Original Article

Individual variation in migratory behavior in a subarctic partial migrant shorebird

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Migratory behavior can differ markedly amongst individuals within populations or species. Understanding the factors influencing this variation is key to understanding how current environmental changes might influence migratory propensity and the distribution and abundance of migratory species across their range. Here, we investigate variation in migratory behavior of the partially migratory Eurasian oystercatcher (*Haematopus ostralegus*) population breeding in Iceland. We use the resightings of color-ringed adults and stable isotopes to determine whether individuals migrate or remain in Iceland during winter and test whether individual migratory strategies vary in relation to sex, body size, and breeding location. We also explore individual consistency in migratory strategy and test whether assortative mating with respect to strategy occurs in this population. The proportion of migrants and residents varied greatly across breeding locations but not with respect to sex or body size. Individuals were consistent in migratory strategy between years and there was no evidence of assortative mating by migratory strategy. We use these findings to explore factors underlying the evolution and maintenance of partial migration at high latitudes.

Key words: individual variation, migratory consistency, migratory strategies, stable isotopes, wader.

INTRODUCTION

Migration is commonly seen as a life-history trait shared by individuals within populations or species. However, many aspects of migratory behavior can differ markedly among individuals, from the direction (e.g., Finch et al. 2017) and routes undertaken (e.g., Vardanis et al. 2016) to the distance (e.g., Alves et al. 2012) and timing (e.g., Conklin et al. 2013; Gill et al. 2014) of migratory journeys. This variation is particularly extreme in partial migrant populations, in which some individuals remain close to the breeding grounds all year, while some undertake migratory journeys to more distant locations (Newton 2008). These behavioral differences among individuals have been linked to differences in individual fitness (Gunnarsson et al. 2005; Alves et al. 2013; Grist et al. 2017; Méndez et al. 2018a) and can influence population distribution in the nonbreeding season and associated strategies for site protection (Méndez et al. 2018b). Understanding individual variation in migratory behavior is, therefore, key to understanding these individual- and population-scale implications.

While migratory behavior can differ among individuals within populations, individuals typically display high repeatability of

migratory routes and strong site and time fidelity throughout the annual cycle (Newton 2008; Gill et al. 2014; Carneiro et al. 2019). Such consistency in site use and timings is likely to be beneficial in terms of prior knowledge of the availability of key resources, locations safe from predators, and mate location and timing (Kokko and Sutherland 2001; Gunnarsson et al. 2004; Gill et al. 2014; Winger et al. 2019).

Adopting one migratory behavior or another could have implications for the potential mates that are likely to be encountered, for example, if assortative mating by timing of arrival occurs and timing of arrival varies with migratory behavior (Bearhop et al. 2005; Gunnarsson et al. 2005, 2006). Assortative mating by timing of arrival could benefit breeding success by both reducing the delay between arrival and breeding and increasing the time available for replacement clutches should early nesting attempts fail (Morrison et al. 2019). Similarly, divorce can be more likely in pairs that differ in arrival time at breeding sites, and this can reduce breeding success (Gilsenan et al. 2017). Understanding the presence and extent of assortative mating by migratory behavior can, thus, be an important step in understanding population variance in reproductive success.

In this study, we investigated variation in individual migratory behavior in a partially migratory population, the Eurasian oystercatcher *Haematopus ostralegus*, breeding in Iceland, particularly, which individuals stay in Iceland and which migrate to Europe. Our study

population is at the northern edge of the species' distribution range and consists of both migrants that migrate over the Atlantic Ocean to winter in coastal sites throughout western Europe and residents that make short-distance movements within Iceland (mostly to western Iceland). Iceland supports an unusually high proportion of wintering Oystercatchers, given its latitude and winter temperatures (Þórisson et al. 2018), and this may be influenced by the transoceanic flight of at least 700 km that migratory individuals must undertake to reach the European wintering sites. Individuals that migrate or stay within Iceland could differ in body size, for example, if size influences the capacity to survive adverse winter conditions, which are likely to be more frequent at higher latitudes. In Icelandic oystercatchers, females tend to be slightly larger, and, thus, sex differences in migratory behavior could reflect differences in body size. The impact of adverse conditions at high-latitude winter sites is also likely to be influenced by the capacity of individual oystercatchers to switch between strategies of migrating or remaining in Iceland. Finally, resident and migrant individuals are known to occur throughout Iceland during the breeding season but their relative abundance across the country, the extent to which they occur within the same local populations, and the consequences for assortative mating are unknown.

Oystercatchers that winter in Iceland use a restricted number of coastal sites (as inland sites are frozen during winter) and forage on marine prey, while, elsewhere in Europe, a much wider range of marine and freshwater resources and environments are commonly used in winter (Goss-Custard 1996). These differences in habitat use and dietary composition are likely to result in differences between migrants and residents in carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios of feathers grown during late winter. Stable isotope analyses of feathers and tissues have successfully been used to identify migratory behaviors of individuals in a wide range of species (e.g., Bearhop et al. 2002; Pérez et al. 2014; Hegemann et al. 2015; Catry et al. 2016). We combined data from observations of color-marked individuals with information on the isotopic composition of their feathers to 1) identify migratory strategies of individual oystercatchers and explore whether migrants and residents differ in sex, body size, or breeding location, 2) assess how individually consistent these strategies are between years, 3) quantify spatial variation in the distribution of migrants and residents across the Icelandic breeding range, and 4) determine whether oystercatchers mate assortatively in relation to migratory behavior.

METHODS

Individual marking and sample collection

The study took place from the south (S) to the northwest (NW) of Iceland during the summers of 2013–2017 and was expanded to the northeast (NE) and east (E) in 2017 (Figure 1). Incubating oystercatchers were captured on the nest using a spring trap (http:www.moudry.cz) and individually marked with unique color-ring combinations. For each individual, we measured tarsus + middle toe length to the nearest millimeter (a very consistent metric between observers) and collected a sample of four or five chest feathers (grown on wintering sites during the prenuptial molt) for isotopic analysis. For a subset of birds, we also collected a sample of blood for molecular sex determination (as the biometrics of males and females overlap; van de Pol et al. 2009). Body feathers are molted during the nonbreeding period on the wintering grounds (Dare and Mercer 1974) and the isotope ratios in chest feathers reflect diet and habitat use during this period when those feathers were grown (Bearhop et al. 2003; Pearson et al. 2003).

Resighting data

Individually marked oystercatchers were observed and recorded at nonbreeding sites within and outside of Iceland during surveys conducted by the authors and colleagues and by observers throughout Europe between the winters of 2013–2014 and 2017–2018. The winter period (during which only resident individuals are likely to be in Iceland) was defined from the beginning of October to the end of February. No migrant individuals have been seen in Iceland after September and the earliest returning migrants have been observed during the first week of March (personal observations).

Molecular sex determination

DNA was extracted from blood samples using a standard ammonium acetate technique (dx.doi.org/10.17504/protocols.io.knycvfw) and diluted to a working concentration of 10–50 ng/μL. The sex of individuals was then determined using the molecular methods set out in Fridolfsson and Ellegren (1999).

Stable isotope analysis

Prior to isotopic analysis, feathers were washed in a 2:1 chloroform/methanol solution, left to dry overnight in a fume cupboard and cut into small fragments. Each sample was then weighed (from 0.45 to 0.55 mg) with a microbalance, packed in tin capsules, and loaded into a combustion Costech elemental analyzer coupled to a Thermo Scientific Delta XP continuous flow isotopic ratio mass spectrometer and a Conflo III interface. Carbon and nitrogen stable isotope ratios are reported as δ values in parts per thousand (‰) deviations from the international standards Vienna Pee Dee Belemnite (V-PDB) for δ^{13}C and AIR N_2 for δ^{15}N. Replicate measurements of the internal laboratory standard (collagen) indicated measurement errors of 0.2‰ and 0.1‰ for δ^{13}C and δ^{15}N, respectively.

Statistical analyses

In order to assign a migratory status to color-marked individuals, we carried out a discriminant analysis using the *MASS* R package (Venables and Ripley 2002). First, we used the isotopic signatures of 113 individuals that were observed during winter within (residents) or outside (migrants) Iceland as a training set. A preliminary analysis showed that a quadratic discriminant analysis (QDA) performed better than a linear (LDA), with 9.3% and 17.4% misclassified, respectively. Therefore, results from QDA are reported here. We set prior probabilities of migratory strategy at 30% for residents and 70% for migrants as approximately 30% of the breeding population is estimated to be resident (Þórisson et al. 2018). We evaluated model performance and prediction by applying an internal validation technique using 50 bootstrap samples from the training data set. We then used the discriminant function to assign migratory strategy (resident in Iceland or migrant wintering in western Europe) to 424 individuals for which the isotopic signatures described by the δ^{13}C and δ^{15}N values were attained but no winter observations were available. Posterior probabilities of being migrant or resident were calculated for each individual, and these were classified into one strategy or the other when the posterior probability for a given strategy was at least twice than for the other (≥67 %). We then carried out a sensitivity analysis by systematically varying this threshold and assessing the influence on the models of spatial variation and assortative mating described below (Supplementary Material). The 71 individuals that did not meet the ≥ 67% threshold were excluded from further analysis.

To determine the annual consistency in the migratory strategy of individuals, we quantified the proportion of those that were
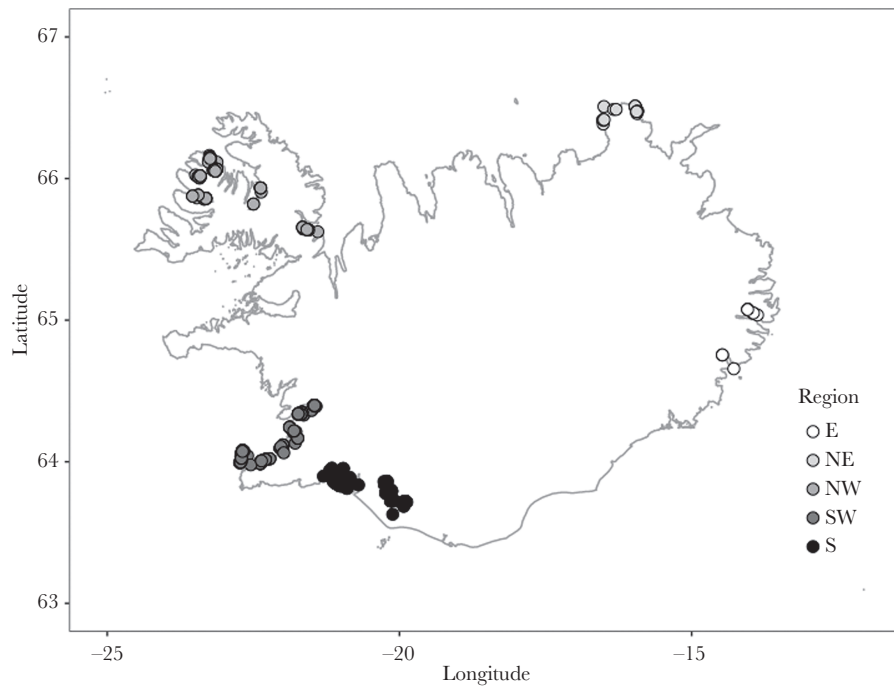
Figure 1
Locations at which breeding oystercatchers have been marked across Iceland. Locations are colored by region.

recorded in more than one winter, either in Iceland or western Europe. In addition, using feather samples collected in different years for 13 individuals, we quantified the consistency of isotopic signatures of each individual and used the QDA to examine whether both samples resulted in similar posterior probabilities and consequent classification as migrant or resident.

To investigate variation in the likelihood of being migrant or resident in relation to sex, body size, and breeding location, we used a generalized linear model with a binomial error distribution and logit link function, where migratory strategy (migrant or resident) was modeled as a function of the region of Iceland (see Figure 1 for regions), sex, body size (tarsus + middle toe length [millimeters]), and all two-way interactions. The significance of each variable was assessed with Wald statistics. At the population level, we then explored spatial variation in the frequency distribution of migrants and residents breeding in each region with a chi-square test of independence. For the subset of individuals of known sex, we also used a chi-square test to explore spatial and sex-related variation in the frequency of migrants and residents in the population.

Finally, to explore whether oystercatchers mate assortatively with respect to migratory strategy, we used all pairs for which the migratory strategy of both members has been either assigned through resightings or predicted by the QDA. We used chi-square tests to investigate whether the frequency of pairs with different migratory strategies varied regionally and in relation to the spatial distribution of migrant and resident individuals. All the statistical analyses were carried out using R 3.4.3 (R Core Team 2018).

RESULTS

Assignment of migratory strategy

We captured, color ringed, and collected feather samples from 537 oystercatchers, of which 113 (55 residents and 58 migrant) were assigned migratory status through observations of color rings during winter (mean observations ± standard deviation [SD] = migrants: 26 ± 15; residents = 32 ± 19). The isotopic signatures of feathers from the 55 resident birds clustered in the center of the δ^{13}C–δ^{15}N isotope space (Figure 2a), with δ^{15}N values significantly lower than those of the 58 migrant birds (residents: mean = 12.39‰ ± 0.09 standard error; migrants: 13.54 ± 0.2; Wilcoxon test, W = 2,584; Z = −5.55; P < 0.0001) but with no differences apparent in their δ^{13}C values (residents: −17.35 ± 0.14; migrants: −17.62 ± 0.36; Wilcoxon test, W = 1,783; Z = −0.58; P = 0.26). The QDA predicted a posterior probability ≥67% of being a migrant or resident for 353 of the 424 individuals with measured isotopic signatures but no winter observations (Figure 2b).

Consistency of migratory strategy

The 18 individuals that were observed in more than one winter were all consistent in migratory behavior (10 residents and 8 migrants) and occurred in the same location (Iceland or western Europe) in both winters. For the 13 individuals with feather samples collected in different years, the QDA predicted a posterior probability ≥67% for 10 individuals and these were also assigned the same strategy on both occasions (Figure 3). However, for the remaining three individuals, the QDA predicted a low posterior probability (≤67%) on at least one of the occasions, and the migratory strategy was, therefore, unassigned as the isotopic signatures of these three individuals fell in the overlap area between migrants and residents (Figure 3).

Factors influencing individual migratory strategies

We found significant variation among regions in the probability of individuals being migrant or resident but no effect of sex or body size (Table 1). The probability of being resident was greatest in the
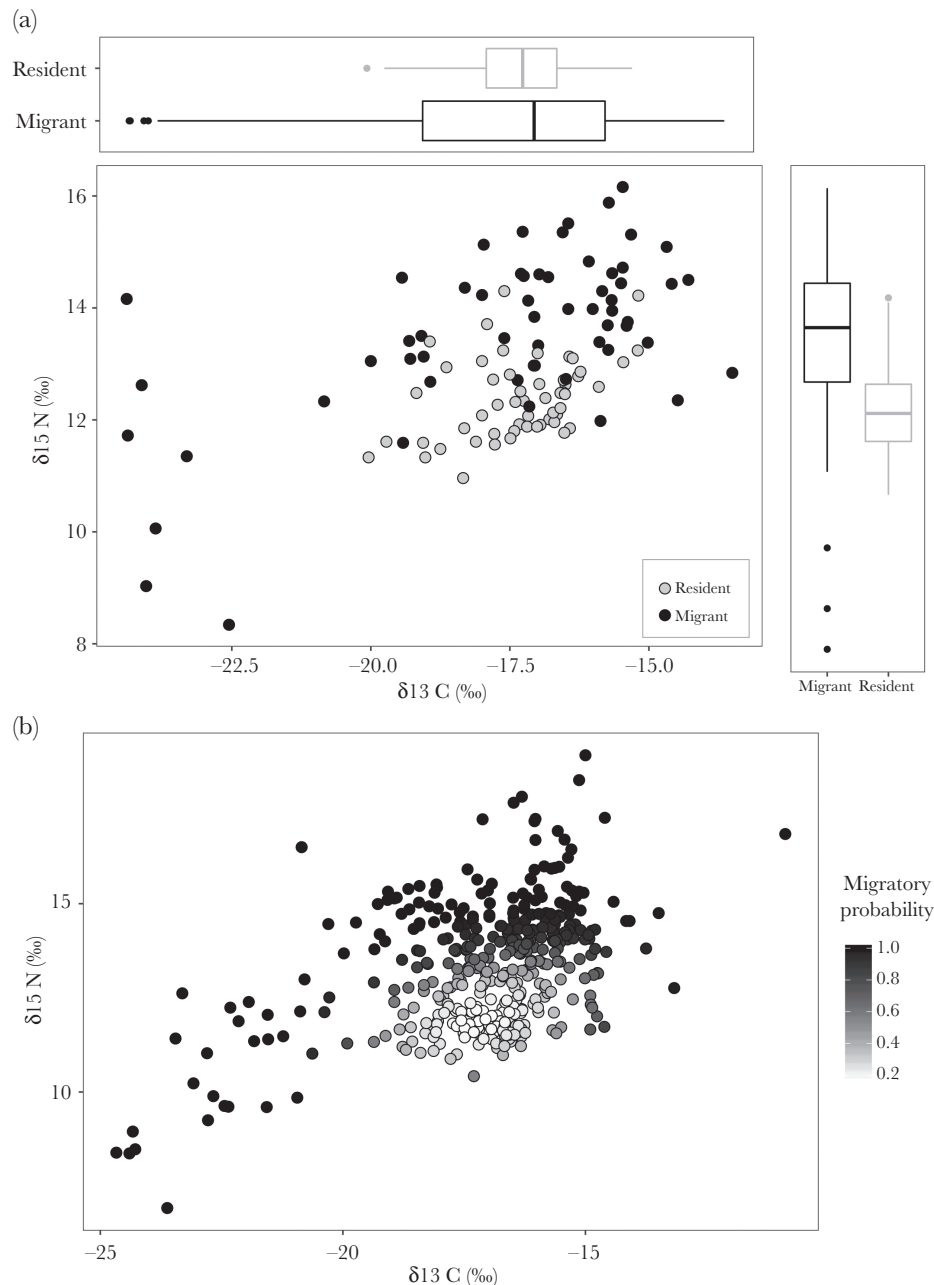
Figure 2

Stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios assimilated into chest feathers of Icelandic oystercatchers during postbreeding body molt from individuals with (a) confirmed migratory status through resightings in winter and (b) predicted migratory status (derived from a quadratic discriminant function) for individuals of unknown wintering location.

NW (probability = 0.94, 95% confidence intervals [CIs] = 0.76–0.99), followed by the southwest (SW; 0.73, 0.52–0.87), but decreased in the south (S; 0.31, 0.15–0.55) and the NE (0.29, 0.14–0.47). The probabilities of using one strategy or the other differed significantly between NW and S, NW and NE, and SW and S (Tukey's comparison, $P < 0.008$).

Spatial and sex-related variation in the frequency of migrants and residents

The frequency of migrant and resident birds varied significantly among regions ($\chi^2_{(4, N = 469)} = 103.23$, $P < 0.001$). In the SW, the

frequency of migrants and residents was similar (54% and 46%, respectively), whereas the breeding population largely comprised residents in the NW and migrants in the S, E, and NE (Figure 4a). The regional distribution of migrants and residents is highly robust to the threshold used for assigning strategy in the QDA (Supplementary Figure S1).

Using the subset of data for individuals with known sex, we found no evidence of sex-related variation in the frequency of migrants and residents ($\chi^2_{(1, 272)} = 1.01$, $P = 0.31$) and the regional variation remained significant within each sex (female $\chi^2_{(3, 127)} = 21.86$, $P < 0.0001$; male $\chi^2_{(3, 145)} = 35.66$, $P < 0.0001$; Figure 4b).
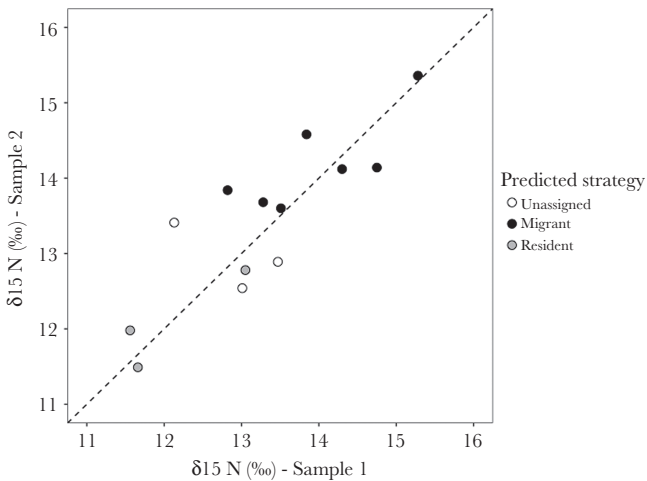
Figure 3

Stable nitrogen (δ^{15}N) isotope ratios from individuals with feather samples collected in 2 years. Color shows the predicted strategy (from a quadratic discriminant function) for both samples of the same individual.

Table 1

Results of generalized linear models of the effects of region, sex, body size, and all two-way interactions on the probability of individual Icelandic breeding oystercatchers ($N = 269$) migrating out of Iceland in winter

Variables	df	Full model		Minimal model	
		Wald χ^2	P	Wald χ^2	P
Intercept	1	0.0002	0.99	4.8	0.028
Region	3	0.37	0.95	41.2	<0.0001
Sex	1	1.3	0.26		
Tarsus + middle toe (TT)	1	0.002	0.97		
Sex × Region	3	2.9	0.41		
Region × TT	3	0.61	0.89		
Sex × TT	1	1.3	0.25		

df, degrees of freedom.

Assortative mating by migratory strategy

We were able to assign the migratory strategy of both members of the pair (either by resighting or QDA) for 162 pairs. Among these, 75 pairs (46%) were both migrants, 32 pairs (20%) were both residents, and 55 pairs (34%) were mixed. The frequency of full-migrant, full-resident, or mixed pairs varied significantly among regions ($\chi^2_{(6, 160)} = 67.91$, $P < 0.001$; Figure 5a). However, we found no evidence for assortative mating among migrant and resident individuals as mixed pairs were frequent in all regions, particularly, in the SW where similar numbers of migrants and residents are present and the proportion of migrant pairs closely matches the proportion of migrant individuals in each region (Figure 5b).

We found no difference in the predicted QDA probabilities for migrant individuals from migrant pairs and mixed pairs (mean ± SD: migrant.migrant = 0.94 ± 0.09; migrant.mixed = 0.93 ± 0.10; Wilcoxon test, $W = 1,157.5$; $\mathcal{Z} = 1.3$; $P = 0.90$; Supplementary Figure S2) and for resident individuals from resident pairs and mixed pairs (resident.resident = 0.24 ± 0.04; resident.

mixed = 0.23 ± 0.04; Wilcoxon test, $W = 845.5$; $\mathcal{Z} = -0.84$; $P = 0.19$; Supplementary Figure S2); thus, our definition of migratory status is no less robust for individuals in mixed pairs.

DISCUSSION

By using stable isotope signatures in combination with tracking data to distinguish migratory strategies in oystercatchers breeding in Iceland, we found that individuals are consistent in migratory strategy between years and that the frequency of each strategy varies regionally across Iceland. We also found no indication of assortative mating among individuals with the same strategy, with migrant pairs being most common in areas dominated by migrants and pairs of mixed strategy occurring most frequently in areas with similar proportions of migrants and residents. We discuss our findings and highlight the possible factors underlying the evolution and maintenance of partial migration at high latitudes.

The use of stable isotope tracers has proven to be a useful tool for identifying individual migratory strategies in this and other species (e.g., Atkinson et al. 2005; Pérez et al. 2014; Hegemann et al. 2015). We found that residents clustered on the isotopic landscape and displayed more restricted ranges for both isotopes. Residents and migrants differed significantly in δ^{15}N but overlapped in δ^{13}C values, reflecting the fact that individuals wintering in Iceland are likely to feed on a narrower range of items with respect to trophic level and to be more restricted in feeding habitats than migrants. Resident individuals forage almost exclusively on estuarine mudflats in the SW and west (W) of Iceland (Þórisson et al. 2018), whereas in other parts of the winter range, oystercatchers also forage on saltmarshes, sandy and rocky shores, and grass pastures, where a broad spectrum of prey types is consumed (Goss-Custard 1996). The incorporation of additional geographically structured isotopes, such as strontium (Chamberlain et al. 1997; Evans and Bullman 2009) or deuterium (Bowen et al. 2005), might have allowed the assignment of migratory status to a greater number of individuals but, for this study, nitrogen and carbon isotopes proved to have enough discriminant power, with only 16% of marked individuals not being assigned to a strategy.

We found no effect of body size or sex on the tendency to migrate in Icelandic oystercatchers but we did find strong regional variation, with individuals that breed in the NW and SW of Iceland being more likely to be residents. In addition, the consistent repeatability of individual migratory strategy suggests that this is not a facultative response to annual variation in environmental conditions in postbreeding and wintering locations, although tracking over a larger number of years and with a broader range of environmental conditions may be needed to confirm this pattern. Movements of oystercatchers within mainland Europe during periods of cold weather have been reported (Camphuysen et al. 1996; van de Kam et al. 2004), but the extent to which this reflects annual variation in the timing of winter movements or in the proportion of individuals undertaking such movements is unknown. The 700 km sea crossing between Iceland and Europe may constrain resident oystercatchers from undertaking mid-winter migratory movements.

The consistency of adult migratory behavior suggests that migratory strategy is determined in early life, and the regional
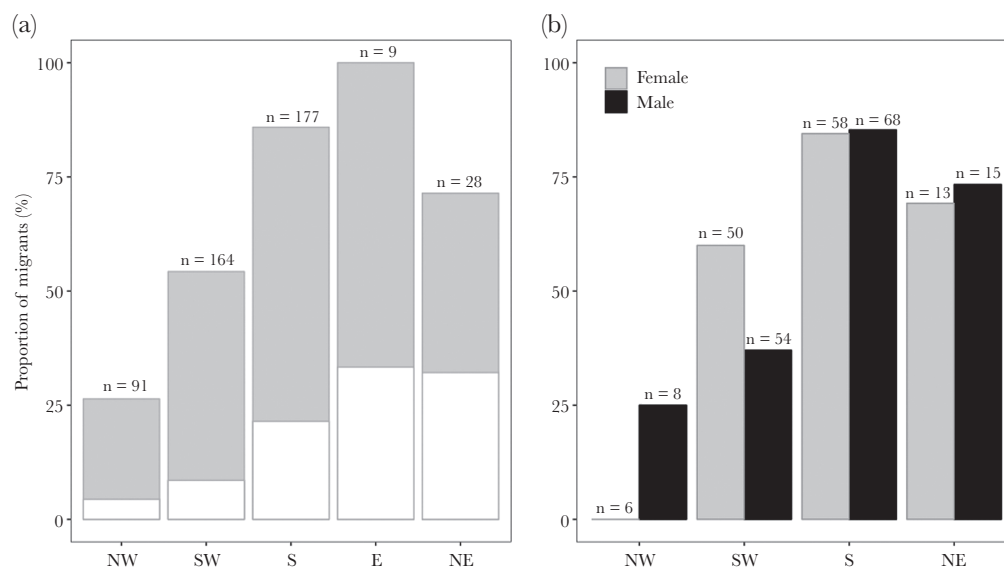
Figure 4

Regional variation in the proportion of (a) migrant oystercatchers around Iceland, with white and gray bars showing the contribution of individuals with confirmed (from observations) and predicted (from isotopes) migratory status, respectively, and (b) migrant male and female oystercatchers (no individuals from the east region were sexed). Sample size for each group is provided above each bar.
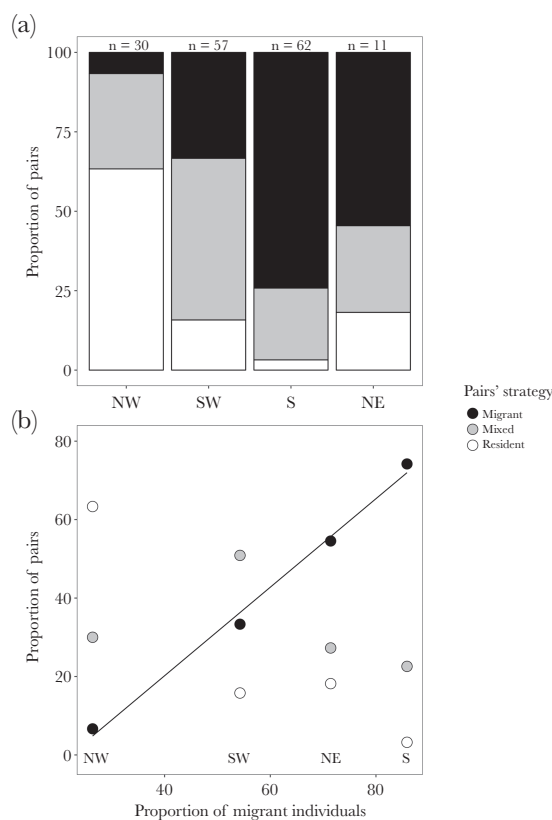
Figure 5

(a) Regional variation in the frequency of oystercatcher pairs of different migratory strategy (sample size for each group is provided above each bar; no pairs of known strategy were available from the east region) and (b) the association between the frequency of pairs of different migratory strategy and the frequency of migrant individuals across regions (solid line indicates the significant correlation for the migrant strategy). Individuals with confirmed (from observation) and predicted (from isotopes) migratory status are included.

variation in the frequency of migrants and residents may, thus, reflect variation in the conditions encountered by individuals during this life stage. The frequency of residents is greatest in the NW and SW of Iceland, and these breeding sites are closest to the main wintering locations in the W and SW of Iceland (Þórisson et al. 2018). Juveniles from the NW and W are, therefore, more likely to encounter these locations (and their resident flocks) when moving S than juveniles from the S, NE, and E, which are more likely to encounter migrating adults on their southward migration. The regional variation in migratory strategy could, thus, arise through the influence of social cues, with juveniles adopting the behavior of the conspecifics that they encounter and then recruiting back into their natal locations (Verhoeven et al. 2018; Gill et al. 2019).

The regional variation in the frequency of migrants and residents reflects the regional variation in the strategies of pairs, with mixed pairs being most common in regions with similar frequencies of migrants and residents and migrant–migrant and resident–resident pairs being common in regions comprising mostly migrants or residents, respectively. This suggests that residents and migrants do not differ consistently in behaviors likely to influence the probability of pair formation, such as timing of arrival on the breeding grounds. The lack of sympatric reproductive isolation between strategies suggests a lack of genetic differentiation or structure in resident and migrant Icelandic oystercatchers (Anderson et al. 2016).

Understanding the factors influencing migratory behavior and the consequences for spatial variation in the distribution and frequencies of individuals with differing migratory behaviors is important for predicting how the abundance and distribution of species may respond to future environmental changes and the implications for protected area networks designed to protect migratory species (Méndez et al. 2018b). Our study suggests that individual migratory behavior may be strongly influenced by social and cultural experiences in Icelandic oystercatchers, which interacts with spatial structure of suitable habitats at the population

scale. This results in large-scale spatial variation in the distribution of migrants and residents across the breeding grounds. Future tracking of juveniles during the early years of life will help to identify the conditions influencing migratory behavior and the demographic consequences of adopting different migratory behaviors in such long-lived species.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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