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1 **The impact of past climate change on genetic variation and population connectivity in**
2 **the Icelandic arctic fox**

3

4 **Running head:** Climate change and Arctic fox migration

5

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18

19 **Summary**

20 Previous studies have suggested that the presence of sea ice is an important factor in
21 facilitating migration and determining the degree of genetic isolation among contemporary
22 arctic fox populations. Because the extent of sea ice is dependent upon global temperatures,
23 periods of significant cooling would have had a major impact on fox population connectivity
24 and genetic variation. We tested this hypothesis by extracting and sequencing mitochondrial
25 control region sequences from 17 arctic foxes excavated from two late 9th-12th century AD
26 archaeological sites in northeast Iceland, both of which predate the Little Ice Age (~16th-19th
27 century). Despite the fact that five haplotypes have been observed in modern Icelandic foxes,
28 a single haplotype was shared among all of the ancient individuals. Results from simulations
29 within an approximate Bayesian computation framework suggest that the rapid increase in
30 Icelandic arctic fox haplotype diversity can only be explained by sea ice-mediated fox
31 immigration facilitated by the Little Ice Age.

32

33 **Keywords:** island biogeography, phylogeography, ancient DNA, approximate Bayesian
34 computation

35 INTRODUCTION

36

37 The last millennium witnessed dramatic environmental and ecological change in Iceland. The
38 effects of human settlement in the 9th century AD were exacerbated by hemispheric climate
39 change, both of which led to widespread environmental degradation at an unprecedented
40 rate[1]. Although a great deal of research has focussed on the human impacts on soil and
41 vegetation systems (*e.g.* [2, 3]), less is known about the effects of settlement or climate
42 change on the wild animal populations of the island. The arctic fox (*Vulpes lagopus*) is
43 particularly interesting since it is the island's only indigenous mammal. Foxes arrived in
44 Iceland by crossing arctic sea ice well before human settlement[4] and have a long-standing
45 antagonistic relationship with people. The population history of the arctic fox in Iceland prior
46 to the 20th century, however, is poorly understood. The use of ancient DNA in a population
47 genetics framework presents an effective means of addressing this issue. Generating
48 empirical evidence of population genetic diversity through time can elucidate past patterns
49 and processes that may be difficult or impossible to ascertain using contemporary data
50 alone[5].

51

52 Genetic diversity within small or isolated wild populations can be strongly affected by human
53 interaction. During the early 20th century, overhunting reduced the size of the Fennoscandian
54 arctic fox population to 100-200 individuals, from which it has failed to recover[6].

55 Comparisons of museum specimens and modern samples indicate a loss of both
56 mitochondrial and microsatellite diversity during this period[7]. More recently, sustained low
57 population levels have promoted further spatial fragmentation and subdivision, in spite of
58 putative gene flow from northern Russia[8].

59

60 In Iceland, the arctic fox has been considered vermin because of its ostensible role in killing
61 sheep and the disruption of eider (*Somateria mollissima*) colonies. Fox hunting has been
62 encouraged and legislated since the 13th century, and is still coordinated and subsidised by the
63 Wildlife Management Institute[9]. The most effective law targeted at the extermination of the
64 arctic fox was passed in 1957 and by the 1970s the population had declined to approximately
65 1,300 individuals[10]. Since this bottleneck, foxes have rebounded substantially and
66 contemporary estimates suggest there are now ~10,000 individuals[11]. No significant
67 signature of the 1970s bottleneck has been found in the population using microsatellite data,

68 though the genetic diversity of Iceland foxes remains comparable to that of the threatened
69 population in Fennoscandia[12].

70

71 Though humans can significantly affect arctic fox population size at a local level, the effects
72 of hunting and trapping on global population dynamics are limited. A more influential factor
73 in determining regional fox population structure is the propensity for long distance migration
74 during periods of nutritional stress[10, 13]. Adult foxes of both sexes are known to habitually
75 travel thousands of kilometres in a single year while spending substantial periods on arctic
76 pack ice [14, 15].

77

78 High mobility across both land and sea ice is believed to have had an important influence on
79 the distribution and maintenance of genetic diversity of the arctic fox across its range (Fig 1).
80 Previous studies using both mitochondrial and microsatellite markers have demonstrated that
81 the presence of sea ice is the most important factor in explaining arctic fox global population
82 structure [16-18]. Genetic differentiation between North America, North Greenland and
83 Svalbard is low, implying extensive movement across the sea ice between these areas [17,
84 19]. In fact, the genetic proximity of these areas to Siberia has prompted suggestions that
85 Svalbard may act as a central junction for gene flow across the entire Arctic, mediated by sea
86 ice[17, 18].

87

88 Islands surrounded by open water year round, such as the Commander Islands, Pribilof
89 Islands and Iceland, show a distinct pattern of genetic isolation[20]. Unlike the small islands
90 of the Bering Sea, however, Iceland may have been connected to the rest of the Arctic more
91 frequently during the last millennium than at present, a possibility reflected in the presence of
92 both indigenous mitochondrial haplotypes (I1 and I2) and Holarctic haplotypes (H2, H5 and
93 H8) that have been observed in specimens from regions across the circumpolar distribution of
94 the arctic fox[21].

95

96 Records dating from the Little Ice Age cooling event (~16th-19th century[22, 23]) suggest that
97 grounding of Arctic sea ice on Iceland's northern shore may have been a relatively common
98 occurrence, thus connecting Iceland and Greenland for several months per year[23]. Such a
99 sea ice bridge, though transient, may have persisted for sufficient time to enable gene flow
100 into Iceland, resulting in an influx of genetic diversity during the last millennium[20].

101

102 In order to test this hypothesis, we generated mitochondrial DNA sequences from
103 archaeological specimens dated to the 9th-12th century AD and compared them with
104 contemporary Icelandic foxes. We then employed an approximate Bayesian computation
105 approach to assess whether the shift in haplotype frequencies through time was larger than
106 would be expected from genetic drift alone, or whether it was necessary to invoke sea ice
107 mediated gene flow to explain the genetic variation in modern Icelandic foxes.

108

109 **MATERIALS AND METHODS**

110

111 We analysed 25 adult arctic fox specimens obtained from different areas of 12 stratigraphic
112 units from six archaeological sites. The deposits span the chronological sequences of the sites
113 and comprise extensive sheet middens accumulated over generations of human occupation.
114 Even those specimens from the same stratigraphic units (ESM Table 1) were derived from
115 individual, non-articulated bones representing the discard of single bones from single kills
116 into the midden. As a result, the bones are unlikely to be derived from related individuals and
117 do not represent a group kill of a family unit. Nineteen of the specimens were derived from
118 six extensive stratigraphic units at Sveigakot, an abandoned farm dwelling containing
119 numerous zooarchaeologically rich midden deposits. Specimens were also acquired from
120 other sites in the Mývatn region in northeast Iceland including two from Hofstaðir and single
121 bones from Hrísheimar and Skútustaðir (Fig 2). Collectively, these sites possess multiple
122 phases of occupation which together have been dated using radiocarbon and
123 tephrochronology to between the late 9th-12th centuries AD[24].

124

125 We successfully extracted and amplified a ~330bp fragment of the mitochondrial control
126 region[7] from 17 bones excavated at Sveigakot and Hofstaðir in the Mývatn region of
127 northeast Iceland (ESM Table 1). Sequences were assigned haplotypes based on comparison
128 with data encompassing the modern and Late Pleistocene mitochondrial variation (GenBank
129 accession numbers AY321123-AY321148; DQ500881-DQ630747; EF95220-EF95229). The
130 data were compared against a previously published set of 23 mitochondrial sequences
131 obtained from modern Icelandic fox specimens[21] (ESM Fig 1). Further details regarding
132 sample preparation, DNA extraction, PCR amplification and sequencing are presented in the
133 electronic supplementary material.

134

135 The most parsimonious explanation for temporal change in observed haplotype frequencies is
136 likely genetic drift and/or sampling error. To statistically test if the observed changes in
137 haplotype frequency could be the result of genetic drift, sampling error, or unobserved
138 variation, we employed a simulation approach described by Sandoval-Castellanos[25]. Since
139 the amount of genetic drift is dependent on the (in this case unknown) effective female
140 population size (N_{ef}), we executed the test for a range of plausible N_{ef} values (100-100,000).

141

142 The results from this simulation demonstrated that the observed change in haplotype
143 frequency was unlikely to be the result of genetic drift alone. We therefore employed an
144 approximate Bayesian computation approach to account for the possibility of sea ice
145 facilitated immigration to Iceland during the Little Ice Age. This approach makes use of
146 extensive simulations using prior distributions for key unknown parameters such as N_{ef} ,
147 migration rate and initial haplotype frequencies. Following the simulations, a rejection
148 approach was employed in order to select a subset of the simulations that have summary
149 statistics that are similar to those of the empirical data set. Finally, posterior probability
150 distributions of the unknown parameters (see above) were approximated from the subset of
151 non-rejected simulations [26, 27]. Additional details of the approximate Bayesian
152 computation analysis are located in the ESM.

153

154 Our model assumed a lack of mitochondrial phylogeographic structuring of modern
155 haplotypes in Iceland. In order to test this assumption, we performed a simulation of one
156 million generations, assuming either two or three genetically differentiated populations
157 within Iceland. These two putative population structures were Northeast vs. West (with
158 sample sizes of 7 and 16) and Northeast vs. Northwest vs. Southwest (sizes 5, 5 and 10,
159 respectively), which correspond with the most obvious pattern following the distribution of
160 the modern haplotypes in Iceland[21] (Fig 2). This simulation is equivalent to a
161 randomisation test but haplotype frequencies are simulated from a Dirichlet prior distribution
162 conditioned on the contemporary haplotype frequencies in Iceland. The Euclidean distances
163 among haplotype frequencies across the simulations were compared with the Euclidean
164 distances calculated from the empirical data set, with the modern samples grouped according
165 to the hypothesised population structures outlined above. The proportion of simulated
166 distances equal to or higher than the observed among the modern samples is equivalent to the
167 p -value in a statistical test.

168

169 **RESULTS**

170

171 All 17 samples for which sequence data could be obtained possessed the identical, previously
172 reported I2 haplotype (Fig 2). This sequence is an Iceland-specific lineage that makes up 61%
173 of the modern population. The four remaining haplotypes present in modern Iceland were not
174 detected, suggesting that each of their frequencies rose from 0% in the ancient sample to 4%
175 (H5), 9% (H2 and H8) and 17% (I1). Although I1, like I2, is an Iceland-specific haplotype,
176 H2, H5 and H8 are Holarctic haplotypes that have been observed in specimens from regions
177 across the circumpolar distribution of the arctic fox[21].

178

179 The test for modern-day geographical structure in Iceland with contemporary haplotypes
180 yielded non-significant p -values ($p = 0.22$ for the North-East-South structure and $p = 0.18$
181 for the East-West structure), suggesting that the contemporary population is not
182 phylogeographically structured.

183

184 The simulation test for temporal changes in haplotype frequencies, however, demonstrated
185 that the observed change in haplotype frequencies was unlikely to be due to genetic drift
186 alone ($p \leq 0.009$ for all simulated population sizes). Assuming some female immigration
187 during the Little Ice Age, the ABC analysis suggested that the observed change in haplotype
188 frequencies was consistent with a long-term effective female population size of ~7,000-8,000
189 individuals (Fig 3), with a 95% Credible Interval (CI) ranging from 610 to 18,600 effective
190 females (Table 1). The estimate for immigration was ~4.0 with a 95% C.I. of 0.5 to 9.5 (Fig
191 3). The estimated ~4.0 Bayes Factor suggested that the Little Ice Age-mediated immigration
192 hypothesis was more strongly supported than the drift hypothesis.

193

194 **DISCUSSION**

195

196 The genetic composition of the ancient samples indicates that the Icelandic fox population
197 ~1,000-1,100 years ago was genetically homogeneous relative to the modern population (Fig
198 2). There are three possible explanations for the presence of just a single haplotype in the
199 ancient population, but five haplotypes, including three found across the Holarctic, in the
200 modern population.

201

202 Firstly, because all of the successfully amplified ancient samples were excavated from two
203 sites in close proximity to each other in the Lake Mývatn region of northeast Iceland, it is
204 possible that the lack of haplotype variation in the ancient samples is the result of our
205 regionally restricted sample set. If foxes on Iceland possessed a strong phylogeographic
206 signal, it is possible that other haplotypes existed in regions outside the Lake Mývatn region.
207 The fact that all five modern fox sequences obtained from this location also possess the I2
208 haplotype (Fig 2) provides superficial support for this argument.

209

210 A recent study of microsatellite data from Icelandic foxes, however, concluded that nuclear
211 gene flow occurs extensively over the majority of the island[12]. Since arctic fox dispersal is
212 not sex biased[28], it is unlikely any mtDNA phylogeographic structure exists. In addition,
213 our simulation analysis found no significant signature ($p = 0.18-0.22$) of geographic
214 structuring of mitochondrial haplotypes in the modern population. As a result, it is unlikely
215 that phylogeographic structuring could be responsible for the observed homogeneity in the
216 ancient samples.

217

218 Secondly, it is possible that the elevated number of haplotypes in the modern population is
219 the result of recent hybridisation with farmed arctic foxes. Imported blue foxes have been
220 farmed on Iceland since the 1930s, and escaped farmed foxes have been observed breeding
221 with wild individuals in southwest Iceland[9]. In addition, hybridisation between farmed
222 arctic foxes and their wild counterparts, with ensuing shifts in haplotype frequencies, has
223 been observed in other regions of the arctic fox's distribution[29]. However, because all
224 farmed foxes in Iceland are fixed for a haplotype (H9)[30] that has not been observed in the
225 contemporary wild population, introgression from farm foxes cannot account for the
226 observed difference between the ancient and modern populations.

227

228 The most likely explanation for the observed increase in diversity is therefore sea ice
229 mediated gene flow from adjacent areas of the Arctic during the Little Ice Age. The results of
230 our simulation test strongly suggest that the novel variation observed in the modern sample
231 was introduced into Iceland during the second half of the last millennium as Arctic foxes
232 migrated across a transient sea ice bridge (Fig 1).

233

234 Sea ice proliferation around Iceland was once highly variable and many severe sea ice years
235 were recorded during the late 18th and 19th centuries[31]. The last recorded grounding event

236 of sea ice on the shores of Iceland occurred in 1877, after which sea ice abundance in the
237 North Atlantic declined significantly[23]. Such grounding events are likely to have been
238 more common during the Little Ice Age, owing to the increased frequency and severity of
239 cold years. An intermittent sea ice bridge between Greenland and Iceland would have
240 facilitated migration between these regions, a scenario consistent with the dispersal
241 characteristics of the arctic fox[15].

242

243 The most extensive annual movements are generally made by “lemming” foxes that are
244 reliant upon microtine rodents as their primary resource base. Unstable ‘boom and bust’
245 rodent population cycles create discordance between fox numbers and resource availability,
246 promoting dispersal during periods of prey scarcity[10, 13, 15, 17, 18, 20]. “Coastal” foxes
247 are found in areas where rodents are absent, including Iceland, Svalbard and parts of
248 Greenland[32] and they do not disperse to the same degree since their resource base is more
249 stable[13].

250

251 In Svalbard, the genetic composition of the arctic fox population, which belongs to the
252 “coastal” ecotype, is influenced by pulses of “lemming” foxes immigrating from
253 neighbouring Siberia and North America, stimulated by crashes in the rodent population[18].
254 A similar process involving the nearby eastern Greenland population may have been
255 responsible for the introduction of novel haplotypes into the coastal fox population of Iceland
256 during the Little Ice Age. This would also explain why the I2 haplotype is found only in
257 Iceland and did not spread to Greenland during the Little Ice Age, since the Icelandic stable
258 resource base would not have provided an ecological basis for long-distance dispersal pulses
259 even in the presence of a sea ice bridge[18].

260

261 The non-native haplotypes introduced during the Little Ice Age increased in frequency to
262 eventually account for nearly 40% of the modern variation in less than 500 years. The
263 approximate Bayesian computation analyses suggest that this rate of change is consistent
264 with an effective female population size of approximately 7,000-8,000 (600-18,000)
265 individuals during the time period between the Little Ice Age and the bottleneck in the 1970s.
266 Assuming an equal sex ratio and that ~33% of all adult females do not breed[11], this
267 corresponds to a census population size of approximately 1,800-46,000. This figure matches
268 well the $10,500 \pm 3,000$ foxes estimated in the most recent Iceland census[11]. This data also

269 suggests that no additional bottlenecks (pre-dating the 1970s) are required to explain the
270 observed change in haplotype frequencies.

271

272 **CONCLUSION**

273

274 Our collective results suggest that a single, indigenous mitochondrial haplotype was present
275 in Iceland prior to the Little Ice Age. The advent of cooler temperatures led to more frequent
276 sea ice grounding events that facilitated arctic fox migration from Greenland (and possibly
277 the rest of the Arctic) into Iceland. These immigrants possessed four additional haplotypes
278 that, once established, increased in frequency until they reached their modern proportions.

279

280 Our analyses contribute to an accumulating body of evidence indicating the importance of sea
281 ice in creating and maintaining the genetic population structure of the arctic fox across its
282 distribution. The incidence of sea ice around Iceland, and hence the potential for immigration,
283 has decreased significantly during the 20th century, a trend which global warming has
284 accelerated[33]. Increasing isolation from the rest of the Arctic will promote genetic
285 divergence, further differentiating the Icelandic population from their mainland relatives.

286

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293 Hersteinsson provided invaluable advice on the biology of the arctic fox, and the history of
294 Iceland. Novel genetic sequences possess Genbank accession numbers JX495788-JX495804.

295

296

297 **Tables**

298

299 **Table 1.** Estimates of the posterior for female effective population size (N_{ef}) between the first
300 sample and the 1970s bottleneck; and for the effective number of immigrating females per
301 generation (NM_f).

302

	N_{ef}	NM_f
Expectation	8201.8	4.53
Median	7186.5	4.14
Upper limit (95%C.I.)	18621.0	9.60
Lower limit (95%C.I.)	610.0	0.51

303

304

305 **Fig. 1** A map depicting the approximate current distribution of the Arctic fox in blue[10]. The
306 dashed black line indicate the median sea ice maximum for the period 1979-2000[31].

307

308 **Fig. 2** A map of Iceland showing the sample locations and sizes for both the modern and
309 ancient data sets. Pie charts show the proportion of individuals at each locality assigned to
310 each haplotype shown at the bottom of the figure. Median-joining networks to the right of the
311 maps depict the relationships between the ancient and modern haplotypes present on Iceland.
312 Black circles indicate the absence of modern haplotypes in the ancient population. White
313 circles represent inferred haplotypes.

314

315 **Fig 3** A) A joint density graph showing high (yellow) and low (blue) probability regions for
316 the combination of two parameters: a logarithmic scale of effective female population size
317 (N_{ef}) and effective number of female immigrants per generation (NM_f). The square and
318 diamond represent median and expected values and the black dashed line shows the borders
319 of the 95% highest density region (HDR). B) A depiction of the posterior probability
320 distribution of the effective female population size (N_{ef}) on a logarithmic scale. C) A
321 depiction of the posterior probability distribution of the effective number of female
322 immigrants per generation (NM_f). In B and C, vertical lines correspond to the median (left)
323 and expected values (right) and the lighter blue bars encompass the 95% HDR.

324

325

326

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328

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