given site in a given year, thus promoting relatively high flexibility in timing between years.

It is somewhat paradoxical that marsh harriers, despite their high individual consistency in annual timing of migration, have advanced their autumn passage through southern France (i.e. including the Swedish population) twice as much as ospreys have over the last 30 years (Filippi-Codaccioni et al., 2010). While the mechanisms driving this population-level advance in a species with little individual plasticity remains elusive, this pattern has also been observed among Icelandic black-tailed godwits, *Limosa limosa islandica* (Gill et al., 2014) and migratory black kites, *Milvus migrans* (Sergio et al., 2014).

Timing performance may also change with experience and learning. Sergio et al. (2014) found that the most dramatic individual 'improvement' in migratory timing occurs among young prebreeding birds. However, in our study we included only adult birds, and we assumed no difference in experience between birds within the two species. An additional possible limitation could be due to the differential timing (Alerstam et al., 2006) and duration (Strandberg et al., 2008) of migration between the sexes. However, the small sample size precludes testing for sex effects, but the balanced sex ratio in our study makes such a potential effect less likely to bias our results.

Individual Consistency Versus Flexibility in Different Migratory Traits

A considerable number of repeatability studies have provided evidence supporting significant consistency in the timing of bird migration among a variety of species (Conklin et al., 2013; Gill et al., 2014; Lopez-Lopez et al., 2014; Lourenço et al., 2011; Pulido, 2007b; Thorup et al., 2013), whereas evidence for relatively low and sometimes nonsignificant repeatability in routes has been reported for three raptor species (marsh harrier: Vardanis et al., 2011; Egyptian vulture, *Neophron percnopterus*: Lopez-Lopez et al., 2014; black kite: Sergio et al., 2014), one songbird (Stanley et al., 2012) and one pelagic long-distance migrant (Dias et al., 2013). Even though it may be difficult to compare repeatability estimates across studies because of variation in measurement precision, the present set of published

studies would make it tempting to suggest that a higher repeatability in timing compared to routes may be a general feature in bird migration. This may be a consequence of constraints set by genetic/endogenous mechanisms controlling the timing of bird migration, while advanced navigation capabilities allow flexibility in routes (associated with environmental variation in wind and resources), also for species with a rather strict fidelity to breeding and wintering sites.

However, the case of the osprey shows a contrasting pattern with relatively lower repeatability in timing and higher repeatability estimates in routes. Thus, the relative level of individual variation present in different time- and space-associated behavioural traits across avian migrants may not reflect general adaptations or constraints in long-distance migration common to all long-distance migrants (Piersma, Pérez-Tris, Mouritsen, Bauchinger, & Bairlein, 2005), but might, instead, be shaped by species-specific differences in life history and ecological characteristics, as well as the importance of selective forces (time, energy and safety).

Future Directions

Estimating repeatability is a tool to facilitate inferences about the evolutionary ecology of behavioural traits, and, thus, its estimation may not be an aim in itself. Despite the large heterogeneity of repeatability studies in the bird migration literature, comparisons of r estimates between different groups of birds (e.g. sexes, populations, species within and between different migratory systems, as well as different stages of the annual cycle) hold great potential in furthering our understanding of the adaptive value of individuality in migratory behaviour. Comparisons across species and annual stages may, for example, identify suitable traits accommodating genetic variation and, thus, possibly larger potential for evolutionary change (van Noordwijk et al., 2006). Furthermore, such an approach, in combination with additional lines of data (e.g. stopover behaviour, mortality patterns, etc.) can help determine the relevant ecological conditions (Pulido, 2007b) and optimization factors (e.g. time, energy, mortality risk; Alerstam, 2011) that shape different migratory strategies. Finally, future repeatability analyses of individual migration histories, including the initial journeys in the life of an individual (McKinnon, Fraser, Stanley, & Stutchbury, 2014; Schiffner, Pavkovic, Siegmund, & Wiltshko, 2011; Sergio et al., 2014; Stout, Greene, & Postupalsky, 2009), will be needed in order to disentangle the relative importance and interaction between genetic and environmentally induced responses, as well as experience-based learning and cultural and social influences on the observed strategies in migratory vertebrates.

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Appendix

Table A1

Possible intermediate goal areas (i.e. areas used for repeated stopover or passage) by four ospreys that were tracked for at least 2 complete years

Individual	Country (coordinates)	Autumn			Spring		
		Year	Use	Duration (days)	Year	Use	Duration (days)
OM1	1. France (47°42'N, 6°35'E)	2006	SO	15	2007	P	
		2007	SO	30	2008	SO	5
		2008	SO	31	2009	SO	5
		2009	SO	31	2010	SO	5
		2010	SO	22	2011	SO	6
	2. France (44°23'N, 3°12'E)	2006	—		2007	P	
		2007	P		2008	—	
		2008	—		2009	—	
		2009	—		2010	P	
		2010	SO	2	2011	P	
	3. Algeria (29°11'N, 7°12'W)	2006	P		2007	—	
		2007	P		2008	—	
		2008	P		2009	—	
		2009	N		2010	—	
		2010	—		2011	—	
	4. Mauritania (19°36'N, 13°5'W)	2006	—		2007	P	
		2007	P		2008	P	
		2008	P		2009	P	
		2009	P		2010	—	
		2010	P		2011	P	
OM2	1. Poland (53°6'N, 16°11'E)	1998	P		1999	—	
		1999	—		2000	—	
		2000	SO	2	2001	—	
	2. Poland (52°36'N, 14°18'E)	1998	—		1999	SO	5
		1999	P		2000	—	
		2000	—		2001	P	
	3. Poland (51°N, 15°18'E)	1998	SO	16	1999	P	
		1999	SO	10	2000	SO	1
		2000	SO	8	2001	SO	2
	4. Italy (45°30'N, 13°18'E)	1998	P		1999	P	
		1999	—		2000	—	
		2000	P		2001	P	
	5. Tunisia (35°17'N, 10°24'E)	1998	SO	8	1999	—	
		1999	P		2000	—	
		2000	P		2001	—	
OF1	1. Germany (51°23'N, 10°54'E)	2007	SO	16	2008	SO	11
		2008	SO	20	2009	SO	6
		2009	SO	34	2010	P	
	2. W. Sahara (25°11'N, 11°11'W)	2007	—		2008	P	
		2008	P		2009	—	
		2009	P		2010	P	
	3. France (44°17'N, 0°30'E)	2007	P		2008	—	
		2008	P		2009	—	
		2009	P		2010	x	

Table A1 (continued)

Individual	Country (coordinates)	Autumn			Spring		
		Year	Use	Duration (days)	Year	Use	Duration (days)
OF2	4. Spain (36°12'N, 5°24'W)	2007	P		2008	P	
		2008	P		2009	P	
		2009	P		2010	x	
	5. Morocco (34°6'N, 6°17'W)	2007	SO	5	2008	—	
		2008	SO	8	2009	P	
		2009	SO	3	2010	x	
	1. Morocco (33°12'N, 3°36'W)	2006	—		2007	—	
		2007	P		2008	x	
		2008	P		2009	P	
	2. Spain (36°23'N, 5°17'W)	2006	SO	6	2007	P	
		2007	—		2008	x	
		2008	SO	10	2009	—	
	3. Germany (51°17'N, 10°35'E)	2006	P		2007	P	
		2007	—		2008	—	
		2008	P		2009	x	
	4. Spain (41°30'N, 1°6'W)	2006	P		2007	P	
		2007	P		2008	x	
		2008	—		2009	P	
	5. Germany (50°17'N, 12°18'E)	2006	SO	4	2007	P	
		2007	SO	44	2008	x	
		2008	SO	24	2009	x	

SO: stopover; P: passage; —: absence; x: data gap. We used the following criteria as minimum requirements to define an area as a possible goal: (1) one stopover and one passage, (2) two stopovers or (3) three passages (within a radius of 50 km). Duration of stopover is also shown.

Table A2

Possible intermediate goal areas (i.e. areas used for repeated stopover or passage) by three marsh harriers that were tracked for at least 2 complete years

Individual	Area (coordinates)	Autumn			Spring		
		Year	Use	Duration (days)	Year	Use	Duration (days)
MHM1	1. Spain (40°6'N, 1°18'W)	2006	SO	3	2007	—	
		2007	—		2008	P	
		2008	—		2009	—	
		2009	—		2010	—	
		2010	—		2011	—	
		2011	—		2012	—	
	2. Spain (39°N, 2°W)	2006	P		2007	—	
		2007	P		2008	—	
		2008	—		2009	—	
		2009	—		2010	—	
		2010	—		2011	—	
		2011	SO	1	2012	—	
	3. Spain (36°36'N, 5°54'W)	2006	—		2007	—	
		2007	—		2008	—	
		2008	—		2009	—	
		2009	—		2010	P	
		2010	—		2011	P	
		2011	—		2012	SO	16
	4. Morocco (32°12'N, 7°24'W)	2006	—		2007	SO	27
		2007	—		2008	SO	22
		2008	—		2009	SO	20
		2009	—		2010	SO	42
		2010	—		2011	—	
		2011	—		2012	P	
	5. Algeria (31°30'–28°30'N, 4°W) ^a	2006	P		2007	—	
		2007	SO	1	2008	—	
		2008	P		2009	—	
		2009	P		2010	—	
		2010	P		2011	P	
		2011	P		2012	—	
	6. Mauritania (13°30'N, 20°18'W)	2006	SO	1			
		2007	—		2007	P	
		2008	—		2008	—	
		2009	—		2009	—	
		2010	—		2010	—	
		2011	—		2011	SO	12
		2012	—		2012	—	

(continued on next page)

Table A2 (continued)

Individual	Area (coordinates)	Autumn			Spring		
		Year	Use	Duration (days)	Year	Use	Duration (days)
MHF1	1. Germany (52°23'N, 10°18'E)	2012	—		2008	SO	1
		2007	—		2009	—	
		2008	—		2010	—	
		2009	P		2011	—	
		2010	—		2012	—	
	2. Germany (51°17'N, 8°E)	2011	—		2008	—	
		2007	P		2009	P	
		2008	—		2010	P	
		2009	P		2011	P	
		2010	—		2012	—	
	3. France (48°47'N, 6°42'E)	2011	—		2008	SO	2
		2007	P		2009	—	
		2008	—		2010	—	
		2009	—		2011	—	
		2010	—		2012	—	
	4. France (43°12'N, 3°23'E)	2011	—		2008	P	
		2007	—		2009	—	
		2008	SO	5	2010	P	
		2009	SO	2	2011	—	
		2010	P		2012	—	
	5. Spain (40°36'N, 0°36'E)	2011	—		2008	SO	1
		2007	SO	3	2009	—	
		2008	SO	3	2010	P	
		2009	P		2011	—	
		2010	SO	2	2012	—	
	6. Spain (38°N, 0°36'W)	2011	SO	3	2008	—	
		2007	P		2009	—	
		2008	P		2010	—	
		2009	P		2011	—	
		2010	—		2012	—	
	7. (Algeria (28°23'N, 4°30'W)	2011	P		2008	—	
		2007	P		2009	—	
		2008	P		2010	—	
		2009	—		2011	—	
		2010	—		2012	—	
MHF2	1. Germany (50°–53°N, 9°–11°E)	2011	P		2006	—	
		2005	P		2007	P	
		2006	—		2008	P	
		2007	—		2009	—	
		2008	—				
	2. France (46.5°N, 5°E)	2009	P		2006	P	
		2005	—		2007	—	
		2006	SO	1	2008	P	
		2007	S	3	2009	—	
		2008	—				
	3. Spain (36.6°N, 5.7°W)	2009	P		2006	—	
		2005	—		2007	SO	6
		2006	—		2008	SO	5
		2007	—		2009	SO	4
		2008	—				
	4. Algeria (34.5°N, 0°)	2009	—		2006	—	
		2005	P		2007	—	
		2006	P		2008	—	
		2007	P		2009	—	
		2008	P				
	5. Algeria (30°N, 2.5°W)	2009	—		2006	—	
		2005	P		2007	—	
		2006	P		2008	—	
		2007	P		2009	—	
		2008	P				
	6. Morocco (29.7°N, 9.7°W)	2009	—		2006	P	
		2005	—		2007	P	
		2006	—		2008	—	
		2007	—		2009	P	
		2008	—				
		2009	—				

SO: stopover; P: passage; —: absence. We used the following criteria as minimum requirements to define an area as a possible goal: (1) one stopover and one passage, (2) two stopovers or (3) three passages (within a radius of 50 km). Duration of stopover is also shown.

^a Possibly identical flight paths.

Table A3Within- and between-individual variances (s^2), as well as F ratios for routes, timing and duration of migration of ospreys and marsh harriers

Season	Latitude	Species	df	Longitude		Date		Duration	
				Within	Between	Within	Between	Within	Between
Autumn	46°N	Osprey	7	1.90	36.36	73.93	121.28		
		Harrier	5	14.15	3.96	49.41	52.61		
				7.46	9.19	1.50	2.31		
	36°N	Osprey	6	4.10	65.91	98.83	161.43	0.07	0.16
		Harrier	3	12.21	7.95	84.06	128.65	0.06	1.47
				2.98	8.29	1.18	0.80	1.14	9.45
	26°N	Osprey	6	12.15	27.83	202.17	162.81		
		Harrier	3	9.15	2.48	82.98	143.34		
				1.33	11.24	2.44	1.14		
Spring	26°N	Osprey	3	21.90	6.55	36.47	63.08		
		Harrier	2	3.16	0.24	56.49	279.54		
				6.93	27.56	1.55	4.43		
	36°N	Osprey	3	2.78	17.81	36.95	60.02	0.18	0.12
		Harrier	2	1.37	0.13	44.60	34.37	0.04	0.11
				2.02	133.34	1.21	1.75	4.81	1.12
	46°N	Osprey	3	0.21	33.30	56.04	32.89		
		Harrier	2	2.22	0.35	17.93	30.24		
				10.75	95.02	3.13	1.09		

Variances for route (degrees of longitude) and timing (date) were calculated for three latitudes, corresponding to regions in Europe (46°N), the Mediterranean (36°N) and the Sahara (26°N). Index of duration refers to days per degree of latitude (see [Methods](#)). Degrees of freedom (df = number of individuals – 1) are provided for each estimate. Differences between species in variances were tested by Fisher's F ratios (shown in italics); statistical significance based on an F distribution table for $P = 0.05$ are shown in bold.