1 Finescale ecological niche modeling provides evidence that lactating gray seals (*Halichoerus*

2 *grypus*) prefer access to fresh water in order to drink.

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ABSTRACT

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

<u>INTRODUCTION</u>

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).

It has previously been assumed that gray seals meet their water requirements while hauled out through the metabolism of fat reserves (Schweigert 1993), with no clinical evidence having been found for dehydration during this time (Irving 1935, Kooyman and Drabek 1968, Ortiz *et al.* 1978). However, at the Scottish colony of North Rona (59.10°N, 5.83°W; Fig. 1), lactating female gray seals incur a negative water balance (Reilly *et al.* 1996) and have been observed drinking from pools of water of varying salinities (Reilly *et al.* 1996, Redman *et al.* 2001, PPP and SDT, personal observation). Similar drinking behavior has been observed at other UK colonies, including Donna Nook (53.47°N, 0.15° E, JES, personal observation) and the Isle of May (56.18° N, 2.56° W, PPP and SDT, personal observation). Therefore, it is also possible that proximity to water is important because lactating gray seals may need to drink from pools of water to maintain a positive water balance and avoid the water stress that develops during lactation (Reilly *et al.* 1996, Redman *et al.* 2001). The difference between these observations and those of Schweigert (1993) at Sable Island, Nova Scotia (43.93°N 59.92°W) could be a result of the higher average temperatures (approximately 7°C difference) at North Rona (Redman *et al.* 2001) relative to Sable Island (Schweigert 1993), which may be enough to induce additional water requirements. However, despite behavioral observations showing that seals submerge their mouths and appear to drink (PPP and SDT, personal observation), it is difficult to state conclusively, without real-time physiological monitoring, that free-living seals drink water whilst hauled out. However, an alternative approach is to examine the fine scale habitat preferences of individuals, particularly with regards to proximity to pools and to pool salinity. If seals require pools solely for thermoregulation they should not differentiate between salt and fresh water pools. Therefore, we examined the fine spatial scale terrestrial habitat preferences of adult female gray seals based on preestablished preferences (proximity to 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 km^2. 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 m^2 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

Eco-Geographical Variables

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

High resolution aerial photographs of the study site (taken by SMRU for the annual pupping census; Hiby *et al.* 1988) were available for four dates, hereafter "focal dates", during the 2010 breeding season. These focal dates are referred to by the "stage" of the breeding season to which they relate: 30 September 2010 ("Beginning"), 12 October 2010 ("Mid"), 24 October 2010 ("Late") and 03 November 2010 ("End"). Using a geographic information system (GIS; ArcInfo Version 9.3, Environmental Systems Research Institute Inc., Redlands, CA), digital copies of these aerial photographs were georectified. We then digitized as polygons all pools of standing water across the study site. These polygon 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, $r = -0.178$),

162 both variables were retained within the model as the effect sizes were very small.

163

164 <u>Seal Location Data</u>

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 × 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

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 $\times$

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 (*coM*s) for each EGV, which express the degree of

222   correlation between *M* and each EGV. EGVs with large *coM*s contribute more to *M* than

223   those with small *coM*s*;* 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 *coM*s 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 v-1 specialization factors (where v 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   <u>RESULTS</u>

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

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

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

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

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

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

The evidence presented here concurs with results of previous studies (Twiss *et al.* 2003) and indicates that females choose sites near to, but not necessarily within, pools as a means of addressing the pup-pool trade-off (Redman *et al.* 2001). This trade-off arises since newborn pups are vulnerable when the mother is absent whilst travelling to and from pools, 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   <u>Change in Preferences Across the Season</u>

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.

15

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 <u>Broader Implications for Gray Seal and Wider Mammalian Reproductive Ecology</u>

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 communication[1]). 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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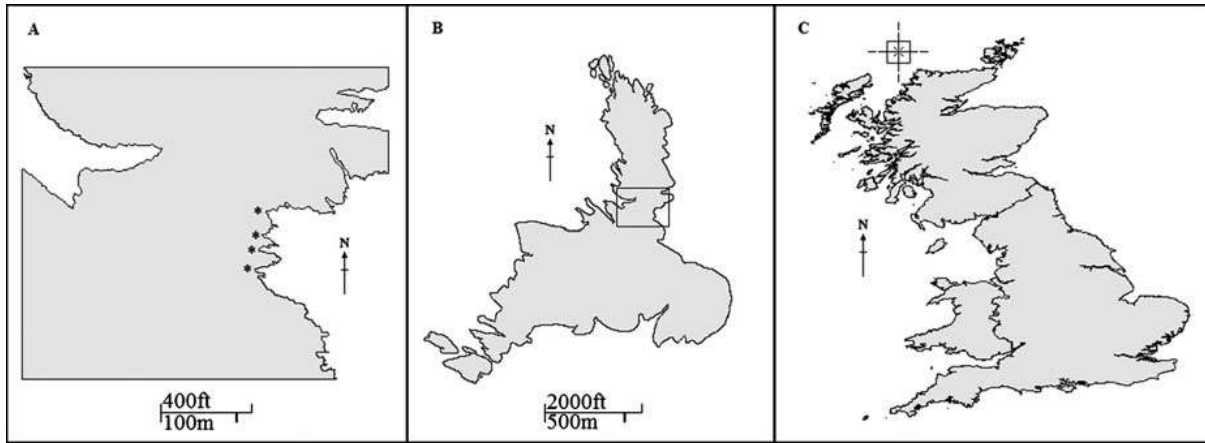526   Ecology and Sociobiology 59: 293-302.

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).
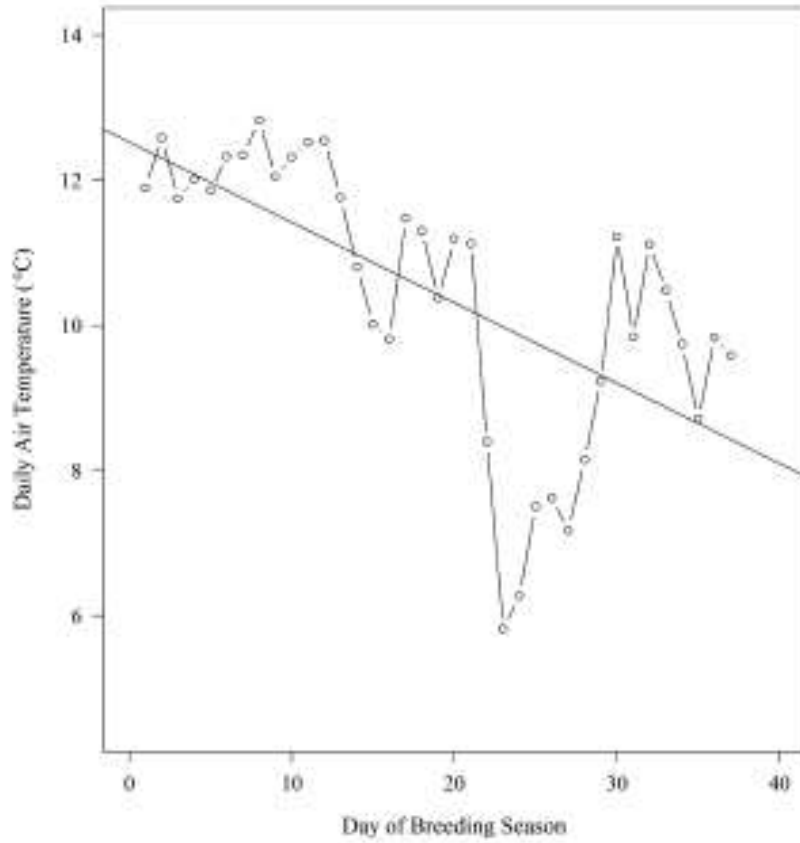
Figure 2: Change in air temperature (°C) over the 2010 breeding season. Day 1 = 28 September. Spearman's rank correlation demonstrates a negative correlation between air temperature and day of breeding season ($r = -0.746$, $n = 36$, $P < 0.001$).
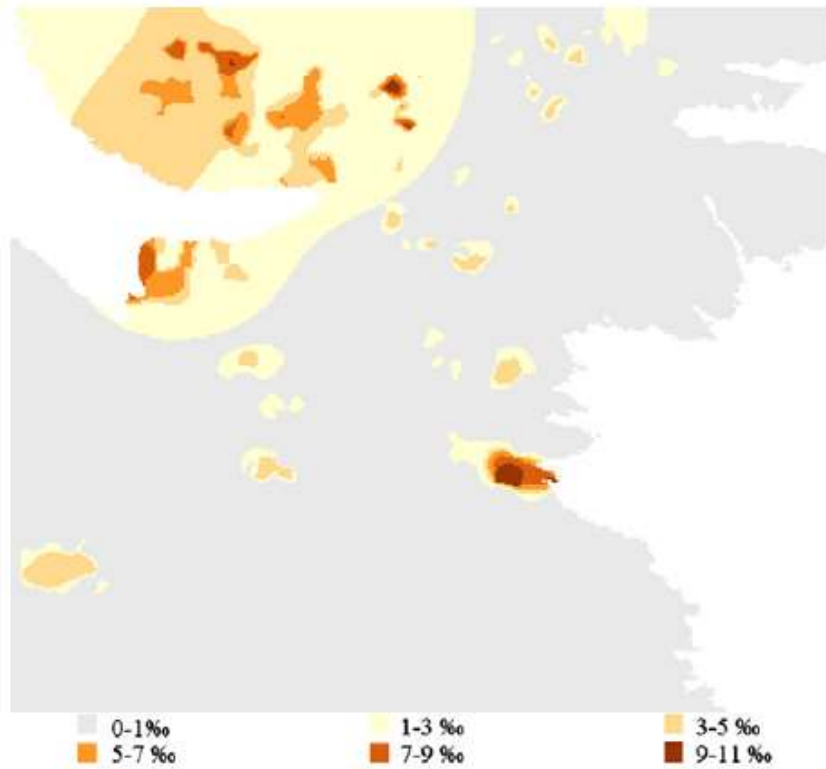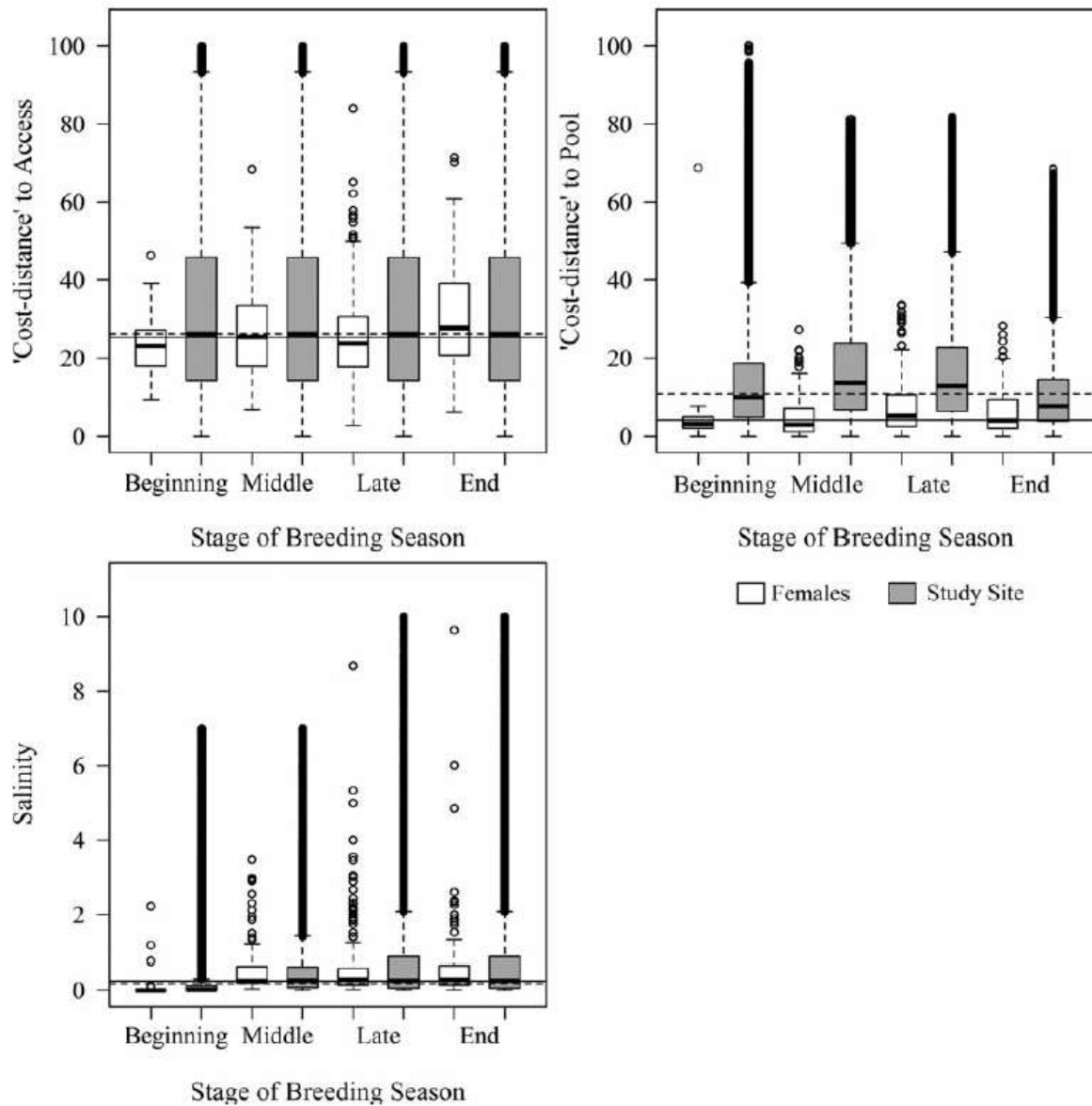
Figure 3: Distribution of salinity values (‰) across the study site on 03 November 2010 ("End" 2010). Dark shades represent high salinity whilst the lower values are represented by lighter shades. Pools are present across the study site, and are not restricted to colored areas.

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	coM^1	-0.402	**-0.843**	-0.357	60
	$coS1^2$	0	0.376	**0.926**	31
	$coS2^2$	**0.872**	0.472	0.132	9
Middle	coM^1	-0.269	**-0.963**	0	49
	$coS1^2$	**0.957**	0.271	0.104	39
	$coS2^2$	0.148	0	**0.989**	12
Late	coM^1	-0.365	**-0.921**	-0.138	34
	$coS1^2$	**0.928**	0.371	0	46
	$coS2^2$	0	0.16	**0.987**	20
End	coM^1	-0.131	**-0.973**	-0.191	37
	$coS1^2$	**0.991**	0.132	0	46
	$coS2^2$	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.