Individual consistency and sex differences in migration strategies of Scopoli's shearwaters *Calonectris diomedea* despite year differences

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Abstract   Recently-developed capabilities for tracking the movements of individual birds over the course of a year or longer has provided increasing evidence for consistent individual differences in migration schedules and destinations. This raises questions about the relative importance of individual consistency versus flexibility in the evolution of migration strategies, and has implications for the ability of populations to respond to climatic change. Using geolocators, we tracked the migrations of Scopoli's shearwaters *Calonectris diomedea* breeding in Linosa (Italy) across three years, and analysed timing and spatial aspects of their movements. Birds showed remarkable variation in their main wintering destination along the western coast of Africa. We found significant individual consistency in the total distance traveled, time spent in transit, and time that individuals spent in the wintering areas. We found extensive sex differences in scheduling, duration, distances and destinations of migratory journeys. We also found sex differences in the degree of individual consistency in aspects of migration behaviour. Despite strong evidence for individual consistency, which indicates that migration journeys from the same bird tended to be more similar than those of different birds, there remained substantial intra-individual variation between years. Indeed, we also found clear annual differences in departure dates, return dates, wintering period, the total distance traveled and return routes from wintering grounds back to the colony. These findings show that this population flexibly shifts migration schedules as well as routes between years in response to direct or indirect effects of heterogeneity in the environment, while maintaining consistent individual migration strategies [*Current Zoology* 60 (5): 631–641, 2014].

Keywords   Avian migration, GLS loggers, Repeatability, Individual strategies

Avian migration evolved to allow the exploitation of seasonal peaks of resource abundance located in geographically distant areas (Berthold, 2001). Migration behaviour is an evolutionarily very labile trait, appearing and disappearing repeatedly throughout the avian phylogeny (Alerstam et al., 2003; Piersma et al., 2005). Although the ancestors of birds were also seasonal migrants, and presumably evolved adaptations that support a migratory lifestyle (e.g. the clock-and-compass navigation system), as the avian clade diversified, new innovations emerged in different lineages that provided a diverse array of physiological and behavioural solutions to the challenges presented by migration (Piersma et al., 2005). Therefore, mechanisms and patterns of migration vary widely between species, as may the degree of individual flexibility in migration behaviour in response to environmental change.

In many areas, availability and distribution of resources varies unpredictably between years, which should favour flexibility in choosing when to migrate and how far to travel. Furthermore, inter-annual variation meteorological factors cause birds to vary migration routes (Gonzalez-Solis et al., 2009) to minimize energetic costs (Sherpard et al., 2013), which promotes flexibility and may obscure individual strategies (Mellone et al., 2011). In fact, the decision to migrate in itself appears to be flexible, switching on or off based on a genetically determined threshold level of external or internal conditions experienced by the individual (Newton, 2012). A similar threshold mechanism may operate, although less dramatically, in determining whether migrant individuals choose to travel long or short distances, and how

long they remain in intermediate staging areas along the migratory route. At the same time, environmental unpredictability has preserved a large degree of genetic variation in migratory traits in many migrant populations (Piersma et al., 2005), presumably because different migration strategies provide differential survival and reproductive success across years. A genetic basis for alternative migration strategies could explain the widely-observed, consistent between-individual differences in migration schedules (e.g. Battley, 2006; Thorup et al., 2013). For example, the timing of migratory restlessness is a trait that is at least partly under genetic control (Newton, 2008). Nevertheless, the degree to which individual differences in migration schedules are genetically controlled vs. condition-dependent still requires further investigation. A first step to studying this is to distinguish the degree to which the observed variation in distances and destinations in migratory journeys are attributable to flexibility within individuals vs. stable differences between individuals.

New technological capabilities for tracking individual movements over the course of a year or longer, have made it possible to track entire migratory journeys, including in successive years by the same individuals. These tools have provided not only additional evidence for individual repeatability in migration timing (Dias et al., 2011; Vardanis et al., 2011; Conklin et al., 2013; Stanley et al., 2012) but also intriguing data pointing to striking differences among species in the extent of individual consistency in migration routes and destinations (Phillips et al., 2005, Dias et al., 2011; Guildford et al., 2011; Dias et al., 2013; Raine et al., 2013).

In this study we tracked adult Scopoli's shearwaters *Calonectris diomedea* of both sexes repeatedly during three consecutive years, and examined variance in several components of migration behaviour that allowed us to assess the relative importance of individual consistency versus flexibility in their migratory journeys. Maximizing survival is considered to be the key determinant of the Darwinian fitness of iteroparous species with long life spans, such as seabirds (Stearns, 1999). Moreover, seabirds are likely to encounter substantial fluctuations in their environment during their long lives. Hence, we expect selection to have maximized the degree to which seabirds are able to flexibly adjust their behaviour. Although, long-lived species presumably vary in the degree to which their environments fluctuate, several recent studies have reported individual consistency in movements at large (Dias et al., 2011) and small scales (Patrick et al., 2013; Patrick and Weimers-

kirch, 2014). The degree of flexibility may, however, vary greatly between species and even populations.

As timing of migratory journeys may be under the control of mechanisms that differ from those influencing decisions about where and how far to travel, we separately examine the importance of within- and between-individual variation in temporal as well as spatial aspects of migration. Furthermore, as sex is a stable trait within an individual, it may account for a substantial portion of between-individual differences in migration strategies; however, to date, most tracking studies investigating consistency in migration have not focused on sex differences (but see Perez et al., 2013). In this study we explicitly test for variation in migration strategies related to sex and we also examine whether sexes differ in the degree of flexibility in migration behaviour.

1 Materials and Methods

1.1 GLS attachment and data processing

The Scopoli's shearwater is a pelagic seabird that breeds in the Mediterranean and is considered to be a sibling taxon (subspecies or separate species) related to the Cory's shearwater (Sangster et al., 2012). Our study population breeds on Linosa, a volcanic island off Sicily, which holds the second largest colony of shearwaters in the Mediterranean (ca. 10,000 breeding pairs, B. Massa, personal communication). The birds breed inside crevices in the lava formation, and are mostly concentrated on the coast of Mannarazza, on the northern side of the island. They lay their single egg from the second half of May onwards, and chicks hatch between mid-July and the first week of August. Fledglings typically leave the colony around the end of October.

Light-level geolocators or Global Location Sensor (GLS) loggers (MK9 from British Antarctic Survey, UK, and MK3006 from Biotrack, UK) were attached to the leg rings of adult Scopoli's shearwaters during the chick-rearing period (first half of August) and were recovered at the beginning of the subsequent breeding season (mid-May).

We obtained 60 complete migrations from 46 individuals (21 females, 25 males) at 31 nests tracked within a period of 3 consecutive years (2009–2011). We repeatedly tracked 12 individuals: 10 individuals for two years (6 males, 4 females), and 2 individuals for three years (1 male, 1 female).

All of these tracks came from individuals that successfully fledged a chick prior to departure on migration. Bird sex was determined on the basis of body measurements (Lo Valvo, 2001) and vocalizations.

Table 1   Device deployment and recovery details

Year	Loggers deployed	Failed loggers	Not recovered	Files analysed	Males tracked	Females tracked
2009	23	1	0	22	15	7
2010	38	5	6	27	12	15
2011	11	0	0	11	6	5

The light data were processed using the BASTrak software suite (British Antarctic Survey, Cambridge). Using a threshold value of 2 in TransEdit, we determined sunrise and sunset transition times, each of which was assigned a level of confidence based on the slope and smoothness of the light curve. Locator software was then used to calculate geographical coordinates based on the day length and timing of mid-day derived from the transition times, using a sun elevation angle of -5. Processing parameters were derived from calibration data collected by five loggers of the same type left at the colony during the whole migration period. Geolocators provide two locations per day (local midnight and noon) with a mean error $\pm$ SD estimated in a previous study of 186 ± 114 km (Phillips et al., 2004).

1.2   Statistical analysis

We defined intervals of migratory movement ("total days in transit") as time periods during which birds advanced at least 0.8 degrees of latitude or longitude per day for at least 3 consecutive days. We defined wintering areas, or periods during which birds paused on migration, as those during which birds stopped rapid directional migratory flight for at least 3 days. Most tracks ($n = 47$) were of birds that used a single wintering area (for a mean $\pm$ SD of 83.4 ± 10.9 days), but 13 individuals visited multiple wintering areas (2 areas: $n = 9$; 3 areas: $n = 3$; 4 areas: $n = 1$, Table 2). The terminal wintering area (i.e. the furthest from the colony) was not always the region in which birds spent the most time (Table 2).

We selected several parameters for our analyses that described different temporal and spatial characteristics of migration routes and wintering areas. This included date and approximate time (local noon or midnight, as geolocators provide two locations per 24 hours) of i) departure, i.e., when a bird initiated migration (defined above) in the autumn, and (ii) return to the colony in the spring. The duration of the intervening period was termed "total migration period". The total number of days in wintering areas was the time away from the colony that was not spent in transit between wintering sites. We calculated the total distance traveled from the sum of the distances between consecutive locations

Table 2   The number of days spent in each wintering area by individual birds (see text for details)

Area 1	Area 2	Area 3	Area 4
20	9	39.5	11.5
23	42	4	–
15	37	10	–
9.5	4	62.5	–
60	5.5	–	–
68.5	13	–	–
27	42	–	–
15	45.5	–	–
5	60.5	–	–
6.5	60.5	–	–
6.5	78.5	–	–
6.5	79.5	–	–
9	80.5	–	–

2 wintering areas: $n = 9$, 3 wintering areas: $n = 3$, 4 wintering areas: $n = 1$.

when birds were in transit, and the straight-line distance between the point of entry to point of exit for each individual in their wintering areas (i.e. no attempt was made to calculate total distance traveled during periods of residency). Migratory routes during the return to the colony varied substantially in terms of maximum longitude west (i.e. how far west each bird travelled in the Atlantic Ocean). We therefore compared maximum longitude west to assess this variation. In addition, we also compared minimum latitude, which reflects the furthest point south that was reached.

We performed linear mixed effects models for the various migration parameters with sex as a fixed factor and nest (results for nest variance components reported elsewhere), individual and year as random factors. All factors were always included together in all models, which allowed us to quantify the variance that each explained. The combined analysis avoids the confounding of one factor with another, which can lead to inflated repeatability values in independent analyses (e.g. it is useful to account for sex before comparing within-

individual consistency). The initial model included all 60 migration journeys, including multiple trips from some individuals, to generate variance components for year and sex (although, as stated above, we also included individual and nest as random factors in the model). We used the regression coefficient for the fixed factor (sex) from this mixed model to identify sex differences in mean values for each migration parameter. We then built a second model, which contained the same factors but used a smaller dataset including only tracks from the 12 individuals tracked in multiple years ($n = 26$ migrations). We used the variance components from this second model to calculate individual repeatability.

We used the variance component for year and individual to calculate repeatability (intra-class correlation coefficient, or the proportion of the variance accounted for by differences within, compared with among, groups) of migratory behavior for different years and individuals. We computed the proportion of variance explained by each of these factors using the method outlined in Lessells and Boag (1987). This approach calculates a repeatability value using the among-groups variance component (the variance component associated with a random factor in the model such as individual), the within-group variance component (the remaining variance in the dependent parameter not associated with the focal factor, including variance associated with the random factors - year and nest - plus the residual variance), n0 (a coefficient related to the sample size per group in the dataset), and an additional value which is computed from two different degrees of freedom (one reflecting the number of groups, the other reflecting the number of individuals in the group). Sex was included in the model as a fixed factor because we anticipated that this was likely to affect migration patterns. The study years and individuals can be considered as random samples, and so variation attributable to individual years or birds was modeled using random factors, which provided variance components used for calculating repeatability.

We then partitioned the data from individuals tracked in multiple years according to sex. We performed the linear mixed models specified above separately for males ($n = 15$ migrations from 7 individuals) and females ($n = 11$ migrations from 5 individuals) and produced variance components to compute individual repeatability for each sex. We used the equation provided by Bonett (2002) to compute 95% confidence intervals around the repeatability estimates to determine if these differed between sexes.

We computed 95% kernel densities of unsmoothed locations in staging and wintering areas separately for each track. Points over land were included so as not to bias the kernel to periods when individuals were further offshore. As kernels were intended to represent wintering areas, we excluded the locations of birds in transit. We then computed the degree of overlap of these 95% kernel densities among all 60 migration journeys in our dataset which created a set of values for each paired comparison that ranged from 0 (no overlap) to close to 1 (almost complete overlap). The overlap values were included in a Poisson mixed model with the binary fixed factors of "same sex" (0 as no and 1 as yes), "same year", "same nest" or "same individual", and the random factors of "nest" and "individual". A significantly positive regression coefficient would indicate a higher overlap (i.e. greater similarity) between individuals from the same classification (sex, year, nest, or individual) than between individuals from different classifications. For example, a positive coefficient for "same sex" would indicate that tracks from birds of the same sex showed greater overlap than tracks from birds of the opposite sex. We used a Lambert Azimuthal Equal Area projection in the spatial analysis.

All analyses were performed using R software (version 2.12.1, R Development Core Team 2010). Analyses of spatial data to perform kernel overlap comparisons were performed using the packages RODBC (Ripley and Lapsley, 2011), adehabitatLT (Calenge, 2006), mapproj (McIlroy, 2011), sp (Pebesma and Bivand, 2005; Bivand et al., 2008), and adehabitatHR (Calenge, 2006). Mixed models were performed using lme4 (Bates et al., 2011).

2 Results

2.1 Individual differences

Among individuals tracked for at least two years, we found significant individual repeatability in the total number of days spent in wintering areas (Fig. 1A, Table 3), total distance traveled (Fig. 1B, Table 3), and total number of days in transit (Fig. 1C, Table 3). There was no significant individual repeatability in dates of departure from the colony, or of return, migration period (in days), the minimum latitude reached during the winter, or the maximum west longitude reached on the return journey back to the colony (Table 3).

2.2 Year differences

We found significant differences among the three study years in several of the migration characteristics, including in dates of departure (Fig. 2A, Table 3), dates
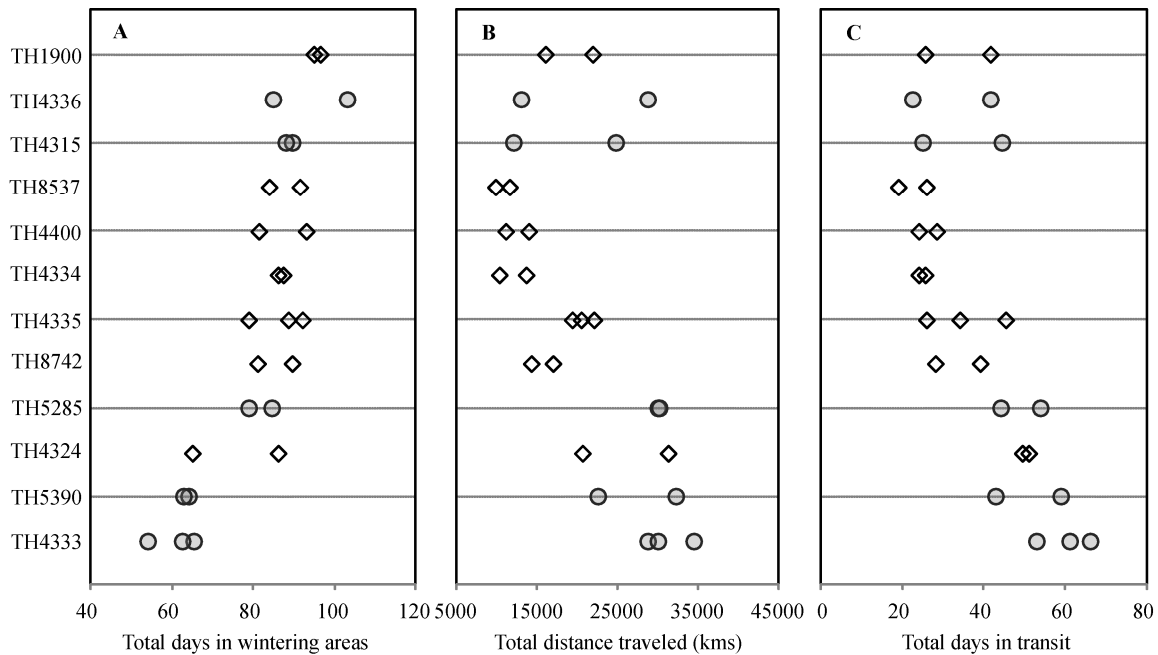
Fig. 1 Individual differences in the total number of days spent in wintering areas (A), the total kilometres traveled during migration (B), and the total days spent in migratory flight (C) by Scopoli's shearwaters tracked in successive years
Open diamonds are males and filled circles are females. Ten individuals were tracked in two years; two individuals were tracked in three years. Codes on y-axis correspond to ring numbers.

Table 3 Repeatability (r and associated P-value) by year (3 years, n = 60 tracks) and individual (12 individuals, n = 26 tracks), and sex differences in mean values (21 females, 25 males, n =60 tracks, negative t-values indicate female values are higher than males') for several migration parameters

	Year		Individual		Sex	
	r	P-value	r	P-value	t-value	P-value
Departure date from colony	0.15	**0.014**	0.36	0.072	-2.11	**0.039**
Return date to colony	0.17	**0.010**	0.09	0.357	-2.64	**0.011**
Migration duration	0.28	**<0.001**	0.03	0.436	-1.43	0.16
Total days in wintering areas	0.00	0.374	0.64	**0.003**	2.26	**0.028**
Total days in transit	0.11	**0.038**	0.49	**0.021**	-2.9	**0.005**
Total distance traveled	0.22	**0.002**	0.46	**0.030**	-2.26	**0.028**
Minimum latitude	0.00	0.374	0.32	0.098	4.32	**<0.001**
Maximum west longitude	0.18	**0.006**	0.14	0.288	-3.27	**0.002**

of return (Fig. 2B, Table 3), and duration of the migration period (Fig. 2C, table 3). Birds also differed between years in how far they traveled (Fig. 2D, Table 3) and the maximum west longitude they during the return journey (Fig. 2E, Table 3). There was no significant effect of years on the minimum latitude (most southerly point) or the number of days birds spent resident in wintering areas (Table 3).

2.3 Sex differences

Males departed earlier from the colony in autumn (Fig. 3A, Table 3) and returned earlier in spring (Fig. 3B, Table 3), but did not differ from females in the duration of the nonbreeding period (Table 3). Compared with males, females traveled further south (Fig. 3F, Table 3), and further west (Fig. 3G, Table 3) on their return migration, covered a longer total distance (Fig. 3E, Table 3) and therefore spent more days in transit (Fig. 3D, Table 3). Females therefore spent a shorter overall period resident in wintering areas (Fig. 3C, Table 3).

We found significant sex differences in the 95% kernel density polygons in wintering areas: the overlap in these kernels was significantly greater between birds of the same than opposite sex (same sex: b = 0.368, SE = 0.117, z = 3.139, P = 0.0017, Fig. 4). In contrast, the

mean overlap did not differ significantly by year ($b = 0.043$, $SE = 0.125$, $z = 0.344$, $P = 0.731$), nest ($b = 0.394$, $SE = 0.352$, $z = 1.118$, $P = 0.263$) or from the same vs. different individuals ($b = 0.144$, $SE = 0.528$, $z = 0.272$, $P = 0.785$).
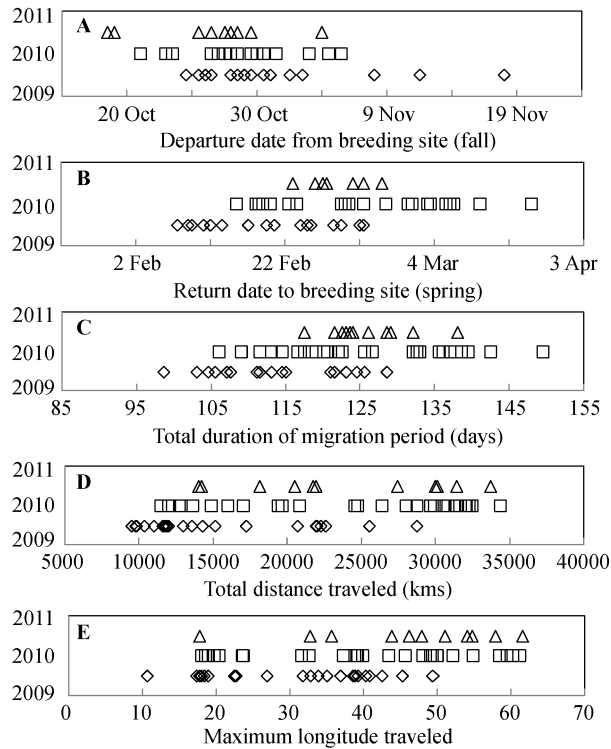

Fig. 2 Differences among years in departure date from breeding colony (A), return date (B), total migration period (days) (C), total distance traveled (km) during migration (D), and maximum west longitude reached on return migration back to breeding colony
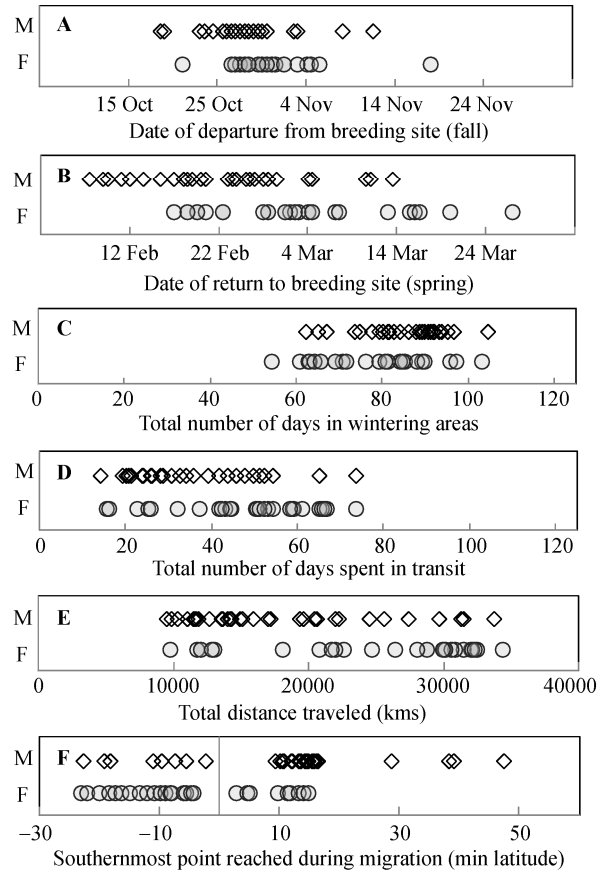

Fig. 3 Sex differences in departure day from breeding colony (A), return date (B), total number of days spent in wintering areas (C), total number of days spent in transit (D), total distances traveled (km) (E), minimum latitude (most southerly location) reached during migration (F) and maximum west longitude reached on return migration to breeding colony (G)
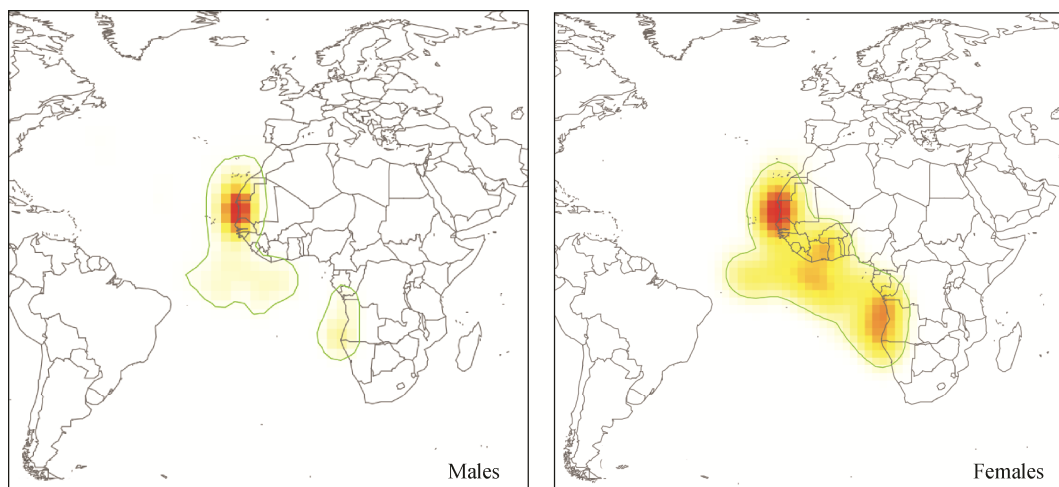Open diamonds are males and filled circles are females.

Fig. 4 Sex differences in kernel densities of wintering areas for males and females
Green lines delineate 95% kernel density.

Sexes also differed in the degree of individual consistency in the total number of days spent in wintering areas: repeatability was high and significant in females, but not significant in males. Furthermore, the 95% confidence intervals surrounding the repeatability estimates for each sex did not overlap (Table 4). There was some evidence for sex differences in individual consistency in three other migration parameters: females but not males showed repeatability in the minimum latitude, males but not females showed repeatability in the total number of days in transit and total distances traveled, but for these parameters, the 95% confidence intervals surrounding repeatability estimates for each sex overlapped (Table 4).

3 Discussion

3.1 Migration distances

Although the Scopoli's shearwaters in our study were obligate migrants, there was a striking level of individual variation in migration distance. All individuals performed at least a short migration along the western coast of Africa as far as the Mauritanian continental shelf, which is part of the very productive Canary Upwelling region (Aristegui et al., 2009), and 45% continued south along the coast, including 15% that travelled as far south as the productive Benguela Upwelling region off Angola and northern to Namibia. These two major upwelling regions are exploited by a wide range of migrant seabirds (Phillips et al., 2005; Stenhouse et al., 2012; Gilg et al., 2013). Furthermore, Cory's shearwaters from some of the Atlantic populations use the Canary Upwelling region also during the breeding season (Ramos et al., 2013).

Individual Scopoli's shearwaters differed consistently in the distances they traveled during migration and in the number of days they spent in transit between the breeding site and wintering areas. In this population, the number of days spent in transit shows an inverse correlation with the number of days spent resident in wintering areas (M. Müller, unpublished data). Therefore, not surprisingly, we also found that the latter differed significantly among individuals. The proximate mechanisms underlying these individual differences in migration characteristics remain poorly understood. In certain other taxa that, like the Scopoli's shearwater, are large, long-lived birds with extended parental care, migration behavior is learned by following parents or migrating flocks to wintering areas (e.g. swans, geese, storks and cranes; Sutherland, 1998) which is likely to reduce the proportion of the total population-level variation in migration destination that is attributable to individual differences. In petrels such as shearwaters, however, juveniles migrating for the first time travel without their parents and largely rely on an endogenous inherited program to control the direction and perhaps also the

Table 4 Individual repeatability (*r*, upper and lower 95% confidence limits and p-value) for males (*n* = 7, 15 tracks) and females (*n* = 5, 11 tracks) tracked in multiple years

		r	lower CI	upper CI	*P*-value
Departure date from colony	Males	0.416	-0.068	0.901	0.093
	Females	0.356	-0.348	1.061	0.155
Return date to colony	Males	0.199	-0.253	0.65	0.261
	Females	0	-0.371	0.371	0.261
Migration duration	Males	0.071	-0.273	0.415	0.398
	Females	0.001	-0.372	0.373	0.467
Total days in wintering areas	Males	0.196	-0.254	0.646	0.264
	Females	**0.819**	**0.659**	**0.979**	**0.003**
Total days in transit	Males	**0.514**	**0.083**	**0.945**	**0.048**
	Females	0.476	-0.173	1.125	0.087
Total distance traveled	Males	**0.665**	**0.38**	**0.951**	**0.012**
	Females	0.33	-0.374	1.035	0.173
Minimum latitude traveled	Males	0.219	-0.245	0.683	0.242
	Females	**0.627**	**0.159**	**1.094**	**0.031**
Maximum west longitude traveled	Males	0.262	-0.221	0.745	0.203
	Females	0	-0.371	0.371	0.467

distance they travel (Akesson and Hedenstrom, 2007; Newton, 2008). After fledging, juveniles accumulate skills, experience, and knowledge of suitable foraging areas to which they may later return in their migrations as adults (Guilford et al., 2011). It remains unclear, however, as to what extent individual differences in migration patterns reflect genetic variation in the internal clock and compass mechanism on which the initial movement as a fledgling appears to be based, rather than variation in experience with extrinsic factors encountered during their first formative years at sea.

Despite this individual consistency in migration distances, we also found clear annual differences in the distances traveled, total number of days spent in transit between the breeding site and wintering areas, the routes back to the colony, and the duration of the migration period. These collective population-level shifts between years in the selection of particular destinations are indicative of substantial flexibility in response to environmental circumstances and may arise due to annual variation in the spatial distribution of resources, i.e., a change in the relative profitability of different feeding areas (Newton, 2008). Between-year differences in migration destinations may also reflect variable resources among breeding seasons (and resulting reproductive costs and carry-over effects) that generate different marginal benefits in traveling farther to more profitable feeding areas (Catry et al., 2013). In any case, the observed variation in migration distances between years indicates birds are able to change their behaviour in response to variable environmental circumstances (see also Dias et al. 2011). These varying environmental circumstances likely include also meteorological factors such as sea surface winds (Gonzalez-Solis et al., 2009) which may have caused the between-year differences in return routes to the breeding site. As individuals can apparently can adjust behaviour to environmental changes, then perhaps the consistent individual differences in migration distances that we observed may not reflect hard-wired programmes but instead be caused by the internal or external circumstances of individuals remaining broadly similar.

3.2   Migration timing

Surprisingly, and in contrast to previous studies of the closely related Cory's shearwater (Dias et al., 2011) and many terrestrial migrants (Vardanis et al., 2001; Conklin et al., 2013; Stanley et al., 2012; Thorup et al., 2013; Lopez and Lopez et al., in press), individuals did not show significant individual consistency in their migratory schedules. In Scopoli's shearwaters, delays in

returning to the colony are due to birds traveling longer distances (and thus, also spending more time in transit and less time in wintering areas), which result in a longer absence from the colony (M. Müller, unpublished data). Therefore, as return dates are essentially a function of the distance traveled, it is surprising that the substantial individual consistency in migration distances did not lead to similar consistency in return dates. The dates of departure from waters around the colony in the autumn, however, do not correlate with the parameters related to migration distance (in this population), which indicates that birds that decide to travel farther do not leave earlier; hence, some other mechanism governs the decision to leave the breeding site. Departure dates were not consistent within individuals, suggesting that variation in environmental conditions may have a larger influence than individual behavioural preference. Indeed, departure dates from the colony appeared to advance in consecutive years. As dates of return to the colony appeared to become later in the three study years (due to farther travel), this resulted in longer absences from the colony. Delayed return would, if anything, be expected to delay laying and, ultimately, departure dates; however, the latter was not the pattern observed.

3.3   Sex differences in migration strategies

Sex differences in migration have previously been described for many species in both timing and in the distances traveled (Newton, 2008). Yet, previous migration studies of Cory's shearwaters found no sex differences in timing (Dias et al., 2011; Catry et al.; 2013, Perez et al., 2013) or destination (Dias et al., 2011; Perez et al., 2013). Our study, however, reveals for the first time several striking sex differences in temporal and spatial aspects of the migration of Scopoli's shearwater. Compared with females, males departed earlier from the colony in autumn and returned earlier the following spring. The high competition for nesting sites (Ramos et al., 1997) and the need for males to spend longer at their burrows to defend them against male conspecifics seems likely to be the motivation underlying early arrival in males (Hedd et al., 2014). Why males depart earlier from the colony in autumn compared to females remains unclear. One could speculate that they leave earlier to accommodate earlier arrival in the following spring (as sexes do not differ in the duration of their absence from the colony).

Previous studies on both partial and obligate migrant species have found that females tend to migrate farther than males (Newton, 2008; Fudickar et al., 2013). We found a similar pattern in Scopoli's shearwaters: fe-

males traveled a longer total distance, wintered further south, returned on a more westerly and indirect route, spent more days in transit, and fewer days in residence in wintering areas. Such patterns can arise if males, which are about 15% heavier than females (Granadeiro, 1993) are more competitive foragers in productive waters located closer to the colony, and force females to travel to more distant wintering areas. However, if this were so, we would expect a difference in migration strategies between males and females in Atlantic populations of Cory's shearwaters, which is not evident (Dias et al., 2011; Catry et al.; 2013). Moreover, Perez et al. (2013) found no association between body size and the decision to migrate in Cory's shearwaters. Alternatively, these sex differences may reflect carry-over effects of differential investment in reproduction. Although both sexes contribute equally to incubation and chick rearing (Hamer et al., 2002), males bear the costs of nest defence at the beginning of the breeding season while females produce an energetically costly egg. A recent study in which reproductive investment in Cory's shearwaters was experimentally reduced showed evidence for sex-specific effects carrying over onto migration behaviour: several manipulated males consequently migrated less far than control males whereas manipulated and control females traveled similar distances on average (Catry et al., 2013). In addition, Perez et al. (2013) found that male Cory's shearwaters were more likely to remain resident than were females, therefore showing more variability in migration decision. In line with this finding, we found intriguing evidence for sex differences in individual consistency in migration behaviour. Females showed significant repeatability in the most southerly point reached during migration and the total number of days spent in wintering areas, whereas only the latter was repeatable in males. On the other hand, males in our study population showed significant individual consistency in the total distances traveled and the total days spent in transit. Females were not consistent in the total distance traveled because a substantial proportion of females in some years traveled much farther west in their return migration (Fig. 3G). This added substantial intra-individual variation in the total distance traveled by many females, but few males.

3.4 Conclusions and future perspectives

Despite the expectation that seabirds should show high behavioural flexibility to cope with changing environments over the course of their long lives, here we show substantial individual consistency in many aspects of migration. This could on the one hand be interpreted

as a limit to individual flexibility, having arisen because maintaining complete flexibility imposes energetic or developmental costs, or reflect the extra risks associated with exposure to new situations or surroundings that the animal is ill-equipped to deal with. Alternatively, the individual consistency we observed may not be a constraint on flexibility, but reflect consistency in individual circumstances that result in similar decisions.

While studies of migration patterns often attempt to make a prediction about whether certain species are able to flexibly adjust to changing environments, it is necessary to disentangle whether behavioural changes at the population level are in fact due to individual plasticity, or to changes in frequencies of certain inflexible behavioural strategies within the population (Charmantier and Gienapp, 2013). Furthermore, even if migratory behaviour is relatively flexible within individuals, certain innate migratory behaviours may be very fine-tuned to particular ranges of stimuli that are highly predictable (e.g. seasonal changes in day length) and may not be adjustable based on the experiences of the animal, whereas other behaviours may be modifiable based on experience (discussed in Wright et al., 2010). The relative contributions of the innate vs. learned flexibility may play an important role in the ability of species to buffer rapid environmental changes.

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