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1 Finescale ecological niche modeling provides evidence that lactating gray seals (*Halichoerus*
2 *grypus*) prefer access to fresh water in order to drink.

3

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9 Key words: pinniped, phocid, habitat preference, Ecological Niche Factor Analysis, ENFA,
10 thermoregulation, water balance, water drinking, salinity.

11

12 ABSTRACT

13 Many phocids are capital breeders, relying on stored reserves to sustain energetic
14 requirements whilst on land. Their large body size, high energy expenditure during lactation,
15 and the insulative effects of the blubber layer can lead to thermal stress from overheating,
16 especially in warm and temperate climates. Thermal stress can influence fine-scale site
17 choice on breeding colonies, and behavioral thermoregulation has been proposed as an
18 explanation for the clear preferences shown by breeding female gray seals for proximity to
19 pools of water. However, anecdotal observations suggest that pools of water may also be
20 preferred for drinking, though water intake is difficult to verify without real-time
21 physiological monitoring. Here, an alternative approach demonstrates that gray seals also
22 require access to water for drinking. Using Ecological Niche Factor Analysis to examine fine-
23 scale physical determinants of pupping site choice at North Rona, Scotland, we found that
24 lactating mothers showed preference for lower salinity pools. This is most pronounced early
25 in the season, when ambient temperatures and presumably thermal stress are greatest. Given
26 that the cooling effect of fresh and salt water should be equivalent, the most parsimonious
27 explanation for this preference for fresh water pools is that lactating females use these pools
28 for drinking.

29 INTRODUCTION

30 Many phocids are capital breeders, and therefore fast continuously throughout the
31 breeding period (Riedman 1990). During their time on the breeding colony, postpartum
32 mothers obtain their energy from the metabolism of stored reserves including lipids in their
33 thick blubber layer (Pomeroy *et al.* 1999). These reserves are also mobilized to provision the
34 pup with a lipid-rich milk in a short lactation period (approximately 18 d in the gray seal,
35 *Halichoerus grypus*; Boness and James, 1979; Pomeroy *et al.* 1999). This results in high
36 energy expenditure during lactation, as demonstrated by increased basal metabolic rates
37 (BMR); for example, the BMR of lactating gray seal mothers is typically approximately 2.3
38 times that of nonlactating females (Reilly *et al.* 1996). This dramatic increase in BMR during
39 lactation can lead to thermal stress from overheating (Twiss *et al.* 2002) as a result of the
40 insulative effects of the blubber layer and large body size, while the burden of lactation can
41 contribute to water stress (Reilly *et al.* 1996). Phocids are unable to pant or sweat (Riedman
42 1990) and cooling on land is primarily achieved by thermal radiation *via* poorly insulated
43 “thermal windows” such as the flippers (Ronald *et al.* 1977, Øritsland *et al.* 1978, McCafferty
44 *et al.* 2011, Paterson *et al.* 2012). However, this can be insufficient to prevent thermal stress
45 on warm days, generating a requirement for behavioral thermoregulation, for example by
46 seeking shade (Campagna and Le Beouf 1988) or bathing in pools of water (Twiss *et al.*
47 2002). These behaviors are common in pinnipeds breeding in warm and temperate climates
48 (Gentry 1973, Campagna and Le Beouf 1988, Twiss *et al.* 2002, Wolf *et al.* 2005) and
49 involve individuals actively seeking fine-scale, heterogeneous landscape features, such as
50 shady cliffs or pools of water. Behavioral thermoregulation has been proposed as an
51 explanation for the clear preferences shown by breeding female gray seals for proximity to
52 pools of water (Redman *et al.* 2001, Twiss *et al.* 2002).

53 It has previously been assumed that gray seals meet their water requirements while
54 hauled out through the metabolism of fat reserves (Schweigert 1993), with no clinical
55 evidence having been found for dehydration during this time (Irving 1935, Kooyman and
56 Drabek 1968, Ortiz *et al.* 1978). However, at the Scottish colony of North Rona (59.10°N,
57 5.83°W; Fig. 1), lactating female gray seals incur a negative water balance (Reilly *et al.*
58 1996) and have been observed drinking from pools of water of varying salinities (Reilly *et al.*
59 1996, Redman *et al.* 2001, PPP and SDT, personal observation). Similar drinking behavior
60 has been observed at other UK colonies, including Donna Nook (53.47°N, 0.15° E, JES,
61 personal observation) and the Isle of May (56.18° N, 2.56° W, PPP and SDT, personal
62 observation). Therefore, it is also possible that proximity to water is important because
63 lactating gray seals may need to drink from pools of water to maintain a positive water
64 balance and avoid the water stress that develops during lactation (Reilly *et al.* 1996, Redman
65 *et al.* 2001). The difference between these observations and those of Schweigert (1993) at
66 Sable Island, Nova Scotia (43.93°N 59.92°W) could be a result of the higher average
67 temperatures (approximately 7°C difference) at North Rona (Redman *et al.* 2001) relative to
68 Sable Island (Schweigert 1993), which may be enough to induce additional water
69 requirements. However, despite behavioral observations showing that seals submerge their
70 mouths and appear to drink (PPP and SDT, personal observation), it is difficult to state
71 conclusively, without real-time physiological monitoring, that free-living seals drink water
72 whilst hauled out. However, an alternative approach is to examine the fine scale habitat
73 preferences of individuals, particularly with regards to proximity to pools and to pool salinity.
74 If seals require pools solely for thermoregulation they should not differentiate between salt
75 and fresh water pools. Therefore, we examined the fine spatial scale terrestrial habitat
76 preferences of adult female gray seals based on preestablished preferences (proximity to
77 access points to the sea and to pools of water; Twiss *et al.* 2000, 2001) and introduced pool

78 salinity as a new parameter. If gray seal mothers do require access to fresh water for
79 addressing water stress, we predict that proximity to pools and positioning relative to access
80 points to and from the colony will remain key determinants of pupping site choice, but that
81 pool salinity will also contribute substantially to pupping site preferences.

82

83 METHODS

84

85 Study Site and Population

86 North Rona is a small island located 75.5 km NNW of Cape Wrath, Scotland, and
87 covers an area of approximately 1.2 km². The gray seal breeding colony at North Rona is
88 concentrated on the Fianuis peninsula, and forms annually between September and November
89 (Pomeroy *et al.* 1999), with individual females generally remaining ashore for approximately
90 22 d. The study site is a 287 m² area in the south of this peninsula (Fig. 1). Due to the
91 locations of cliffs surrounding the island, that rise up to 108 m, access to the study site from
92 the sea is limited to a series of gullies in the east (Fig. 1), which lead to a relatively low-lying,
93 open and boulder-strewn grassy slope. North Rona experiences a decline in daily air
94 temperature over the breeding season (Fig. 2). Adult females tend to give birth within four
95 days of arriving on North Rona (Pomeroy *et al.* 1999), and the colony typically expands
96 inland, further from access points throughout the season (Pomeroy *et al.* 1994). Due to the
97 distance of pupping sites from the sea, females at North Rona typically do not return to the
98 sea during lactation (Pomeroy *et al.* 1994, 1999). The time spent on the colony prepartum is
99 thought to be spent in site selection before individuals give birth to a single pup (Pomeroy *et*
100 *al.* 1999). Adult females show both site fidelity, returning to sites within a median distance of
101 55 m from the previous years' pupping site, and temporal fidelity, pupping within a few days
102 of their pupping date in the previous year (Pomeroy *et al.* 1999).

103

104 Eco-Geographical Variables

105 The study site was characterized in terms of three key eco-geographical variables
106 (EGVs), chosen for their known or hypothesized influence on seal distribution and behavior
107 (Pomeroy *et al.* 1994; Twiss *et al.* 2000, 2001, 2002, 2007; Redman *et al.* 2001): “cost-
108 distance” to access (CACC), “cost-distance” to nearest pool (CPOOL) and pool salinity.
109 Study site topography was quantified using a submeter-accurate Digital Terrain Model
110 (DTM), previously generated from high resolution aerial photogrammetry (Mills *et al.* 1997,
111 Twiss *et al.* 2000). The DTM was stored as a grid of elevation values across the study site,
112 including information on slope and aspect between neighboring 0.2 m × 0.2 m grid cells, and
113 was integrated with a grid of the same resolution and extent depicting land extent and access
114 point availability to provide the CACC surface. The CACC surface represents a cell-by-cell
115 index of the cumulative “cost” incurred from travelling from any location within the study
116 site to the “nearest” (least “costly”) access point to the sea, where cost is a function of the
117 slope traversed between neighboring grid cells, and is represented as a relative index ranging
118 from zero to 100 (Twiss *et al.* 2000, 2001).

119 High resolution aerial photographs of the study site (taken by SMRU for the annual
120 pupping census; Hiby *et al.* 1988) were available for four dates, hereafter “focal dates”,
121 during the 2010 breeding season. These focal dates are referred to by the “stage” of the
122 breeding season to which they relate: 30 September 2010 (“Beginning”), 12 October 2010
123 (“Mid”), 24 October 2010 (“Late”) and 03 November 2010 (“End”). Using a geographic
124 information system (GIS; ArcInfo Version 9.3, Environmental Systems Research Institute
125 Inc., Redlands, CA), digital copies of these aerial photographs were georectified. We then
126 digitized as polygons all pools of standing water across the study site. These polygon
127 coverages were converted to a grid of the same resolution and extent as the study site DTM

128 and used in conjunction with the DTM to create a CPOOL surface for each focal date. The
129 cost-distance surfaces provide a representation of the potential relative costs incurred by
130 individuals moving across the study site towards access points or nearest pools of water, and
131 do not imply a knowledge of the physiological cost to individuals seals (Twiss *et al.* 2000,
132 2001). Based on personal observations of the locomotory abilities of adult gray seals (PPP
133 and SDT), the cost-distance maps also assume that any feature (*e.g.*, stone walls) resulting in
134 a 2 m vertical change in elevation between neighboring grid cells act as impassable barriers
135 to movement (Twiss *et al.* 2000, 2001). Separate CPOOL surfaces were generated for each of
136 the four focal dates due to the spatially and temporally variable nature of the pools, which
137 form as a result of variable rainfall and sea spray throughout the season (Twiss *et al.* 2007),
138 though only one CACC surface was generated as the terrain and positions of access points
139 remain unchanged across the season.

140 Seals have previously been observed drinking from pools of water at North Rona and
141 therefore salinity was quantified to assess whether a preference for less brackish water
142 influenced seal distribution. We recorded pool salinities from seven days of sampling (29
143 September; 5, 9, 10, 11, 19 and 31 October) during the 2010 breeding season on base maps of
144 pools, providing a map of pool salinities for beginning, mid and late in the 2010 breeding
145 season. Salinity was measured in parts per thousand (‰), based on the refractivity index of
146 the water sample. These salinity maps were transferred to the GIS and the salinity at
147 unmeasured locations was predicted using spatial interpolation of salinity values at known
148 locations for each stage of the 2010 season. Interpolation was carried out using a smoothed
149 inverse exponential distance-weighted (IDW) interpolation. The IDW interpolation method
150 operates using the assumption that locations close to each other are more similar than those
151 that are further apart. Measured points close to the prediction location are therefore assigned
152 a higher weighting than those further away, which have relatively little influence on the

153 predicted value (Ball and Luk, 1998). The salinity surface for late 2010 was also used for the
154 end of 2010, as salinity patterns were the same for late and end of season. It was important to
155 quantify CPOOL and salinity over a range of dates during the breeding season due to the
156 changing availability and distribution of pools, and the varying contributions of rainwater and
157 seawater spray to the pools. Generally, the most saline areas are in the northwest of the study
158 site and around access points, due to high seawater contributions from sea spray and runoff
159 from seals arriving to the colony (Fig. 3). Though SAL and CACC are therefore negatively
160 correlated across the study site at each stage in the breeding season (Pearson's product
161 moment correlation, $n = 82,221$, $P < 0.001$; early, $r = -0.225$; mid, $r = -0.050$; late and end, $r =$
162 -0.178), both variables were retained within the model as the effect sizes were very small.

163

164 Seal Location Data

165 Daily locations (28 September to 3 November) of all seals, including adult females
166 with pups, during the 2010 breeding season were recorded on a fine-scale base map of the
167 study site from a hide overlooking the southern half of Fianuis peninsula (Pomeroy *et al.*
168 1994). The number of seals observed on focal dates is summarized in Table 1 (see methods
169 below for an explanation of terminology). All data were recorded with submeter accuracy
170 with the aid of a 10 m \times 10 m grid overlay, using the head of each individual as a standard
171 reference point. Resulting maps were digitally transferred to a GIS database and georectified
172 to real-world coordinates. Points depicting seal locations were digitized to form a point
173 coverage within the GIS for each stage of the 2010 breeding season (Twiss *et al.* 2000, 2002).
174 These points were associated with the age, sex, and, where available, identity (Hiby *et al.*
175 2012) of each individual, allowing coverages to be created depicting the locations of adult
176 females on all focal dates.

177

178 Ecological Niche Factor Analysis (ENFA)

179 Earlier studies of gray seal pupping site choice (*e.g.*, Anderson and Harwood 1985,
180 Twiss *et al.* 2001) have been based on qualitative habitat descriptions or simplistic models
181 utilizing hierarchical selection procedures, rather than using factor analyses of all variables
182 simultaneously, and none have considered the influence of pool salinity. Ecological Niche
183 Factor Analysis (ENFA) was chosen to further investigate gray seal habitat preferences,
184 including the influence of pool salinity. ENFA requires presence-only rather than presence-
185 absence species location data (*i.e.* a knowledge of species' occurrences within a study area,
186 not whether they are consistently absent from specific locations). Presence-absence
187 techniques such as Generalized Linear Models (GLMs; Gu and Swihart, 2004) are not
188 applicable here, as the absence of seals at a given location on the North Rona colony cannot
189 confidently be assumed to be a result of poor suitability at that location, because the colony is
190 in decline (Pomeroy *et al.*, 2010). Absence from a location could therefore occur simply
191 because not all the breeding space is required. Furthermore, the fine-scale nature of our
192 environmental data means that there are many potential locations for individuals to be
193 "absent" from, and assuming that these "false absences" represent actual absences could bias
194 the predictions of the niche model (Hirzel *et al.* 2002, Kéry 2002, Gu and Swihart 2004).

195 EGV maps and Boolean seal presence maps were converted and aggregated to 1 m ×
196 1 m grids, to make the resolution of all maps uniform. Boolean seal presence maps indicated
197 simple presence or absence (1/0) rather than the actual number of seals in each cell. All grids
198 were converted to ASCII files and imported into IDRISI32 (Version I32.11; Clark Labs,
199 Worcester, MA) for conversion into raster maps suitable for Ecological Niche Factor
200 Analysis (ENFA) analysis in BioMapper (Version 4.0.7.373; Hirzel *et al.* 2007). For ENFA
201 analyses on all focal dates one adult female seal presence map was used alongside one of
202 each EGV map for the corresponding date.

203 The ENFA process has been described in detail elsewhere (Hirzel *et al.* 2002) but, in
204 summary, ENFA assesses habitat usage and preferences by comparing the species'
205 distribution on the EGVs (*i.e.*, the values of EGVs at locations with adult female seals
206 present) with the global set of EGV values (the EGV values in all cells of a raster map of the
207 study site). In doing so, it defines the ecological niche in the terms of Hutchinson (1957): an
208 n -dimensional hypervolume that encompasses the ecological requirements of a species. In
209 order to define habitat preferences, ENFA extracts all information relevant to the species
210 niche from the input EGVs whilst discarding the correlations between these variables. It does
211 so by computing two types of uncorrelated factors from the input set of possibly correlated
212 EGVs (composite "global marginality", M , and composite "global specialization", S). These
213 factors are ecologically relevant in that they formally describe some aspect of the species
214 niche relative to the "global" availability of the modelled set of EGVs. Therefore, these
215 factors are easier to interpret in ecological terms than those produced by traditional factor
216 analyses such as principal components analysis (PCA), another method commonly used to
217 assess habitat preferences (Hirzel *et al.* 2001, 2002). The first factor to be extracted is the
218 marginality, M , which summarizes the difference between the species and global mean on all
219 EGVs and ranges between 0 and 1; the larger the value of M , the further the mean of the
220 species distribution lies from average conditions available across the study site. M is
221 composed of marginality coefficients ($coMs$) for each EGV, which express the degree of
222 correlation between M and each EGV. EGVs with large $coMs$ contribute more to M than
223 those with small $coMs$; a low coM value (close to 0) indicates that the species tends to live in
224 average conditions in relation to that EGV, whilst values closer to ± 1 indicate a tendency to
225 live in "extreme" habitats. Positive $coMs$ indicate that the species prefers EGV values that are
226 higher than the global mean, whilst negative coefficients indicate the opposite.

227 The marginality factor accounts for all of the marginality and a certain proportion of
228 the specialization; the residual specialization is accounted for by the subsequently extracted
229 global specialization factors (S), which describe the species' specialization in relation to the
230 range of available EGVs. The ν - I specialization factors (where ν is the number of EGVs) are
231 extracted according to decreasing amounts of explained variance. S is composed of
232 specialization coefficients (coS) for each EGV which range between 0 and ± 1 , with a high
233 absolute coS value indicating a narrow niche breadth relative to the range of available
234 conditions. Note that the sign associated with each coS is redundant and is simply a product
235 of its computation. S is not bounded between zero and one but ranges from one to infinity,
236 with any value exceeding unity indicating a degree of specialization. Thus, the higher the
237 absolute value of coS , the more restricted the species is on the corresponding EGV. As S
238 ranges between one and infinity, it is difficult to interpret meaningfully. Instead it is easier to
239 define the species niche breadth in terms of the computed tolerance value, T . T is simply the
240 inverse of S and, as such, ranges between 0 and 1, with low values indicating lower tolerance
241 (high specialization) and vice versa. Thus, a species with a high T value has a particularly
242 wide niche and is generally widespread across the study site.

243

244 RESULTS

245

246 ENFA showed that female gray seals occupy habitat close to the average of all EGVs
247 (*i.e.*, are only slightly marginal; Table 1) but that they tend to occupy a restricted range of
248 EGV values relative to those which are available (Table 1). That is, females are relatively
249 specialized in terms of their site choice, as shown by S and T . The marginality and
250 specialization displayed is a consequence of avoidance of extreme values, with females
251 typically occupying intermediate values for all EGVs, but avoiding both high and low

252 extreme values (Fig. 4, Table 2). CPOOL contributes the most to female gray seal
253 marginality, and females are typically found closer to pools than would be expected on
254 average (Fig. 4, Table 3).

255 Table 1 shows that all composite marginality values are greater than zero, though
256 none exceed 0.5. There is an overall decrease in composite marginality (*e.g.*, beginning 2010,
257 $M = 0.479$, end 2010, $M = 0.221$; Table 1) and specialization (*e.g.*, beginning 2010, $S =$
258 5.951 , end 2010, $S = 1.434$; Table 1) across the season, as individuals are increasingly found
259 in more average locations across a wider range of EGV values (Fig. 4). Female specialization
260 is especially pronounced at the beginning of the season when the first arrivals are selecting
261 sites on the colony; this is also reflected in the lower tolerance (T) displayed earlier in the
262 season (Table 1).

263 All EGVs influenced gray seal habitat selection (Tables 3 and 4); the *coMs* for each
264 EGV indicate that female gray seals prefer sites close to pools of low salinity near to access
265 points. Throughout the season, CPOOL is the EGV on which the female distribution differs
266 most from the study site average, as indicated by the large and negative CPOOL marginality
267 coefficients, which demonstrate a preference for proximity to pools of water (Table 3).
268 Though salinity contributes less to marginality than does CPOOL (Table 4), what is clear is
269 that individuals avoid those areas with the highest salinity (Fig. 4, Table 2). CPOOL
270 contributes the most to specialization during the beginning and middle stages of the season,
271 though later in the season CACC is the EGV with the greatest contribution to S (Table 4); at
272 the end of the season seals are typically further from access points than earlier in the season,
273 though opt for sites at intermediate rather than extreme high or extreme low CACC and
274 CPOOL values (Fig.3, Table 2). Salinity contributes more to specialization at the beginning
275 of the season (Table 3), when temperatures are higher (Fig. 2), than does CACC, indicating
276 the importance of pool salinity over CACC to the first females to come ashore at the onset of

277 the breeding season, and all EGVs have a demonstrable impact on the marginality and
278 specialization of female distribution throughout the season (Table 4). The results presented in
279 Tables 3 and 4 also suggest that low CACC and salinity are less important to females later in
280 the season, when temperatures are typically lower (Fig. 2), as they are found nearer to the
281 study site average over a wider range of CACC and salinity conditions (are less marginal, less
282 specialized, and more tolerant). The change in CACC and salinity *coMs* demonstrate a shift
283 towards higher values of CACC and salinity closer to the study site average as the season
284 progresses, suggesting that females either prefer or are forced into areas of higher salinity and
285 further from access points as the season progresses (Table 3).

286

287 DISCUSSION

288

289 Habitat Preferences

290 The ENFA has confirmed previous indications that adult female gray seals show a preference
291 for sites near to pools of water at intermediate distances to access points (Pomeroy *et al.*
292 1994, 2000; Twiss *et al.* 2000, 2002, 2003, 2007; Redman *et al.* 2001, Stephenson *et al.*
293 2007). Furthermore, there is a clear preference for fresh rather than brackish or seawater
294 pools, particularly early in the season, when temperatures are typically higher; this has been
295 discovered despite the range of salinity values across the study site being deceptively low (0-
296 10‰). The interpolation technique results in lower salinity values across the study site than
297 were actually observed (max. observed = 32‰), meaning that the results presented here are a
298 conservative metric of the avoidance of high salinity areas, which in reality is likely to be
299 more pronounced. It is concluded that, though pools are demonstrably important for
300 thermoregulation (Redman *et al.* 2001, Twiss *et al.* 2002), they are also likely important
301 sources of drinking water, potentially to avoid a negative water balance. Indeed, it may be

302 that the requirements for thermoregulation mask the requirements for drinking water, with
303 females bathing in any given pool to cool off regardless of the salinity, but showing a
304 preference for lower salinity pools given the option. The water in the more saline pools is
305 more frequently replenished (by sea-spray) than that in less saline pools, and is therefore
306 likely to be relatively cleaner (*e.g.* less concentrated buildup of fecal material). Despite this,
307 individuals show a clear preference for the less saline, potentially more contaminated pools; it
308 may be that amongst these low salinity pools there is a finer scale of selection, with seals
309 avoiding more contaminated pools, though no quantitative data are available to test this.

310 It is likely that females can actively distinguish between the fresher and more saline
311 pools; Friedl *et al.* (1990) demonstrated that California sea lions (*Zalophus californianus*) can
312 discriminate between freshwater and salt water at salinities at least as low as 3.6‰ (0.1M
313 NaCl). Though there are likely some interspecific differences in gustatory threshold, this
314 suggests that gray seals at North Rona are indeed basing their site choices partially on
315 avoidance of high salinity areas, which exhibited salinity readings of over 10‰. Schweigert
316 (1993) suggested that the metabolism of stored lipid reserves was sufficient to offset water
317 losses through lactation, evaporation and urine, and proposed this as an explanation for why a
318 highly concentrated urine or increased osmotic level in blood plasma was not found.
319 However, the oxidation of stored lipids does not contribute to increased urinary water content
320 (Schweigert 1993), further suggesting a likely input from exogenous water to account for
321 additional urinary water output.

322 The evidence presented here concurs with results of previous studies (Twiss *et al.*
323 2003) and indicates that females choose sites near to, but not necessarily within, pools as a
324 means of addressing the pup-pool trade-off (Redman *et al.* 2001). This trade-off arises since
325 newborn pups are vulnerable when the mother is absent whilst travelling to and from pools,
326 for example, to attacks from gulls or starvation if permanent mother-pup separation results

327 (Redman *et al.* 2001) but pups in locations too near to pools may suffer trampling from
328 nearby conspecifics also utilizing the pools (Twiss *et al.* 2003). Similarly, females likely
329 choose sites at intermediate distances to access points to avoid areas directly next to access
330 points which experience greater traffic associated with seals arriving to or leaving the colony,
331 whilst they also avoid greater locomotory costs associated with travelling further inland
332 (Twiss *et al.* 2003, Stephenson *et al.* 2007).

333

334 Change in Preferences Across the Season

335

336 The decrease in composite marginality values across the season may be informative,
337 and is due to females being found in increasingly average sites as the season progresses. Later
338 in the season, maps of females are likely to contain some females in late lactation that are
339 moving to seek mating opportunities or are in the act of departing from the island. These
340 females are likely to be less influenced by pool proximity or salinity, though we expect their
341 contribution to the decrease in marginality values to be minimal. This is because females on
342 North Rona typically depart rapidly after weaning, and only a small proportion (<10%) of
343 females exhibit movements outside the home range of their local male to seek matings (Twiss
344 *et al.* 2006).

345 The decrease in composite marginality may therefore be interpreted in one or more of
346 three ways: (1) as the season progresses, more females choose sites with EGV values closer
347 to the average available across the study site; (2) as the season progresses, more females are
348 forced into more average areas by the presence of females at preferred sites; or (3) as the
349 season progresses, fewer sites with more extreme EGV values are available (for EGVs that
350 vary across the season *i.e.* salinity and CPOOL), with each site having EGV values closer to
351 the global average; as a result the range of sites that females can choose from is less variable.

352 These alternative interpretations are not necessarily mutually exclusive, though for salinity
353 there was generally greater variability, with larger variances and greater spread of values later
354 in the season (Fig. 4, Table 2) so explanation (3) seems unlikely with regards to salinity.
355 Furthermore, the minimum EGV values across the study area did not increase between stages
356 within the breeding season, whilst at no point in the season did the maximum EGV values in
357 occupied areas approach the maximum values seen across the study site, suggesting that a
358 change in availability of preferred sites has not necessitated female movement into less
359 preferred areas. This suggests that the decrease in marginality over each season is due to
360 female choice or exclusion from more preferred sites, rather than declining availability of
361 preferred sites as a result of EGV changes.

362

363 Broader Implications for Gray Seal and Wider Mammalian Reproductive Ecology

364

365 Throughout its range, the gray seal breeds on a variety of substrates. Given the preference for
366 proximity to low salinity pools demonstrated here it is interesting to note that many of these
367 substrates, such as the porous sands of Donna Nook, do not support extensive or widespread
368 pool formation, whilst those pools that do form may be more ephemeral and spatially
369 unpredictable than those at North Rona. This highlights the fact that these are really habitat
370 preferences, as opposed to immutable requirements. The ability to address water deficits by
371 drinking seawater (mariposia) has been recorded in otariids (Gentry 1981, Costa and
372 Trillmich 1988) and phocids, including harp seals, *Pagophilus groenlandicus* (Storeheier and
373 Nordøy 2001, How and Nordøy 2007), hooded seals, *Cystophora cristata* (Skalstad and
374 Nordøy 2000) and harbor seals, *Phoca vitulina* (Hedd *et al.* 1995). Therefore, it is intriguing
375 that this current study demonstrates a preference for freshwater among lactating gray seals. It
376 is possible that, given the option, addressing a water deficit by drinking freshwater is

377 physiologically less costly, and therefore preferable. It is interesting to question what the
378 effects are of a lack of freshwater pools on female distribution, behavior, and physiology (and
379 therefore reproductive success), especially at sites with similar weather patterns to those at
380 North Rona. Conditions at such sites are known to induce thermal stress (Twiss *et al.* 2002),
381 though even gray seals in colder climates may exhibit similar habitat preferences. For
382 example, water ingestion has even been observed at sites such as Sable Island, where gray
383 seals eat snow and drink from tide pools (SDT, personal observation; D. J. Boness, personal
384 communication¹). Records of pinnipeds specifically ingesting freshwater are rare (*e.g.*
385 Antarctic fur seal, *Arctocephalus gazella*, Lea *et al.* 2002), but such findings raise the
386 question of why seals would choose to breed at sites with limited freshwater availability, and
387 what, if any, advantages are conferred to those that drink freshwater during lactation
388 compared to those that have access only to salt water.

389

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391

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401

402 ¹Personal communication from Daryl J. Boness, University of New England, Department of
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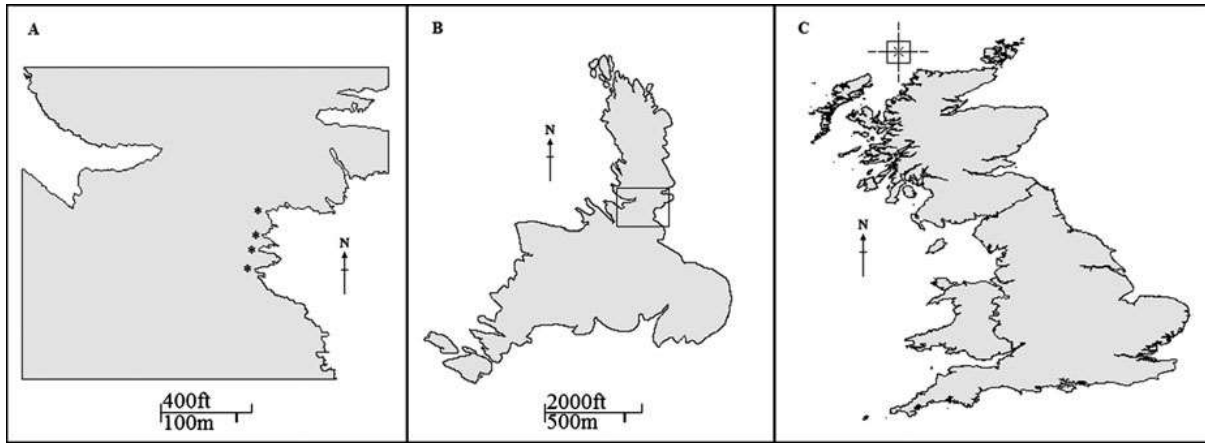


Figure 1: (A) An outline of the Study Site at North Rona; asterisks (*) indicate the location of the main access gullies to and from the sea (B) Location of the Study Site in relation to the rest of North Rona and (C) relative to the rest of the United Kingdom, indicated by crosshairs at 59.1° N, 5.83° W. Areas of land shaded gray. A: outline of Digital Terrain Model of the study site (Stewart, 2013), B: adapted from Google Maps outline view of North Rona (Stewart, 2013), C: adapted from a shapefile of the UK coastline (Stewart, 2013).

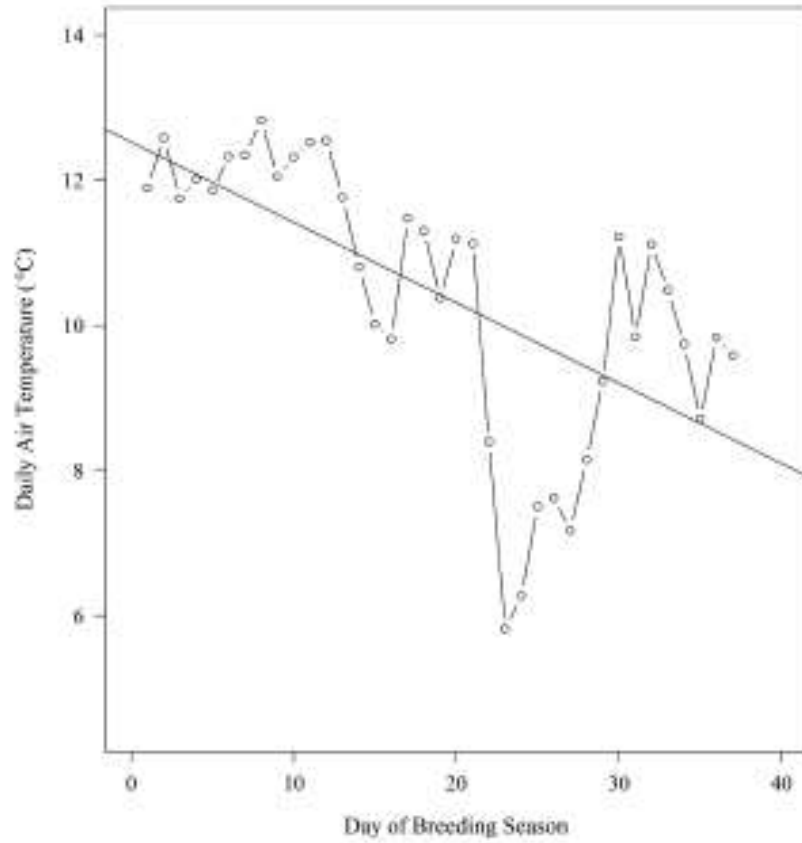


Figure 2: Change in air temperature (°C) over the 2010 breeding season. Day 1 = 28 September. Spearman's rank correlation demonstrates a negative correlation between air temperature and day of breeding season ($r = -0.746$, $n = 36$, $P < 0.001$).

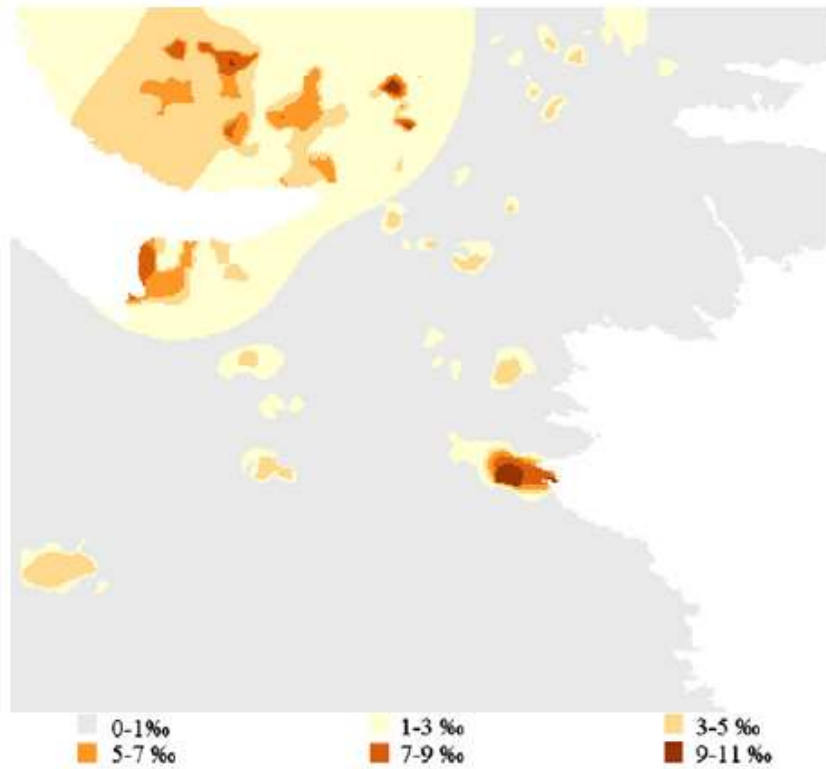


Figure 3: Distribution of salinity values (‰) across the study site on 03 November 2010 (“End” 2010). Dark shades represent high salinity whilst the lower values are represented by lighter shades. Pools are present across the study site, and are not restricted to colored areas.

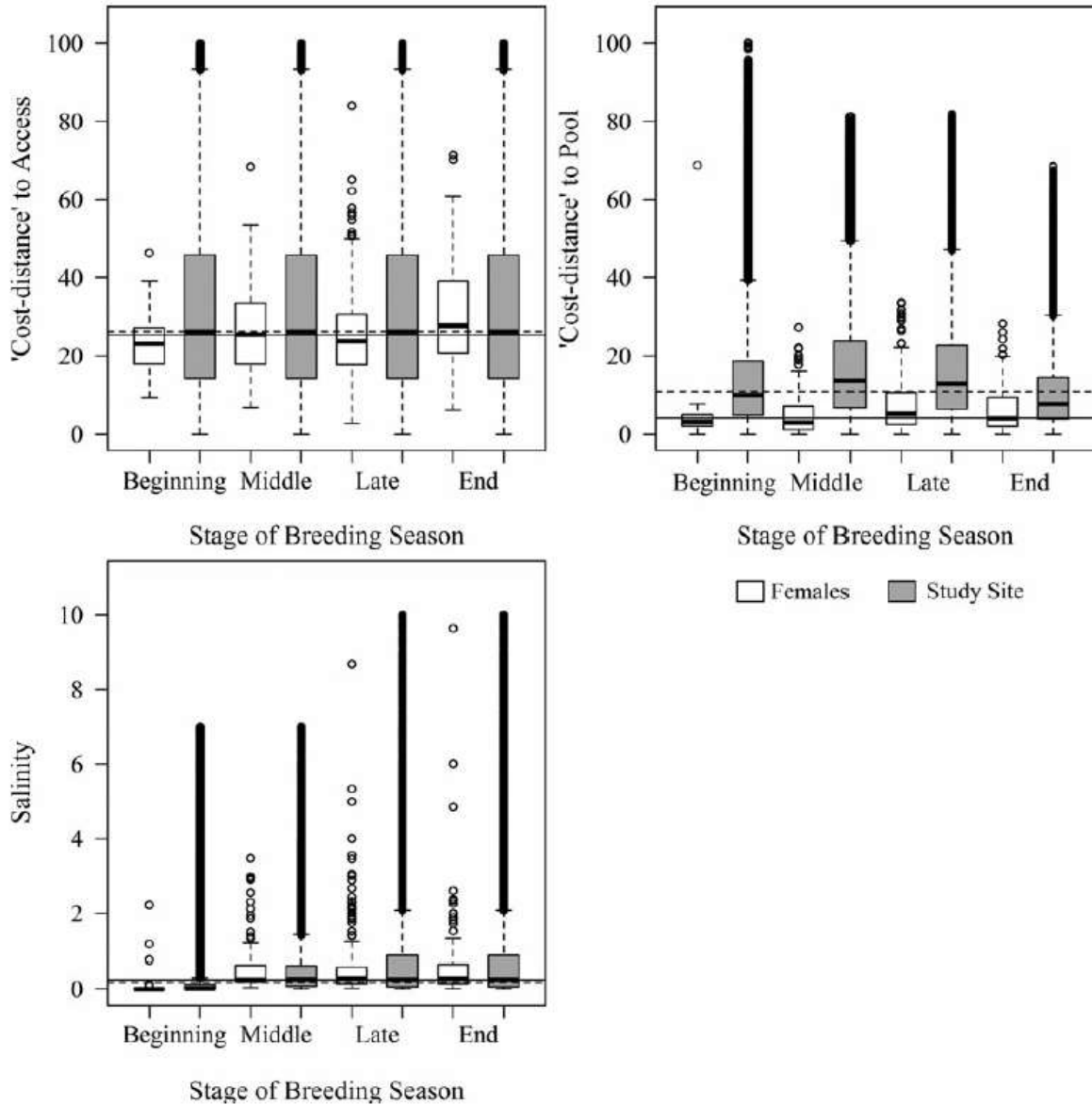


Figure 4: CACC, CPOOL and salinity (%) values at female locations and across the study site in all four stages of the 2010 breeding season. The horizontal dashed line represents the study site (global) median for all focal dates in 2010, whilst the solid horizontal line represents the median across all four focal dates for female locations. Outliers have been included as these represent real measurements from within the study site at locations accessible to seals.

Table 1: Numbers of females in the study site on focal dates, and composite marginality, specialization and tolerance values for females on all focal dates.

Parameter	Stage of Breeding Season	
Number of females	Beginning	48
	Mid	135
	Late	176
	End	106
Marginality (M)	Beginning	0.479
	Mid	0.472
	Late	0.355
	End	0.221
Specialization (S)	Beginning	5.951
	Mid	1.856
	Late	1.557
	End	1.434
Tolerance (T)	Beginning	0.168
	Mid	0.539
	Late	0.642
	End	0.697

Table 2: Summary statistics for CACC, CPOOL and salinity values at female locations and across the study site in all four stages of the 2010 breeding season; CACC = “Cost-distance” to nearest access; CPOOL = “Cost-distance” to nearest pool; SAL = Salinity.

	Females (used habitat)				Study Site (available habitat)			
	Max.	Min.	Median	IQR	Max.	Min.	Median	IQR
(a) CACC								
Beginning	46.28	9.25	23.17	9.52	100.00	0.00	26.17	31.66
Mid	68.38	6.76	25.39	15.57	100.00	0.00	26.17	31.66
Late	83.92	2.64	23.73	12.98	100.00	0.00	26.17	31.66
End	71.42	6.06	27.69	18.51	100.00	0.00	26.17	31.66
(b) CPOOL								
Beginning	7.62	0.00	3.08	2.86	100.00	0.00	9.92	13.82
Mid	27.26	0.00	2.90	6.05	81.28	0.00	13.57	17.09
Late	33.65	0.00	5.14	8.16	81.71	0.00	12.90	16.33
End	28.26	0.00	4.01	7.29	68.48	0.00	7.71	10.63
(c) SAL								
Beginning	1.17	0.00	<0.01	<0.01	7.00	0.00	0.02	0.12
Mid	3.47	0.04	0.25	0.45	7.00	0.00	0.26	0.54
Late	8.67	0.02	0.27	0.45	10.00	0.00	0.25	0.81
End	9.63	0.01	0.27	0.51	10.00 [†]	0.00	0.25	0.81

[†]The maximum value for salinity was not equal to the maximum measured value (32.00) due to the interpolation technique used to create the salinity surface, which reduced the maximum salinity across the study site.

Table 3: Coefficients of Eco-Geographical Variables (EGVs) on each ENFA (Ecological Niche Factor Analysis) factor for female gray seals on each focal day. The marginality factors (M) explain 100% of the marginality and a certain amount of specialization; “%S” indicates the amount of specialization (S) accounted for by each factor; CACC = “Cost-distance” to nearest access; CPOOL = “Cost-distance” to nearest pool; SAL = Salinity. Bold numbers indicate the EGV with the largest coefficient value on each factor.

Stage of Breeding Season	ENFA Output	EGV			
		CACC ³	CPOOL ³	SAL	(% S)
Beginning	<i>coM</i> ¹	-0.402	-0.843	-0.357	60
	<i>coS1</i> ²	0	0.376	0.926	31
	<i>coS2</i> ²	0.872	0.472	0.132	9
Middle	<i>coM</i> ¹	-0.269	-0.963	0	49
	<i>coS1</i> ²	0.957	0.271	0.104	39
	<i>coS2</i> ²	0.148	0	0.989	12
Late	<i>coM</i> ¹	-0.365	-0.921	-0.138	34
	<i>coS1</i> ²	0.928	0.371	0	46
	<i>coS2</i> ²	0	0.16	0.987	20
End	<i>coM</i> ¹	-0.131	-0.973	-0.191	37
	<i>coS1</i> ²	0.991	0.132	0	46
	<i>coS2</i> ²	0.133	-0.209	0.969	16

¹ Positive marginality coefficients indicate that the species was found in locations with higher than average values whilst negative coefficients indicate lower than average EGV values at species locations. A value of 0 indicates no significant differentiation from the global mean.

² Specialization factors (S) one and two (S1 and S2) convey niche breadth. There are two specialization factors because one factor is extracted for each of the three EGVs, one of which is the marginality factor. S will be > 0 whenever female seals were found to occupy a narrower range of conditions than was available across the study site; the greater the absolute value of the coefficient, the more restricted the females’ range on the corresponding EGV.

³ Avoidance of large values of “cost-distance” to a feature (indicated by negative marginality coefficients) may be understood as a preference for proximity to this feature.

Table 4: Eco-Geographical Variable (EGV) contributions to female composite marginality and specialization throughout 2010. CACC = Cost-distance to nearest access; CPOOL = Cost-distance to nearest pool; SAL = Salinity. Bold numbers indicate the EGV with the largest contribution to each factor. Absolute values only reported, sign is unimportant to interpretation.

Stage of Breeding Season	ENFA Output	EGV		
		CACC	CPOOL	SAL
Beginning	M^1	0.402	0.843	0.357
	S^2	35.111	70.527	54.634
Middle	M^1	0.269	0.963	0.029
	S^2	5.416	5.969	1.792
Late	M^1	0.365	0.921	0.138
	S^2	4.037	3.770	1.847
End	M^1	0.131	0.973	0.191
	S^2	3.268	2.836	1.431

¹ Absolute values for EGV contributions to marginality have been reported; a higher coM indicates a greater contribution to M by that EGV whilst a value of 0 indicates no significant difference between the mean at occupied sites and the global mean.

² Specialization factor, which indicates how narrow the range of conditions occupied by the species is (essentially niche width). S varies between 1 and infinity and will exceed unity whenever female gray seals were found to occupy a narrower range of conditions than was available across the study site; the higher this value, the more restricted the females' range on the corresponding EGV.