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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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

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 (δ^{13}C) and nitrogen (δ^{15}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

5

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) 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 δ^{13}C and AIR N_2 for δ^{15}N. Replicate

137   measurements of the internal laboratory standard (collagen) indicated measurement errors of

138   0.2‰ and 0.1‰ for δ^{13}C and δ^{15}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 δ^{13}C and δ^{15}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**

8

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 $\pm$ 15; residents = 32 $\pm$ 19). The

185   isotopic signatures of feathers from the 55 resident birds clustered in the center of the δ^{13}C -

186   δ^{15}N isotope-space (Figure 2A), with δ^{15}N values significantly lower than those of the 58 migrant

187   birds (residents: mean = 12.39‰ ± 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 δ^{13}C values (residents: -17.35 ±

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 ≥ 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 ≥ 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 (≤ 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).

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).

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 ± 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 $\delta^{15}N$, but overlapped in $\delta^{13}C$ 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	d.f.	Full model Wald χ^2	P	Minimal model 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		

Figure legends

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

Figure 2. Stable carbon (δ^{13}C) and nitrogen (δ^{15}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 (δ^{15}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.
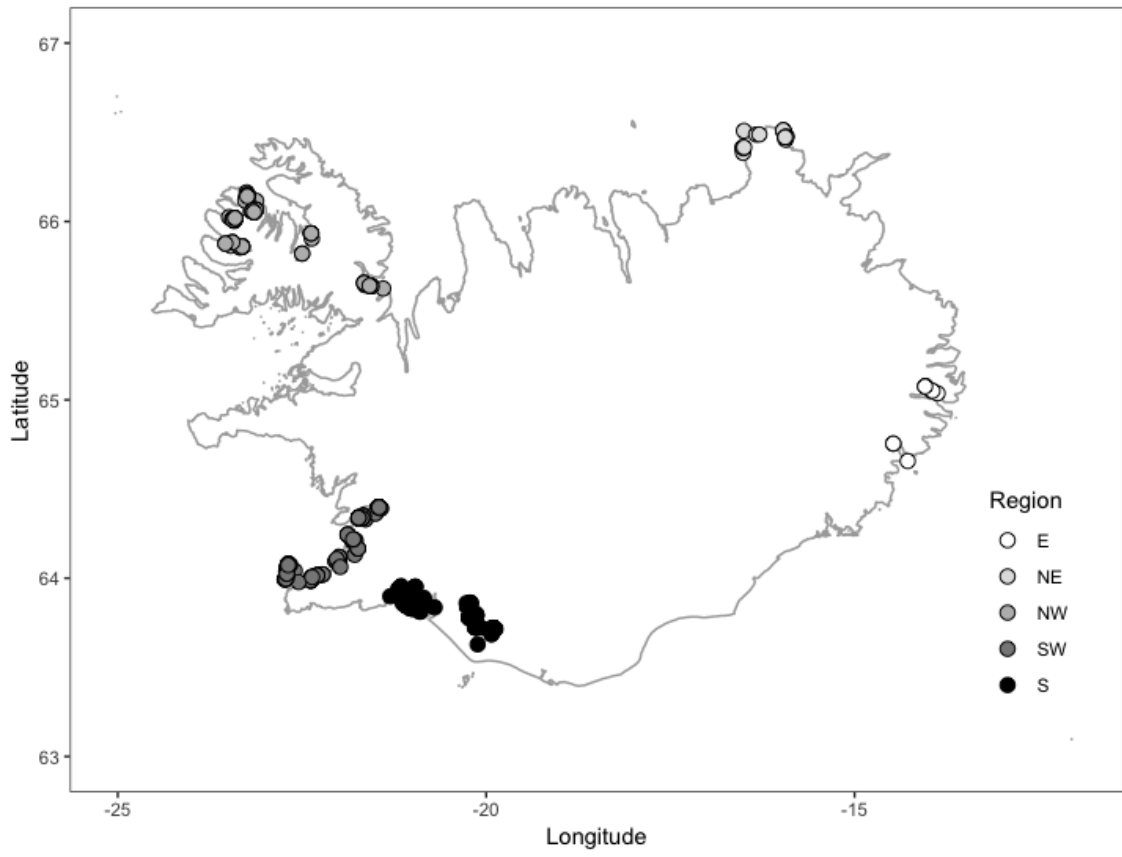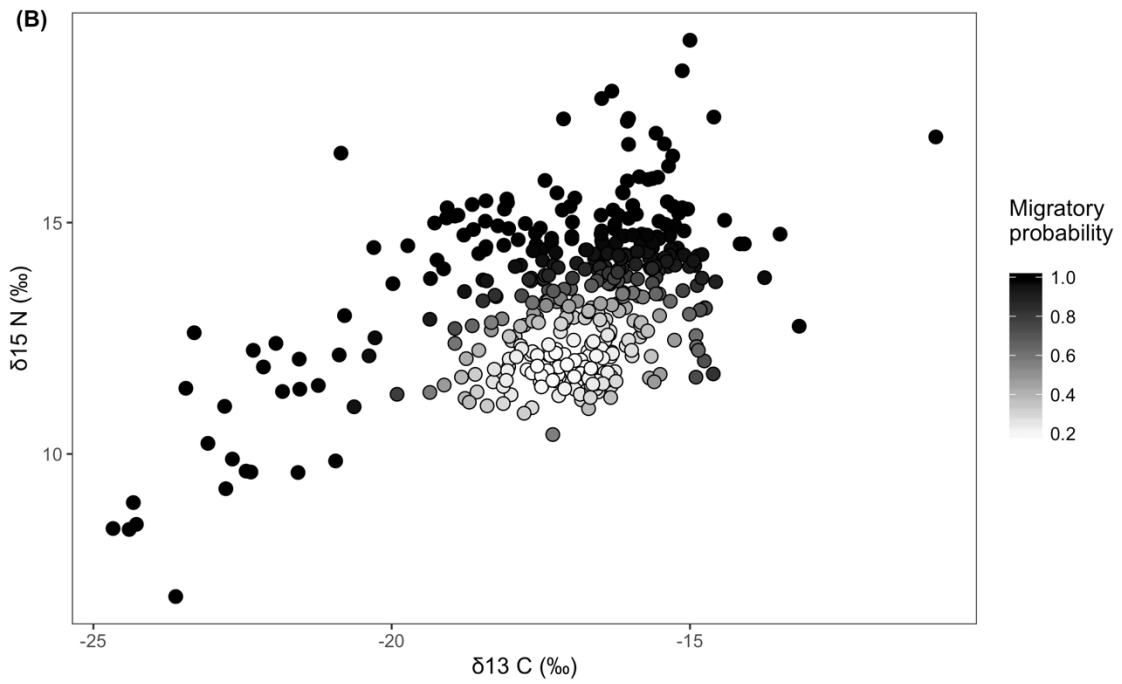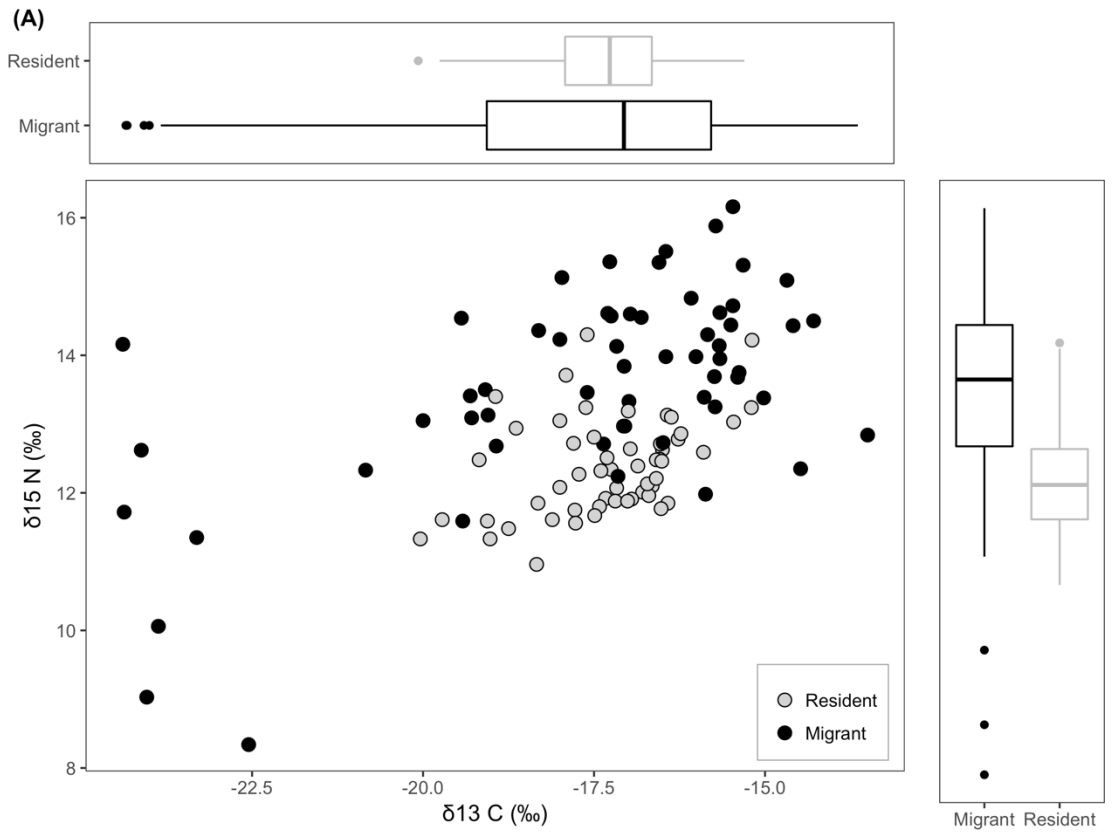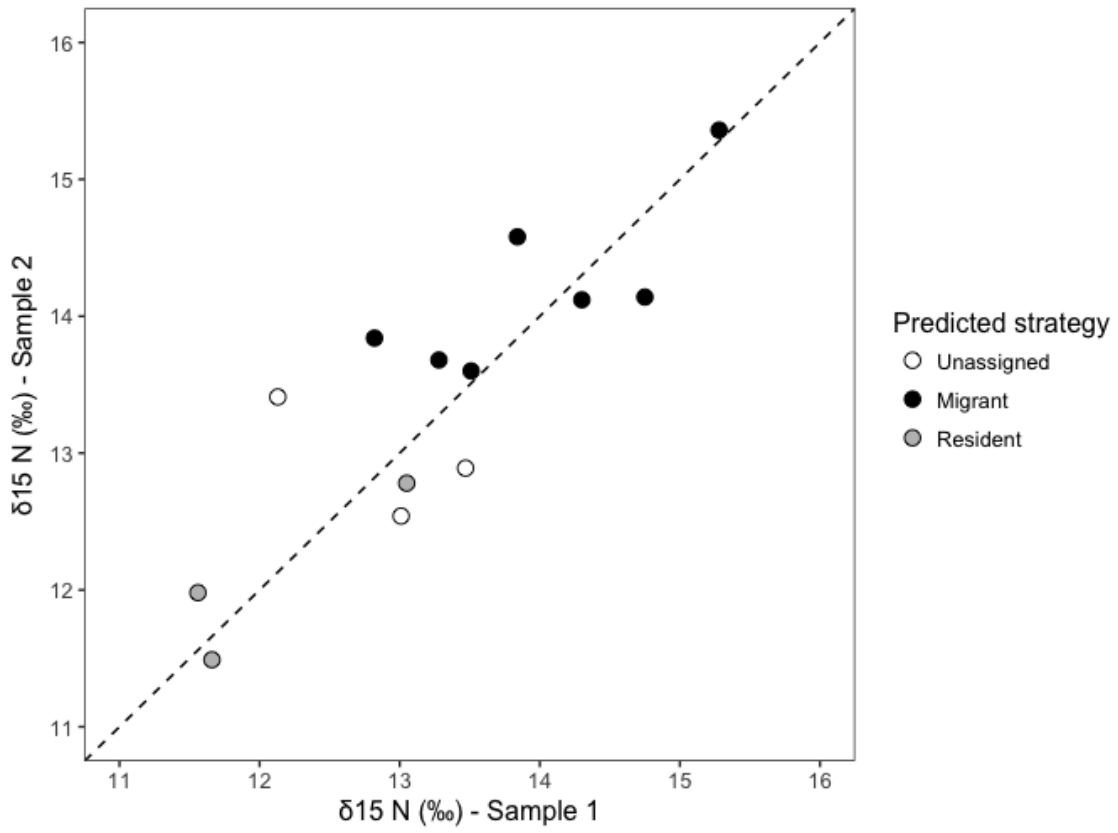
Figure 1

Figure 2

Figure 3

Figure 4

Figure 5