

1 **Title:** Individual variation in migratory behavior in a sub-arctic partial migrant shorebird

2 **Running title:** Partial migration in Icelandic oystercatcher

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18

19 **Data Accessibility Statement**

20 Analyses reported in this article can be reproduced using the data provided by Méndez et al.

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

39 **Keywords:** migratory strategies, individual variation, stable isotopes, migratory consistency,
40 wader

41 **INTRODUCTION**

42 Migration is commonly seen as a life history trait shared by individuals within populations or
43 species. However, many aspects of migratory behavior can differ markedly among individuals,
44 from the direction (e.g. Finch et al. 2017) and routes undertaken (e.g. Vardanis et al., 2016) to
45 the distance (e.g. Alves et al., 2012) and timing (e.g. Conklin et al., 2013; Gill et al., 2014) of
46 migratory journeys. This variation is particularly extreme in partial migrant populations, in which
47 some individuals remain close to the breeding grounds all year, while some undertake migratory
48 journeys to more distant locations (Newton 2008). These behavioral differences among
49 individuals have been linked to differences in individual fitness (Gunnarsson et al. 2005; Alves et
50 al. 2013; Grist et al. 2017; Méndez, Alves, et al. 2018), and can influence population distribution
51 in the non-breeding season and associated strategies for site protection (Méndez, Gill, et al.
52 2018). Understanding individual variation in migratory behavior is therefore key to
53 understanding these individual- and population-scale implications.

54 While migratory behavior can differ among individuals within populations, individuals typically
55 display high repeatability of migratory routes and strong site- and time-fidelity throughout the
56 annual cycle (Newton 2008; Gill et al. 2014; Carneiro et al. 2019). Such consistency in site use
57 and timings is likely to be beneficial in terms of prior knowledge of the availability of key
58 resources, locations safe from predators and mate location and timing (Kokko and Sutherland
59 2001; Gunnarsson et al. 2004; Gill et al. 2014; Winger et al. 2019).

60 Adopting one migratory behavior or another could have implications for the potential mates
61 that are likely to be encountered, for example if assortative mating by timing of arrival occurs
62 and timing of arrival varies with migratory behavior (Bearhop et al. 2005; Gunnarsson et al.
63 2005; Gunnarsson et al. 2006). Assortative mating by timing of arrival could benefit breeding
64 success by both reducing the delay between arrival and breeding and increasing the time

65 available for replacement clutches should early nesting attempts fail (Morrison et al. 2019).
66 Similarly, divorce can be more likely in pairs that differ in arrival time at breeding sites, and this
67 can reduce breeding success (Gilsenan et al. 2017). Understanding the presence and extent of
68 assortative mating by migratory behavior can thus be an important step in understanding
69 population variance in reproductive success.

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

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

102

103 **METHODS**

104 **Individual marking and sample collection**

105 The study took place from the south to the north-west of Iceland during the summers 2013-
106 2017 and was expanded to the north-east and east in 2017 (Figure 1). Incubating oystercatchers
107 were captured on the nest using a spring trap (<http://www.moudry.cz>), and individually marked
108 with unique color-ring combinations. For each individual we measured tarsus + middle toe
109 length to the nearest millimeter (a very consistent metric between observers) and collected a
110 sample of 4-5 chest feathers (grown on wintering sites during the pre-nuptial moult) for isotopic
111 analysis. For a subset of birds, we also collected a sample of blood for molecular sex

112 determination (as the biometrics of males and females overlap; (van de Pol et al. 2009)). Body
113 feathers are moulted during the non-breeding period on the wintering grounds (Dare and
114 Mercer 1974) and the isotope ratios in chest feathers reflect diet and habitat use during this
115 period, when those feathers were grown (Bearhop et al. 2003; Pearson et al. 2003).

116 **Resighting data**

117 Individually-marked oystercatchers were observed and recorded at non-breeding sites within
118 and outside of Iceland during surveys conducted by the authors and colleagues, and by
119 observers throughout Europe between the winters of 2013/14 and 2017/18. The winter period
120 (during which only resident individuals are likely to be in Iceland) was defined from the
121 beginning of October to the end of February. No migrant individuals have been seen in Iceland
122 after September and the earliest returning migrants have been observed during the first week
123 of March (pers. obs.).

124 **Molecular sex determination**

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

129 **Stable isotope analysis**

130 Prior to isotopic analysis, feathers were washed in a 2:1 chloroform/methanol solution, left to
131 dry overnight in a fume cupboard and cut into small fragments. Each sample was then weighed
132 (from 0.45 to 0.55 mg) with a microbalance, packed in tin capsules, and loaded into a
133 combustion Costech elemental analyser coupled to a Thermo Scientific Delta XP continuous flow
134 isotopic ratio mass spectrometer and a ConFlo III interface. Carbon and nitrogen stable isotope

135 ratios are reported as δ values in parts per thousand (‰) deviations from the international
136 standards Vienna Pee Dee Belemnite (V-PDB) for $\delta^{13}\text{C}$ and AIR N_2 for $\delta^{15}\text{N}$. Replicate
137 measurements of the internal laboratory standard (collagen) indicated measurement errors of
138 0.2‰ and 0.1‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

139 **Statistical analyses**

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

159 To determine the annual consistency in migratory strategy of individuals we quantified the
160 proportion of those that were recorded in more than one winter, either in Iceland or western
161 Europe. In addition, using feather samples collected in different years for 13 individuals, we
162 quantified the consistency of isotopic signatures of each individual and used the QDA to examine
163 whether both samples resulted in similar posterior probabilities and consequent classification
164 as migrant or resident.

165 To investigate variation in the likelihood of being migrant or resident in relation to sex, body size
166 and breeding location, we used a generalized linear model with a binomial error distribution and
167 logit link function, where migratory strategy (migrant or resident) was modelled as a function of
168 region of Iceland (see Figure 1 for regions), sex, body size (tarsus + middle toe length (mm)) and
169 all 2-way interactions. Significance of each variable was assessed with Wald statistics. At the
170 population level, we then explored spatial variation in the frequency distribution of migrants
171 and residents breeding in each region with a chi-square test of independence. For the subset of
172 individuals of known sex, we also used a chi-square test to explore spatial and sex-related
173 variation in the frequency of migrants and residents in the population.

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

180 **RESULTS**

181 **Assignment of migratory strategy**

182 We captured, color-ringed and collected feather samples from 537 oystercatchers, of which 113
183 (55 residents and 58 migrant) were assigned migratory status through observations of color-
184 rings during winter (mean observations \pm SD = migrants: 26 ± 15 ; residents = 32 ± 19). The
185 isotopic signatures of feathers from the 55 resident birds clustered in the center of the $\delta^{13}\text{C}$ -
186 $\delta^{15}\text{N}$ isotope-space (Figure 2A), with $\delta^{15}\text{N}$ values significantly lower than those of the 58 migrant
187 birds (residents: mean = $12.39\text{‰} \pm 0.09$ SE; migrants: 13.54 ± 0.2 ; Wilcoxon test, $W = 2584$, $Z =$
188 -5.55 , $p < 0.0001$), but with no differences apparent in their $\delta^{13}\text{C}$ values (residents: $-17.35 \pm$
189 0.14 ; migrants: -17.62 ± 0.36 ; Wilcoxon test, $W = 1783$, $Z = -0.58$, $p = 0.26$). The QDA predicted
190 a posterior probability $\geq 67\%$ of being a migrant or resident for 353 of the 424 individuals with
191 measured isotopic signatures but no winter observations (Figure 2B).

192 **Consistency of migratory strategy**

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

201 **Factors influencing individual migratory strategies**

202 We found significant variation among regions in the probability of individuals being migrant or
203 resident, but no effect of sex or body size (Table 1). The probability of being resident was
204 greatest in the NW (probability = 0.94, 95% CIs = 0.76-0.99), followed by the SW (0.73, 0.52-

205 0.87), but decreased in the S (0.31, 0.15-0.55) and NE (0.29, 0.14-0.47). The probabilities of using
206 one strategy or the other differed significantly between NW and S, NW and NE, and SW and S
207 (Tukey's comparison, $p < 0.008$).

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

209 The frequency of migrant and resident birds varied significantly among regions ($\chi^2_{(4, N=469)} =$
210 103.23, $p < 0.001$). In the SW, the frequency of migrants and residents was similar (54% and
211 46%, respectively), whereas the breeding population largely comprised residents in the NW and
212 migrants in the S, E and NE (Figure 4A). The regional distribution of migrants and residents is
213 highly robust to the threshold used for assigning strategy in the QDA (Figure S1).

214 Using the subset of data for individuals with known sex, we found no evidence of sex-related
215 variation in the frequency of migrants and residents ($\chi^2_{(1, 272)} = 1.01$, $p = 0.31$) and the regional
216 variation remained significant within each sex (Female $\chi^2_{(3, 127)} = 21.86$, $p < 0.0001$; Male $\chi^2_{(3, 145)}$
217 = 35.66, $p < 0.0001$) (Figure 4B).

218 **Assortative mating by migratory strategy**

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

227 We found no difference in the predicted QDA probabilities for migrant individuals from migrant
228 pairs and mixed pairs (mean \pm sd: migrant.migrant = 0.94 ± 0.09 , migrant.mixed = 0.93 ± 0.10 ;
229 Wilcoxon test $W = 1157.5$; $Z = 1.3$, $p = 0.90$; Figure S2), and for resident individuals from resident
230 pairs and mixed pairs (resident.resident = 0.24 ± 0.04 , resident.mixed = 0.23 ± 0.04 ; Wilcoxon
231 test $W = 845.5$; $Z = -0.84$, $p = 0.19$; Figure S2), thus our definition of migratory status is no less
232 robust for individuals in mixed pairs.

233

234 **DISCUSSION**

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

243 The use of stable isotope tracers has proven to be a useful tool for identifying individual
244 migratory strategies in this and other species (e.g. Atkinson et al., 2005; Perez et al., 2014;
245 Hegemann et al., 2015). We found that residents clustered on the isotopic landscape and
246 displayed more restricted ranges for both isotopes. Residents and migrants differed significantly
247 in $\delta^{15}\text{N}$, but overlapped in $\delta^{13}\text{C}$ values, reflecting the fact that individuals wintering in Iceland are
248 likely to feed on a narrower range of items with respect to trophic level and to be more restricted
249 in feeding habitats than migrants. Resident individuals forage almost exclusively on estuarine

250 mudflats in the south-west and west of Iceland (Þórisson et al. 2018) whereas, in other parts of
251 the winter range, oystercatchers also forage on saltmarshes, sandy and rocky shores and grass
252 pastures, where a broad spectrum of prey types is consumed (Goss-Custard 1996). The
253 incorporation of additional geographically structured isotopes such as strontium (Chamberlain
254 et al. 1997; Evans and Bullman 2009) or deuterium (Bowen et al. 2005) might have allowed the
255 assignment of migratory status to a greater number of individuals but, for this study, nitrogen
256 and carbon isotopes proved to have enough discriminant power, with only 16% of marked
257 individuals not being assigned to a strategy.

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

270 The consistency of adult migratory behavior suggests that migratory strategy is determined in
271 early life, and the regional variation in the frequency of migrants and residents may thus reflect
272 variation in the conditions encountered by individuals during this life stage. The frequency of
273 residents is greatest in the north-west and south-west of Iceland, and these breeding sites are

274 closest to the main wintering locations in the west and south-west of Iceland (Þórisson et al.
275 2018). Juveniles from the north-west and west are therefore more likely to encounter these
276 locations (and their resident flocks) when moving south, than juveniles from the south, north-
277 east and east which are more likely to encounter migrating adults on their southward migration.
278 The regional variation in migratory strategy could thus arise through the influence of social cues,
279 with juveniles adopting the behavior of the conspecifics that they encounter and then recruiting
280 back into their natal locations (Verhoeven et al. 2018; Gill et al. 2019).

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

289 Understanding the factors influencing migratory behavior and the consequences for spatial
290 variation in the distribution and frequencies of individuals with differing migratory behaviors is
291 important for predicting how the abundance and distribution of species may respond to future
292 environmental changes, and the implications for protected area networks designed to protect
293 migratory species (Méndez, Gill, et al. 2018). Our study suggests that individual migratory
294 behavior may be strongly influenced by social and cultural experiences in Icelandic
295 oystercatchers, which interacts with spatial structure of suitable habitats at the population
296 scale. This results in large-scale spatial variation in the distribution of migrants and residents
297 across the breeding grounds. Future tracking of juveniles during the early years of life will help

298 to identify the conditions influencing migratory behavior and the demographic consequences of
299 adopting different migratory behaviors in such long-lived species.

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409

Table 1. Results of GLMs of the effects of region, sex, body size and all 2-way interactions on the probability of individual Icelandic breeding oystercatchers ($N = 269$) migrating out of Iceland in winter.

Variables	<i>d.f.</i>	Full model		Minimal model	
		Wald χ^2	<i>P</i>	Wald χ^2	<i>P</i>
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 \times Region	3	2.9	0.41		
Region \times TT	3	0.61	0.89		
Sex \times TT	1	1.3	0.25		

Figure legends

Figure 1. Locations at which breeding oystercatchers have been marked across Iceland. Locations are colored by region.

Figure 2. Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios assimilated into chest feathers of Icelandic Oystercatchers during post-breeding body moult 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.

Figure 3. Stable nitrogen ($\delta^{15}\text{N}$) isotope ratios from individuals with feather samples collected in two years. Color shows the predicted strategy (from a quadratic discriminant function) for both samples of the same individual.

Figure 4. Regional variation in the proportion of (A) migrant Oystercatchers around Iceland, with white and grey 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.

Figure 1

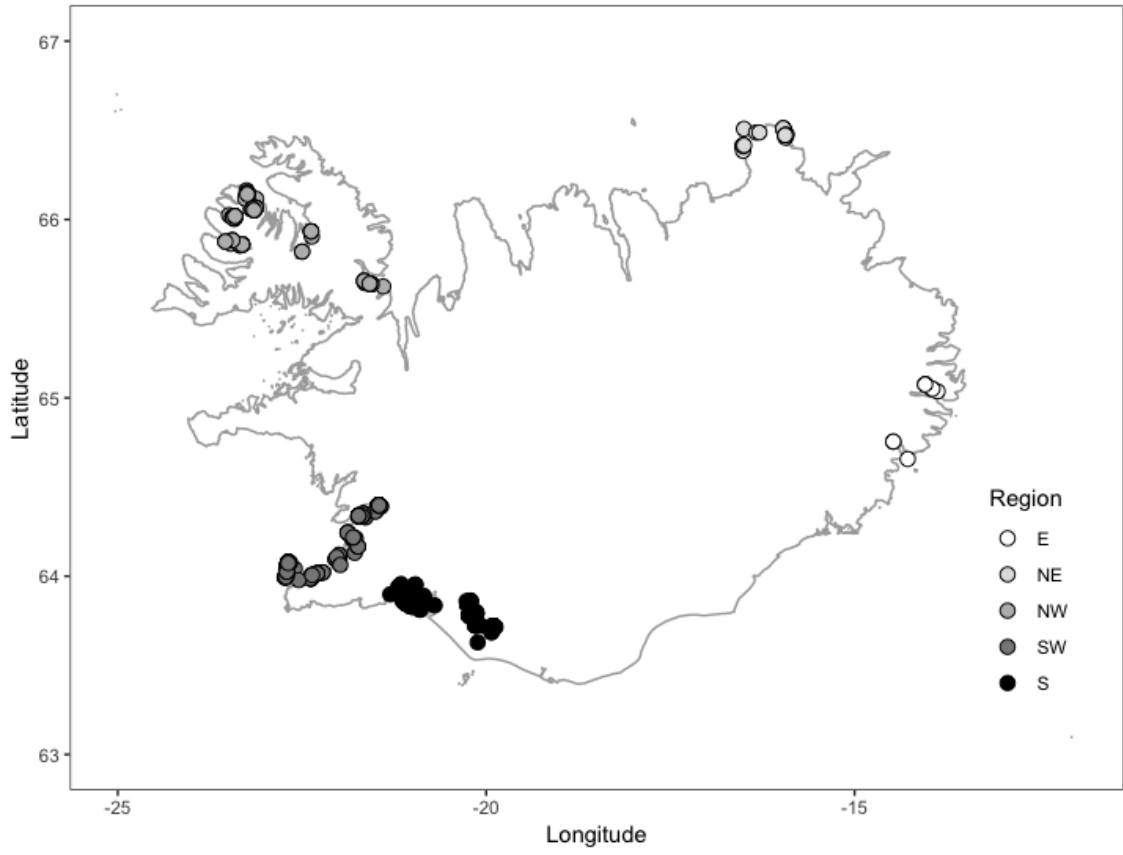


Figure 2

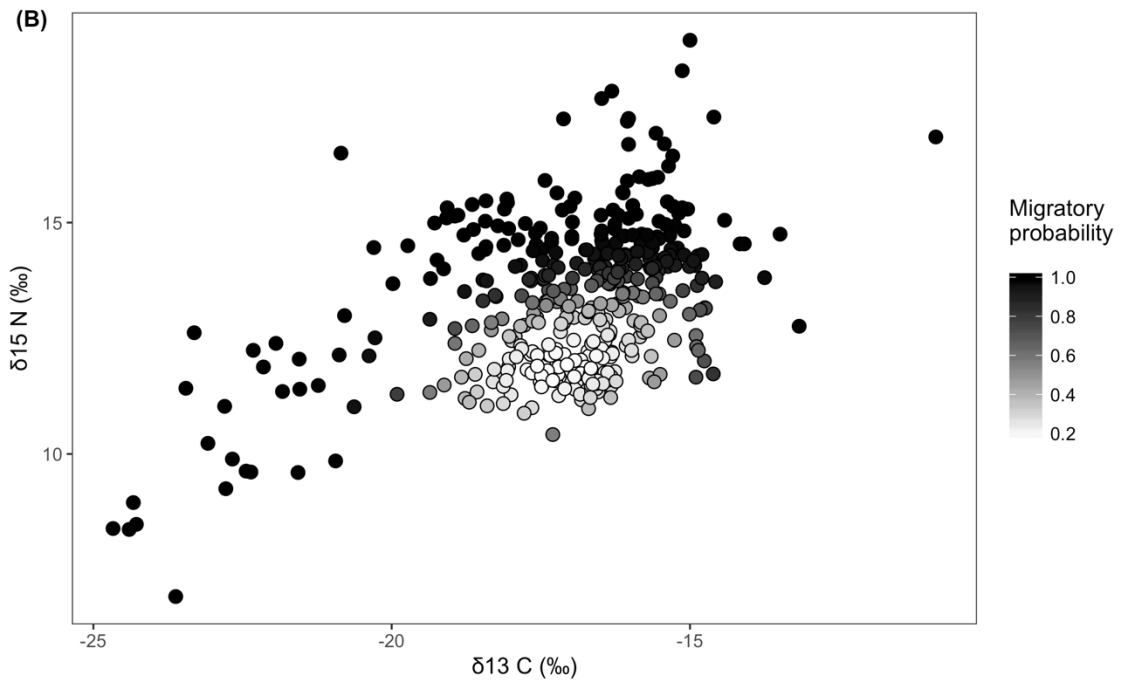
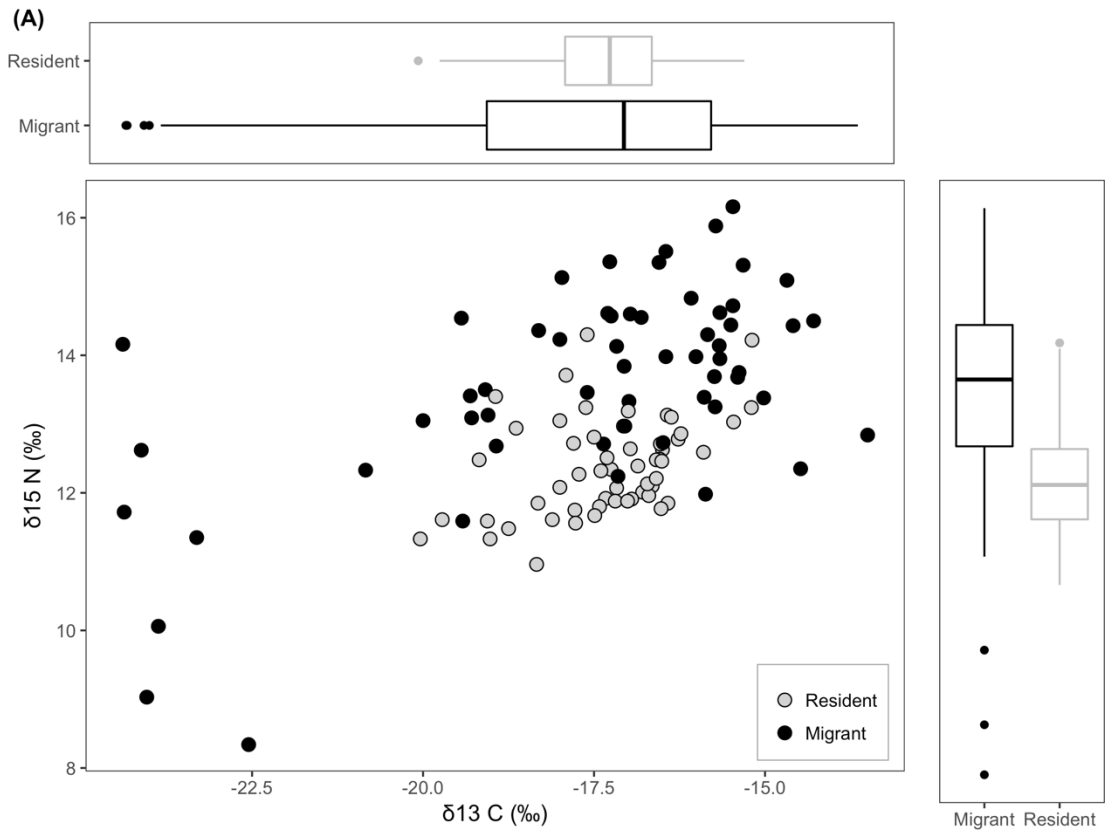


Figure 3

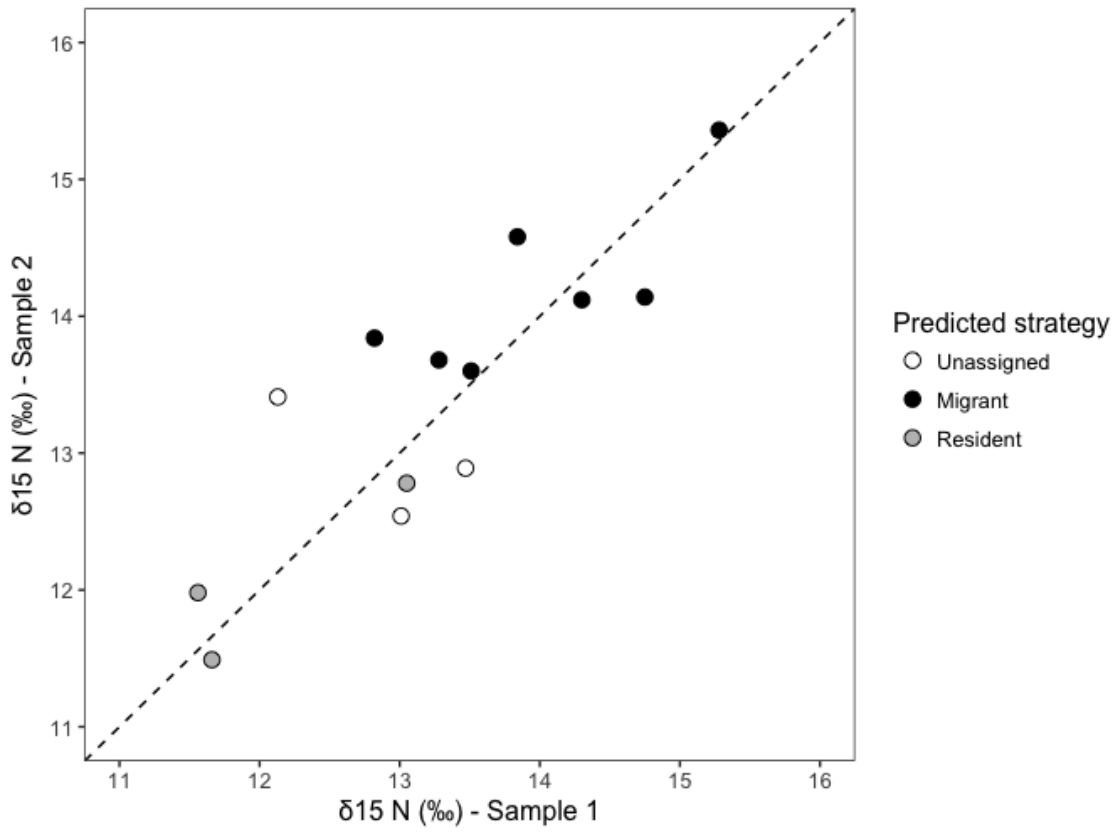


Figure 4

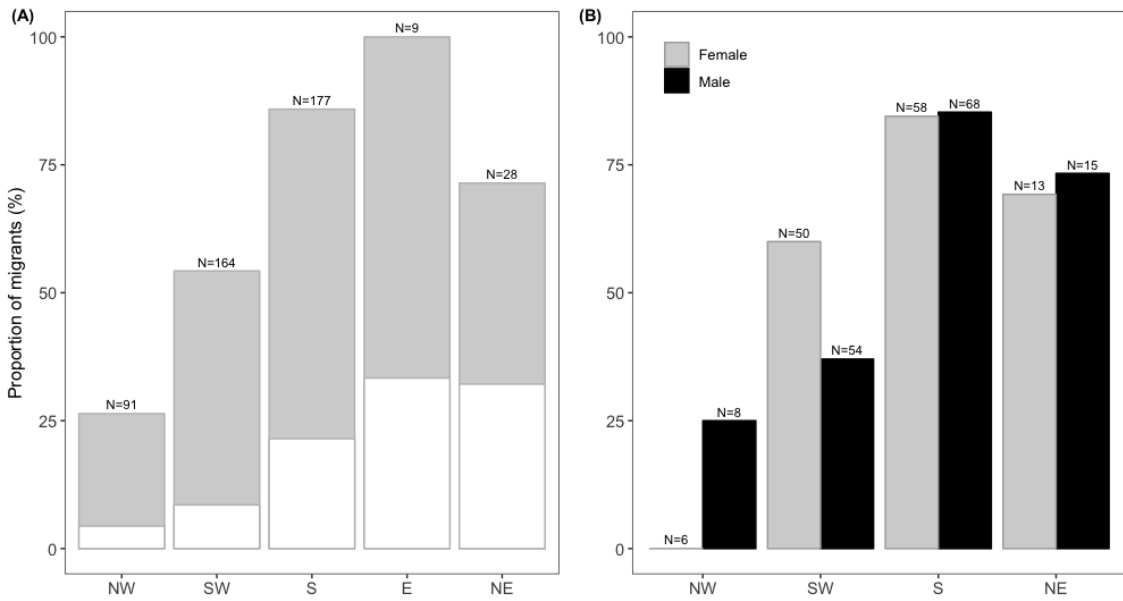


Figure 5

