

1 **Density-dependent, central-place foraging in a grazing herbivore:**
2 **competition and trade-offs in time allocation near water**

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25 **Abstract** (297 words): Optimal foraging theory addresses one of the core challenges of ecology:
26 predicting the distribution and abundance of species. Tests of hypotheses of optimal foraging, however,
27 often focus on a single conceptual model rather than drawing upon the collective body of theory,
28 precluding generalization. Here we demonstrate links between two established theoretical frameworks
29 predicting animal movements and resource use: central-place foraging and density-dependent habitat
30 selection. Our goal is to better understand how the nature of critical, centrally placed resources like
31 water (or minerals, breathing holes, breeding sites, etc.) might govern selection for food (energy)
32 resources obtained elsewhere—a common situation for animals living in natural conditions. We
33 empirically test our predictions using movement data from a large herbivore distributed along a
34 gradient of water availability (feral horses, Sable Island, Canada, 2008–2013). Horses occupying
35 western Sable Island obtain freshwater at ponds while in the east horses must drink at self-excavated
36 wells (holes). We studied the implications of differential access to water (time needed for a horse to
37 obtain water) on selection for vegetation associations. Consistent with predictions of density-dependent
38 habitat selection, horses were reduced to using poorer-quality habitat (heathland) more than expected
39 close to water (where densities were relatively high), but were free to select for higher-quality
40 grasslands farther from water. Importantly, central-place foraging was clearly influenced by the type of
41 water-source used (ponds vs. holes, the latter with greater time constraints on access). Horses with
42 more freedom to travel (those using ponds) selected for grasslands at greater distances and continued to
43 select grasslands at higher densities, whereas horses using water holes showed very strong density-
44 dependence in how habitat could be selected. Knowledge of more than one theoretical framework may
45 be required to explain observed variation in foraging behavior of animals where multiple constraints
46 simultaneously influence resource selection.

47 Optimal foraging theory, a foundation of behavioral ecology, generally focuses on how animals
48 maximize energy intake per unit of foraging time under various constraints (Stephens and Krebs 1986).
49 Expansions on foraging theory include models of density-dependent habitat selection (Rosenzweig
50 1981, 1991) such as the ideal-free distribution (Fretwell and Lucas 1969), which continues to base
51 much research in modelling animal distributions and population dynamics. Another well-known
52 extension is the central-place foraging model of Orians and Pearson (1979). The latter is a corollary of
53 the marginal value theorem of Charnov (1976) and describes foraging behavior of an animal that must
54 periodically return to some location between foraging bouts. Central-place foraging relaxes one of the
55 main assumptions of ideal-free distribution: the unhindered movements of individuals among habitat
56 patches. However, despite the importance of competition on foraging behavior (Rita et al. 1996),
57 density of conspecifics is rarely considered explicitly in models of central-place foraging and only
58 implicitly by considering rate of resource depletion.

59 Classical models of central-place foraging consider animals that harvest food from a patch at
60 some distance and then return with items to a central place, typically a nest or colony. There are
61 numerous examples of this behavior from a variety of taxa (e.g., ants [Holway and Case 2000],
62 passerines [Andersson 1981, Bryant and Turner 1982], hummingbirds [Tamm 1989], seabirds [Patrick
63 et al. 2014, Wakefield et al. 2014], rodents [Jenkins 1980, McAleer and Giraldeau 2006], humans
64 [Houston 2011]). A key prediction is a declining probability of using areas farther from the focal point
65 (Schoener 1979). Predictions often imply a loading effect or size of food item-distance relationship.
66 Foragers are expected to become more selective for a smaller range of prey size farther from the central
67 place as pursuit and/or provisioning times increase with prey size, and because a specific range of prey
68 sizes may be more profitable at a distance (Schoener 1979, Jenkins 1980, McAleer and Giraldeau
69 2006). In the case of grazing herbivores, however, which obtain food directly on selected patches (and
70 eat while travelling), foraging is exempted of loading effects.

71 Non-loading effects in models of central-place foraging may involve cases where the central
72 place is or contains an essential resource for survival, such as feeding stations for large herbivores (van
73 Beest et al. 2010), breathing holes for marine mammals under ice (Kramer 1988) and water holes for
74 terrestrial vertebrates in arid environments (e.g., hippopotamus, *Hippopotamus amphibious* [Lewison
75 and Carter 2004]). Many species must drink water as part of their daily activities and this is known to
76 influence foraging decisions (Redfern et al. 2003), leading to space-use patterns that resemble those of
77 central-place foragers (Chapman 1988). In cases like the above, the energetic cost of the outbound trip
78 for foraging and the return trip to the central place is roughly the same and the 'loading effect' of the
79 classical model is eliminated. The latter is, however, replaced by a food 'quality effect': the rate of
80 energy gain is linked to distance to the central place, its quality, and the availability or quality of food
81 in the foraging patch. Quality in this respect may be a function of density, which can increase
82 substantially around points of attraction used by multiple individuals (Redfern et al. 2003), leading to
83 so-called 'piosphere' effects (reviewed in James et al. 1999). The latter includes foraging and trampling
84 impacts of large herbivores (e.g., African elephants, *Loxodonta africana* [Landman et al. 2012]) on
85 vegetation dynamics and soils in relation to water (radial symmetry in grazing intensity that develops
86 around watering points).

87 There remains a need for empirical studies that go beyond testing assumptions of single models
88 of classical foraging theory (Chudzinska et al. 2015). Here we seek to highlight common links between
89 central-place foraging and density-dependent habitat selection. Specifically, we test the general
90 prediction that habitat or resource selection by animals around points of attraction on a landscape (like
91 water holes) will be a fundamentally density-dependent process shaped by time constraints reminiscent
92 of central-place foraging. For our analysis, we use six years of movement data from the individual-
93 based study of an island population of feral horses (*Equus ferus caballus*; Sable Island, Nova Scotia,
94 Canada, 2008–2013). Sable Island presents an idealized system as horses are known to compete for
95 space and forage resources (van Beest et al. 2014) yet live in a natural though simplified system

96 without predation, human interference, or interspecific competition (they are the island's only
97 terrestrial mammal). The population is subject to an individual-based monitoring program of
98 movements, behavior, and life history, where all members of the population ($N = 559$ horses in 2013)
99 are identified and followed (801 life histories from 2008–2013; see van Beest et al. 2014). The whole-
100 island system allows us to meaningfully test ecological theory at larger scales than most researchers of
101 optimal foraging are accustomed (Owen-Smith et al. 2009). Although central-place foraging has the
102 potential to shape movement and habitat selection patterns, few studies have addressed the mechanisms
103 underlying habitat use at the landscape scale (Shrader et al. 2012, Patenaude-Monette et al. 2014).

104 A unique feature of Sable Island, which is a long (49 km) and narrow (1.25 km at its widest)
105 vegetated sand bar (Fig. 1), is a longitudinal gradient in water availability (Contasti et al. 2013). Horses
106 occupying west-central Sable Island can drink at permanent ponds where freshwater is abundant, while
107 in eastern Sable Island horses must obtain water from self-excavated holes or wells (Contasti et al.
108 2012). Home ranges on Sable Island are relatively small ($2.79 \pm 1.17 \text{ km}^2$ [$\bar{x} \pm \text{SD}$]; Welsh 1975), and
109 our observations suggest most individuals specialize on either drinking from ponds or excavated holes.
110 If water acts as a point of attraction, and ponds vs. excavated holes present horses with different time
111 budgets for obtaining daily water requirements (and thus time to forage), we expect foraging decisions
112 of horses around water to be constrained by distance to water, local density, and/or quality of water
113 source. In particular, we can predict a shift in selectivity away from higher-quality (in terms of forage
114 productivity) vegetation associations (grasslands) toward poorer-quality habitat (heathlands) as density
115 increases closer to water, following core expectations of density-dependent habitat selection
116 (Rosenzweig 1981, 1991). That is, the ability for horses to select for grasslands should erode (and use
117 of heathlands increase) where density effects (crowding and the depletion of high-quality forage)
118 increase (Prediction 1). Horses should also demonstrate selection for higher quality grasslands as the
119 energetic cost of travelling increases with distance from water (Prediction 2), following principles of
120 central-place foraging (Orians and Pearson 1979). Extending upon these predictions we can add the

121 hypothesis that the quality of the water source (resource defining the central place) will lead to
122 differences in where on the distance gradient selection patterns switch because of differential time
123 constraints on how individuals access water. For example, the constraint of being away from large,
124 permanent ponds where water may not be as limiting should be less compared to where horses must
125 queue and dig for water at wells. The daily time constraints presented by having to obtain water at self-
126 excavated holes may not exist (or is reduced substantially) where horses obtain water from ponds;
127 hence, any switch in selection between low and high quality vegetation associations should occur at a
128 relatively greater distance from ponds compared to holes (Prediction 3).

129

130 **Materials and Methods**

131 **Study area**

132 Sable Island National Park Reserve (43° 55' N, 60° 00' W) is a crescent-shaped sand bar (Fig. 1)
133 located approximately 275 km southeast of Halifax, Nova Scotia, Canada. The climate is temperate
134 oceanic with warm summers and cool, wet winters. The island is treeless and the vegetation (Tissier et
135 al. 2013) is dominated by American beach grass, or marram (*Ammophila breviligulata*). The climax
136 vegetation association on the island is shrub-dominated heath (*Empetrum nigrum*, *Juniperus communis*,
137 *Myrica pensylvanica*, *Rosa virginiana*, *Vaccinium angustifolium*). Confined to western and central areas
138 of the island and covering approximately 20 ha in total are several permanent freshwater ponds used by
139 horses (Figs. 1 and 2). Ephemeral melt- and rain-water ponds largely occur on the east half of the
140 island but these generally disappear in summer, and horses on east Sable Island must excavate drinking
141 holes to access freshwater (Figs. 1 and 2; Contasti et al. 2012). Introduced in the mid-1700s, the Sable
142 Island horses have always been free-ranging with minimal interference with humans (Christie 1995).
143 The horses are the only terrestrial mammal on the island and are protected and unmanaged.

144

145 **Horse location data**

146 We obtained location data from horses through direct observations of individuals via systematic ground
147 censuses on Sable Island (weekly observations from July–September between 2008 and 2013). This
148 includes whole-island censuses ($N = 375, 437, 503, 448, 534,$ and 559 individuals known to be alive at
149 September 1 for years 2008 through 2013, respectively). During each daily sampling effort (in one of 7
150 sections of the island, stratified to allow complete coverage of a section in one day and roughly
151 complete coverage of the island in one week), we approached horses on foot (which largely ignored our
152 presence) and recorded the location of an individual using a hand-held Global Positioning System
153 (GPS) with location error to within 5 m, the horse's identity from facial features and other
154 distinguishing marks (verified using digital photographs at every sampling event), sex, field age,
155 reproductive status, and group membership. On average, each horse was observed 5 ± 2 times ($\bar{x} \pm SD$)
156 a year, with a maximum of 17 times a summer. In total, we collected 16120 locations of horses (2008 =
157 1005; 2009 = 2429; 2010 = 2702; 2011 = 1402; 2012 = 4048; 2013 = 4534). We evaluated whether our
158 censuses were accurate by comparing summer count data of non-foals in 2010 with data obtained from
159 high-resolution aerial photography in January 2010 (prior to births). This procedure confirmed that our
160 2010 census accounted for >99% of the horses expected to be present (Contasti et al. 2013). Using
161 mark-recapture analysis, we also observed that resighting probability was very high across the period
162 of study (0.99 for each sex). All collection and sampling methods (strictly observation) were approved
163 by the University of Saskatchewan's Animal Research and Ethics Board, under University of
164 Saskatchewan Animal Care Protocol 20090032 and guidance of the Canada Council on Animal Care.

165

166 **Use of vegetation**

167 Vegetation data for the island were obtained using high-resolution aerial photography and a Light
168 Detection and Ranging (LIDAR) map (2009) classified and ground-truthed by the Applied Geomatics

169 Research Group (AGRG) at Nova Scotia Community College, Middleton, Nova Scotia, Canada. This
170 included locations of dense and sparse grasslands of marram; dense and sparse patches of sandwort
171 (*Honckenya peploides*); dense and sparse heathlands; patches of beach pea (*Lathyrus japonicus* var.
172 *maritimus*); non-vegetated areas (dunes, beaches); buildings and fenced areas; and permanent water
173 ponds. We merged vegetation types into three categories (following van Beest et al. 2014), including:
174 a) grasslands of marram and other forage species, containing sandwort and beach pea where present
175 (total annual forage [non-woody plant] production: 549–1566 g/m² [Welsh 1975]); b) heathlands of
176 shrubs and some grasses (forage production: 53–529 g/m² [Welsh 1975]), and c) ‘non-vegetated’ areas
177 which included sand dunes and beaches with minimal coverage of plants. These vegetation classes
178 have previously been shown to influence resource selection patterns of horses on Sable Island (van
179 Beest et al. 2014), with horses showing a strong preference for grasslands compared to heathland when
180 effects of density (competition) are controlled. For all spatial analyses here and below we used a
181 Geographical Information System (ArcGIS 10.1, ESRI, 380 New York Street, Redlands, CA 92373-
182 8100, USA).

183

184 **Use of water**

185 In addition to having mapped water ponds, each year we recorded the locations of excavated water
186 holes, which were typically located in depressions (e.g., valleys and sand dune blow-outs) and were
187 accessed and re-excavated over multiple years (Figs. 1 and 2). We computed the mean distance in
188 meters (m) of both water ponds and holes from vegetation associations. We quantified time costs for
189 individual horses drinking at excavated water holes on Sable Island compared to horses drinking at
190 permanent ponds (Fig. 2), as our conceptual model assumed that drinking from excavated holes would
191 be more costly than drinking from ponds. To confirm this, we collected data on the duration of time
192 spent drinking at either ponds or water holes for a series of focal observations in summer 2012 (93
193 drinking bouts from 55 horses: 32 at holes, and 23 at ponds). We defined start of time spent drinking

194 when a horse approached water and lowered its head to drink, and end of each drinking bout by a horse
195 walking away or being forced away from the water by another individual. A complete start-end
196 drinking cycle was considered a drinking bout, excluding instances of feeding on submerged
197 vegetation. We compared individual times to finish drinking water (all bouts) at holes vs. ponds using a
198 *t*-test assuming unequal variances (square root-transformed data); and a Wilcoxon Rank Sum test for
199 group drinking times, as the data could not be transformed to a normal distribution.

200

201 **Resource Selection Functions (RSFs)**

202 A powerful analytical approach to quantifying how animals select habitat and resources therein is the
203 Resource Selection Function (RSF; Manly et al. 2002). An RSF is typically defined as any function
204 describing habitat or resource use that is proportional to the probability of use by an organism (Manly
205 et al. 2002). A particular strength of the RSF modelling approach is that multiple continuous and
206 categorical variables that influence selection can be incorporated simultaneously. We estimated RSFs
207 for Sable Island horses as a function of vegetation associations and distance to water sources (ponds,
208 holes and both).

209 For each horse, in each year, we created a mean location for a horse (centroid based on UTM *x*-
210 *y* locations). Centered on this point for a horse we then created a circular buffer with a radius of 4000
211 m, bounded by the island shoreline. Our choice of buffer radius corresponded roughly to the 95th
212 percentile of the within-summer range of movements of horses on Sable Island (4438 m, 2008 to 2010;
213 as used in Marjamäki et al. 2013). We then categorized each buffer for a horse according to water
214 sources available within: a) ponds only, b) excavated holes only, or c) both ponds and holes. We then
215 merged buffers of the same category to create three map layers on the island to determine habitat
216 availabilities and compute RSFs; i.e., models for horses that had access to ponds, only excavated holes,
217 or both ponds and holes. We excluded from analysis observations that were not located within 4000 m
218 of any known source of freshwater ($n = 210$).

219 For each horse location we then created a random location in the same availability layer as that
220 based on the classification for a horse's centroid. These random locations described the available
221 resources based on a theoretical, homogeneous distribution of the horses across the landscape. For each
222 actual and random location we extracted the vegetation association at the point and distance to nearest
223 water source. This structuring allowed us to classify the dependent variable in our RSF models as a
224 binomial variable with observed = used (1) and random = available (0) points, and independent
225 variables describing vegetation association and distance to water (a continuous variable); and the
226 interaction between vegetation association and distance to water. Our intent here was to present a
227 simple description of vegetation associations suitable for constructing comparable RSF models, rather
228 than detail the intricacies of horse resource selection on the island. We discuss potential effects of
229 functional responses (Mysterud and Ims 1998) on our results, but did not explicitly include random
230 coefficients in addition to a random intercept in our models for this purpose (Gillies et al. 2006).

231 Because our RSFs were based on use-availability sampling designs (design III data; Thomas
232 and Taylor 2006), we employed mixed-effect logistic regression to estimate coefficients (Gillies et al.
233 2006). For this, we used the "lme4" package (Bates et al. 2014) in R (R Development Core Team
234 2014). Our RSF analyses corresponded most closely to that of second-order selection (Johnson 1980).
235 The application of distance-based models is preferred when analyzing resource selection for animals
236 for which a central place can be identified because they incorporate potential spatial clustering of
237 habitats surrounding the central place and, therefore, account for potential bias in selection estimates
238 (Rosenberg and McKelvey 1999). To account for unbalanced data across years, we used year as a
239 random intercept in each RSF (Gillies et al. 2006). We did not include Group ID as an additional
240 random intercept or nesting within year as neither resulted in better models as determined by AIC. We
241 evaluated predictive success of RSFs using the k -fold cross-validation procedure as proposed by Boyce
242 et al. (2002). For this we calculated cross-validated Spearman rank correlations (r_s) between ten RSF-

243 bin ranks and 10 test-training sets. We repeated this procedure 100 times to determine if the r_s was
244 significantly different from random (t -test).

245

246 **Horse density and distance to water**

247 An assumption underlying our predictions is that water sources act as points of attraction (i.e., central
248 places) in the landscape and that local density should decrease as distance from water increases. To
249 confirm this, we calculated for each of the random points created for the RSF analysis (estimation of
250 the available resources) distance to nearest water source and the type of water source (water hole, water
251 pond, or both), and the local density of horses associated with each random point. We defined this local
252 density from the count of horse centroids for the year associated with a random location contained
253 within the 4000 m-radius buffer centered on that location, divided by the area of the buffer
254 (horses/km²). To quantify relationships between local density and distance to water we computed a
255 general additive mixed model using the “mgcv” package (Wood 2006) in R (R Development Core
256 Team 2014). We used local density as the response variable and included class of water availability as
257 a 3-level factor. In addition, distance to water was included as the smoothing parameter (i.e., the non-
258 linear effect following a natural cubic spline relationship). We estimated the number of knots (k) using
259 cross-validation. Here, k refers to the number of points by which the non-linear function is bent to pass,
260 meaning that $k + 1$ is the number of intervals in the distance to water range where density is described
261 by a different polynomial function. If $k = 1$ the relation is considered linear and no smoothing is
262 applied. We used the year associated with the random location to estimate a random intercept.

263

264 **Results**

265 Focal horses ($n = 23$) drinking at ponds on Sable Island typically drank water in a single bout, with
266 bouts lasting on average 135 ± 23 s ($\bar{x} \pm SE$) and most horses of a group drinking at or near the same

267 time (Fig. 2). Focal horses ($n = 32$) drinking at excavated holes, however, typically queued to drink
268 (Fig. 2) and often drank in multiple bouts (range 1–5). Mean (total) drinking time for a horse using an
269 excavated hole was 633 ± 89 s. The difference in time spent drinking from holes vs. ponds was
270 significant among individuals ($t = -5.34$, $df = 35$, $P < 0.0001$). Drinking bouts were ended by
271 conspecifics in 23% of the observations at ponds but 45% of the observations at water holes. Focal
272 horses drinking at holes were in groups of 2–6 horses ($\bar{x} = 3.8$ individuals), and mean drinking time for
273 a group was >25 minutes 1510 ± 255 s [$\bar{x} \pm SE$]; median 1523 s). Focal horses at ponds were in 7
274 groups of 2–7 horses ($\bar{x} = 5.1$ individuals). Average time for 9 groups to drink at ponds was less than 8
275 minutes (439 ± 132 s; median 420 s). Drinking times for groups at holes and ponds were significantly
276 different (Wilcoxon Rank Sum test; $W = 10$, $P = 0.026$).

277 Horses only accessing excavated holes were, on average, located 754 ± 15 m ($\bar{x} \pm SE$) from
278 water ($SD = 844$ m, range 0–4678 m, $n = 5598$ locations). Horses drinking from ponds only were
279 located $879 \text{ m} \pm 16$ m from water ($SD = 1087$ m, range to 4205 m, $n = 5046$ locations). Horses that
280 were able to access both ponds and holes were located 281 ± 11 m from water ($SD = 223$ m, range 0–
281 1664 m, $n = 5266$ locations). Local density (horses/km²) was greatest in areas with both holes and
282 ponds (Fig. 3a), and declined in a linear fashion as distance from water increased ($k = 1$, $F = 74.2$, $P <$
283 0.001). Local density around water holes decreased non-linearly but steadily (Fig. 3b) as distance from
284 water increased ($k = 2$, $F = 272.7$, $P < 0.001$). Local density around ponds showed a strong non-linear
285 relation (Fig. 3c) with distance from the source ($k = 4$, $F = 635.4$, $P < 0.001$). Here, density decreased
286 to just under 1000 m from ponds (2.4 to 1.5 horses/km² respectively), beyond which density increased,
287 peaking at approximately 2500 m from water with densities slightly higher (2.7 horses/km²) than
288 observed at ponds. The model explained 65.4% of the observed variation in local density of horses.

289 Irrespective of the water source, horses were found in heathland in the immediate vicinity of
290 water more than expected from random and greater than that observed for the selection of grasslands
291 (Fig. 4, Table 1). This was despite relatively close proximity of grasslands to both holes and ponds.

292 Water holes ($n = 45$) were predominately excavated within or adjacent to grasslands (mean distance to
293 nearest grassland 11 ± 4 m [$\bar{x} \pm \text{SE}$], 95% CI 4–18 m), though ponds ($n = 30$) were located farther (69
294 ± 9 m, 95% CI 49–88 m) from grasslands than were excavated holes.

295 The RSF for horses with access to water holes only (Table 1; Fig. 4a) showed that in the
296 immediate vicinity of water, horses selected strongly for heathland while grasslands and non-vegetated
297 areas were used in proportion to availability (95% CI of selection estimates overlapped with 0;
298 Supplementary material Appendix 1, Fig. A1). A switch in selection from heathland to grassland was
299 evident at approximately 165 m from water beyond which heathland was used less than available,
300 while selection for grasslands increased (Fig. 4a). Selection for non-vegetated sites decreased as
301 distance from water holes increased. The RSF showed good predictive performance (Spearman-rank
302 correlation across 10 cross-validation sets was $r_s = 0.765$, $P < 0.001$).

303 The RSF for horses with access to both water holes and ponds showed that selection of all
304 vegetation classes changed with increasing distance from holes (Table 1; Fig. 4b). Close to water,
305 heathland was selected most strongly though not significantly more than grasslands as the 95% CI of
306 selection estimates overlapped near water (Supplementary material Appendix 1, Fig. A1). Selection for
307 both heathland and grassland declined with increasing distance from water with grassland being
308 selected slightly more than heathland beyond 265 m away from water sources (selection switch). Use
309 of non-vegetated sites was proportional to availability close to water sources and steadily decreased as
310 distance from water increased. The RSF for horses accessing both water holes and ponds showed very
311 good predictive performance ($r_s = 0.977$, $P < 0.001$).

312 The RSF for horses only accessing permanent ponds revealed that selection for grassland and
313 heathland also changed with increasing distance from water, while selection for non-vegetated areas
314 was low and remained stable, irrespective of changes in distance from water (Table 1; Fig. 4c;
315 Supplementary material Appendix 1, Fig. A1). Similar to patterns found around water holes, horses
316 selected for heathland in the direct vicinity of ponds whereas grasslands were used in proportion to

317 availability. As distance from ponds increased the relative probability of using grasslands increased and
318 use of heathland became proportional to availability. The switch in selection from heathland to
319 grassland occurred at 1100 m from ponds, which is almost seven times farther than the observed
320 selection switch point for horses using only water holes and four times farther than the observed
321 selection switch point for horses using water holes and ponds. The pond-only RSF also had good
322 predictive performance ($r_s = 0.763$, $P < 0.001$).

323

324 **Discussion**

325 Resource selection in the vicinity of water by feral horses on Sable Island showed signatures of both
326 density-dependent habitat selection and central-place foraging. As predicted, horses concentrated the
327 majority of their summer movements close to water, confirming that ponds and water holes act as
328 points of attraction on the landscape. Our data suggest that local density and hence competition for
329 food resources declined as distance from water increased, in all cases, for approximately the first 1000
330 m around the water source (Fig. 3). Although this is an important assumption of classical central-place
331 foraging theory, which relies on exploitation of a resource around the central place prior to moving on
332 to the next site, the pattern has rarely been quantified using empirical data on animal densities and
333 resource selectivity. Consistent with our predictions, horses selected primarily for lower-quality
334 heathland when in the vicinity of water where density constrained selection for higher-quality grassland
335 and depletion of forage was likely (Prediction 1). When horses moved away from water their selection
336 patterns gradually shifted towards grassland, which we expected as the energetic costs of moving away
337 from the central place increases while at the same time constraints presented by local density generally
338 declines (supporting Prediction 2). What is especially notable about our study, however, is that we also
339 demonstrate how the shift in selection varied with the quality of the non-food resource defining the
340 central place (freshwater pond vs. excavated hole). Horses, and by extension groups, required much

341 longer times to drink at water holes compared to ponds. The switch in selection from use of lower
342 quality to higher quality vegetation as a function of distance to water occurred closer to water for
343 horses drinking at self-excavated holes compared to ponds, with horses drinking at both water sources
344 as an intermediate along this gradient (supporting Prediction 3). Ours is the first study to our
345 knowledge that explicitly accounts for density-dependent habitat selection by a grazing herbivore as it
346 may be constrained by use of a centrally-placed, non-food resource (water).

347 We hypothesized that constraints on resource selection by horses would be due to both density
348 (intraspecific competition) and distance to water. One case did not follow our predictions completely:
349 that of horses drinking at ponds (Figs. 3c and 4c). Although we observed the predicted decline in
350 density to beyond the average distance from water for pond-drinking horses; at farther distances horse
351 density increased while selection for high quality grasslands remained. This pattern may be explained
352 by reduced intraspecific competition between horses in the far west Sable Island (west of the ponds),
353 which is an area able to support higher densities due to unique vegetation features; in particular,
354 nitrogen-enriched patches of beach pea and sandwort that are not found in abundance outside of the
355 spits of Sable Island (Contasti et al. 2012). These patches of vegetation show high nitrogen content
356 traced (using stable isotope analysis) to fertilization by seal colonies (Lysak 2013).

357 We also considered whether our results presented in Fig. 4 were due to functional responses in
358 habitat selection (Mysterud and Ims 1998). A functional response to habitat selection is expected where
359 there exists possible interactions between time allocation relative to different resources, their relative
360 abundance, and spatial arrangement. In this sense, we clearly observed functional responses to forage
361 resources in response to water availability (as also recently observed for African savannah elephants
362 [Roever et al. 2012]). However, we were also concerned whether the extent to which observed shifts in
363 habitat selection for each scenario of water availability may have resulted from availability of
364 vegetation associations. Due to the known environmental gradient in water and vegetation on Sable
365 Island (Contasti et al. 2012), we expected differences in vegetation among the three regions of water

366 availability we mapped. Indeed, heathlands were more common where horses drank from ponds only
367 (14.1%) and both holes and ponds (13.1%), compared to holes only (7.7%); and proportional
368 availability of grasslands was inversely related to these values (30.2%, 43.5%, and 50.2%,
369 respectively). This likely influenced the elevation of slopes of the lines presented in Fig. 4; however,
370 we do not believe that the shift in selection as a function of distance to water (and hence density) was
371 spurious (our main conclusion). The mean distance of patches of heathland to water was 375 ± 663 m
372 ($\bar{x} \pm SD$) for horses drinking from ponds only, 396 ± 361 m from horses using both ponds and holes,
373 and 379 ± 215 m for horses drinking from holes only—values too similar for a functional response to
374 account for the striking shift in selectivity patterns with distance from water we observed (Fig. 4). The
375 more likely explanation for our observation is a trade-off in time available for horses to move and
376 forage vs. acquire water in each region. This shift seems to be apparent as the region of the island
377 where both ponds and holes were available to horses (central Sable Island) produced results that were
378 intermediate between regions where access to water was from ponds or holes only.

379 Central-place foraging is, at its core, a process of time management (Charnov 1976, Orians and
380 Pearson 1979). Maximizing energy intake per unit foraging time as a currency of fitness is often
381 assumed for central-place foragers (Lewison and Carter 2004). In this context, we believe the
382 contrasting time budgets observed for horses drinking at different water sources are biologically
383 important and may be conservative. Indeed, we did not measure group wait times prior to initiation of
384 timed drinking sequences. We suspect these wait times at the periphery of active water holes (queuing)
385 add considerably to time spent away from foraging, and so would exacerbate differences in time
386 budgets for hole- vs. pond-drinking horses. It may thus be that where horses are accessing water from
387 holes vs. ponds, acquisition of water, rather than energy, becomes the currency that horses must
388 maximize on a daily basis to optimize fitness. This may be particularly true in summer (our sampling
389 season) where lactating females must have regular access to water to provide for offspring (Berger
390 1986). The implications of this to the population dynamics of Sable Island horses are beyond the scope

391 of this study, but different densities, sex ratios, and population dynamics across the length of Sable
392 Island from west to east associated with the observed gradient in water availability have already been
393 documented (e.g., Contasti et al. 2012, 2013, van Beest et al. 2014).

394 The multi-theoretical approach we adopted here may serve as a basis to exploring spatial
395 distribution and resource selection patterns of other species in other environments. Further
396 development of our approach is recommended, as the Sable Island horses exist in a simplified system
397 without predators, and in most grazers predator avoidance and foraging behavior seem to be
398 functionally inseparable (Street et al. 2013). Nevertheless, as competition for (and access to) critical
399 resources influences the behavior of most animal species, our findings may apply widely. In particular,
400 we expect parallels for species occupying arid and semi-arid ecosystems, like deserts and savanna,
401 where animals frequently congregate around water (Trash et al. 1995, James et al. 1999, Redfern et al.
402 2003, Landman et al. 2012). The importance of water holes in structuring animal distribution has
403 already been shown in these environments, though not generally explained, for both large herbivores
404 and carnivores (Valeix et al. 2009, 2010). Our results may help predict species distributions in this
405 context.

406 We also expect the processes we describe herein to apply not only to scenarios where animals
407 are accessing water, but also other centrally located points containing critical resources for survival and
408 reproduction. Examples may include breathing holes for aquatic animals under sea-ice; polynyas or
409 open-water areas; access to concentrated sources of minerals or mineral licks; or access to breeding
410 sites (e.g., lekking areas). We conclude that where these non-food resources are centrally located and
411 limiting we should expect constraints on optimal foraging and resource selection from competition.
412 Overall, a single theoretical framework may be insufficient to explain observed variations in foraging
413 behavior as multiple constraints are expected to influence resource selection patterns simultaneously.

414

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524 **Figure Legends**

525 Figure 1. Sable Island, Nova Scotia, Canada, and location of different water sources available to feral
526 horses (2008–2013). Crosses indicate locations of wells excavated by horses (water holes)
527 and circles indicate locations of freshwater ponds on the island. Grey zones indicate
528 locations of vegetated areas.

529 Figure 2. Sable Island horses (a) queuing to drink at self-excavated water holes vs. (b) drinking at
530 freshwater ponds (photographs in 2013 by S. A. Medill).

531 Figure 3. Predicted density of horses on Sable Island, Nova Scotia (horses per km² in a 4000 m buffer
532 at a sampling point; years 2008–2013) as a function of distance to water source for horses
533 with access to (a) both freshwater ponds and excavated holes; (b) water holes only; and (c)
534 ponds only. Functions are plotted out along the *x*-axis to follow the 90th percentile of all
535 horse observations with distance from water for each class of water availability. Lines are
536 fitted means (\pm 95% confidence interval) of densities estimated with a generalized additive
537 mixed model.

538 Figure 4. Estimates of resource selection functions (log odds ratio) for three vegetation associations
539 used by Sable Island horses, 2008–2013, where horses accessed: (a) self-excavated water
540 holes only; (b) water holes and ponds; and (c) ponds only. Estimates overlapping 0 (black
541 dotted line) indicate that use of a vegetation association is proportional to its availability,
542 whereas estimates higher than 0 indicate selection of a vegetation association relative to its
543 availability; values below 0 indicate reduced selection of a vegetation association relative to
544 its availability. The red-dotted, vertical line indicates the distance from a water source where
545 a switch in selection occurs. Note the difference in scale on the *x*-axis between panels, which
546 follows the 90th percentile of all horse observations with distance from water for each type
547 of source (as in Fig. 3). Confidence intervals (95%) around regression lines were not drawn

548 to facilitate plot interpretation but these are presented in Supplementary material Appendix
549 1, Fig. A1.

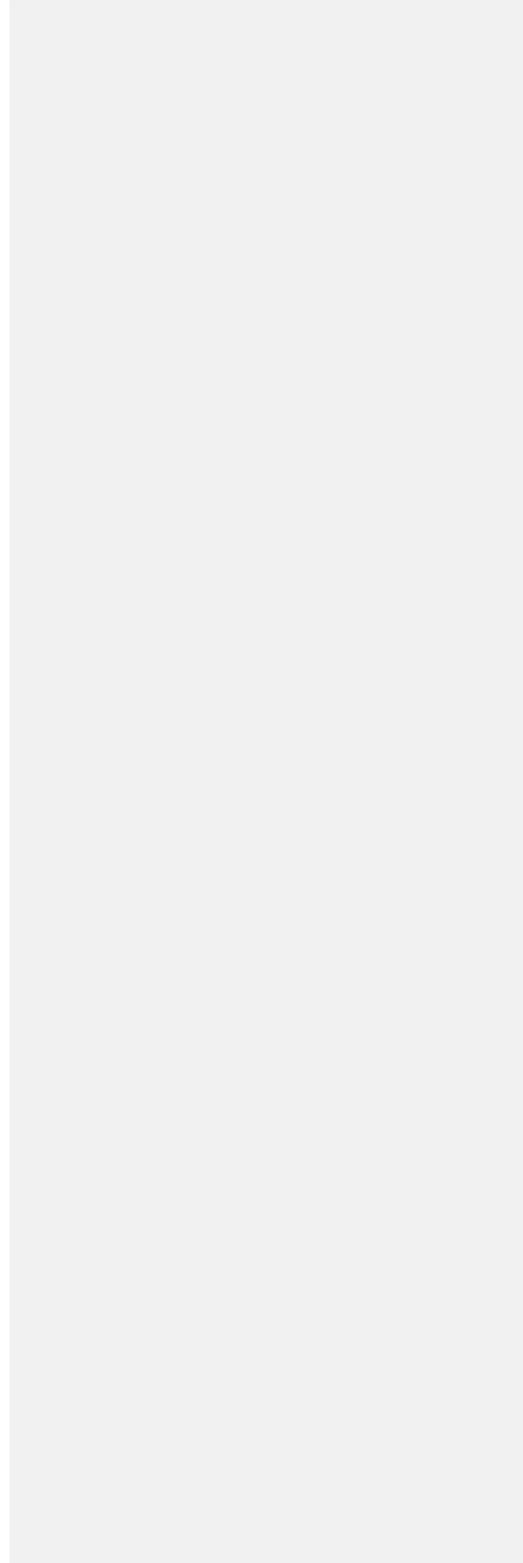


Table 1. Summary of the mixed-effects logistic regressions (RSFs) predicting resource selection by feral horses during summer as a function of vegetation association and distance to water source (where horses area accessing excavated water holes only, ponds only, or both holes and ponds) on Sable Island, Canada, 2008–2013. Year ($n = 6$) was included as a random intercept in all models. The output forms the analytical basis for Figure 4.

Accessed water source	RSF variables	β	SE	95% CI (lower, upper)	P
Water hole	Intercept	1.073	0.37	0.345, 1.801	0.003
	Grassland (G)	-0.779	0.37	-1.507, -0.051	0.034
	Heathland (H)	0.736	0.41	-0.070, 1.542	0.072
	Non-Vegetated (N)	-1.428	0.37	-2.156, -0.700	< 0.001
	Distance to Water (DW)	-0.00006	0.0002	-0.0004, 0.0003	0.734
	G \times DW	0.0002	0.0002	-0.0002, 0.00059	0.258
	H \times DW	-0.009	0.0007	-0.0104, -0.0076	< 0.001
	N \times DW	-0.0003	0.0002	-0.0007, <0.00001	0.066
Random effects	Var	SD			
Year	0.007	0.086			
Water pond	Intercept	1.156	0.21	0.743, 1.569	< 0.001
	Grassland (G)	-1.35	0.168	-1.680, -1.020	0.001
	Heathland (H)	-0.278	0.17	-0.612, 0.056	0.103
	Non-Vegetated (N)	-2.745	0.172	-3.083, -2.407	< 0.001
	Distance to Water (DW)	-0.0002	0.0001	-0.0004, 0.0001	0.202
	G \times DW	0.0005	0.0001	0.0003, 0.0008	< 0.001
	H \times DW	-0.0005	0.0002	-0.0008, -0.0002	0.007
	N \times DW	-0.0003	0.0001	-0.0006, <0.00001	0.036

Random effects		Var	SD		
Year		0.517	0.719		
Both water hole and pond	Intercept	1.601	0.287	1.036, 2.166	< 0.001
	Grassland (G)	-0.590	0.291	-1.162, -0.018	0.042
	Heathland (H)	-0.303	0.296	-0.885, 0.279	0.306
	Non-Vegetated (N)	-1.550	0.298	-2.136, -0.964	< 0.001
	Distance to Water (DW)	-0.008	0.002	-0.012, -0.004	0.003
	G × DW	0.006	0.002	0.002, 0.010	0.023
	H × DW	0.005	0.002	0.001, 0.009	0.051
	N × DW	0.005	0.002	0.001, 0.009	0.043
Random effects		Var	SD		
Year		0.001	0.039		

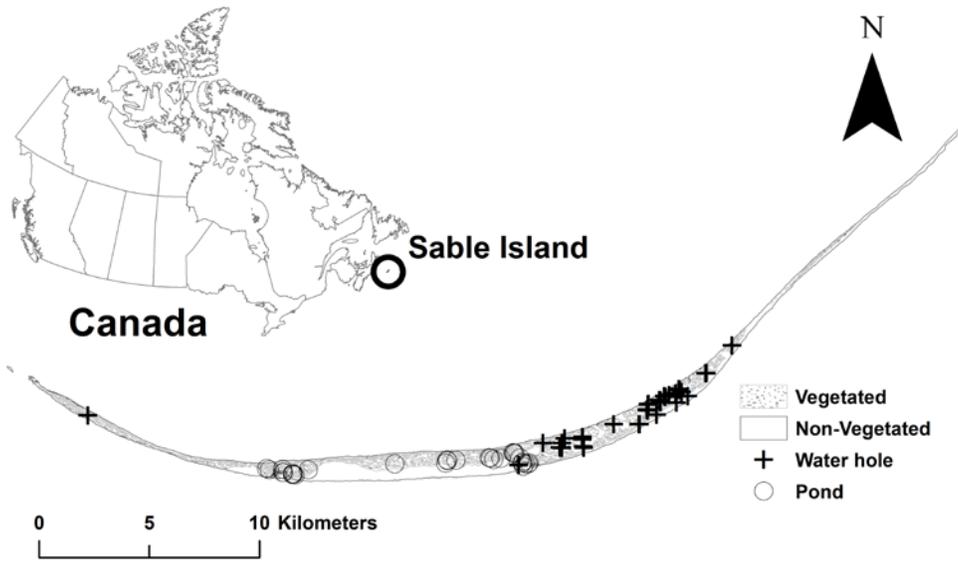


Figure 1.



Figure 2.

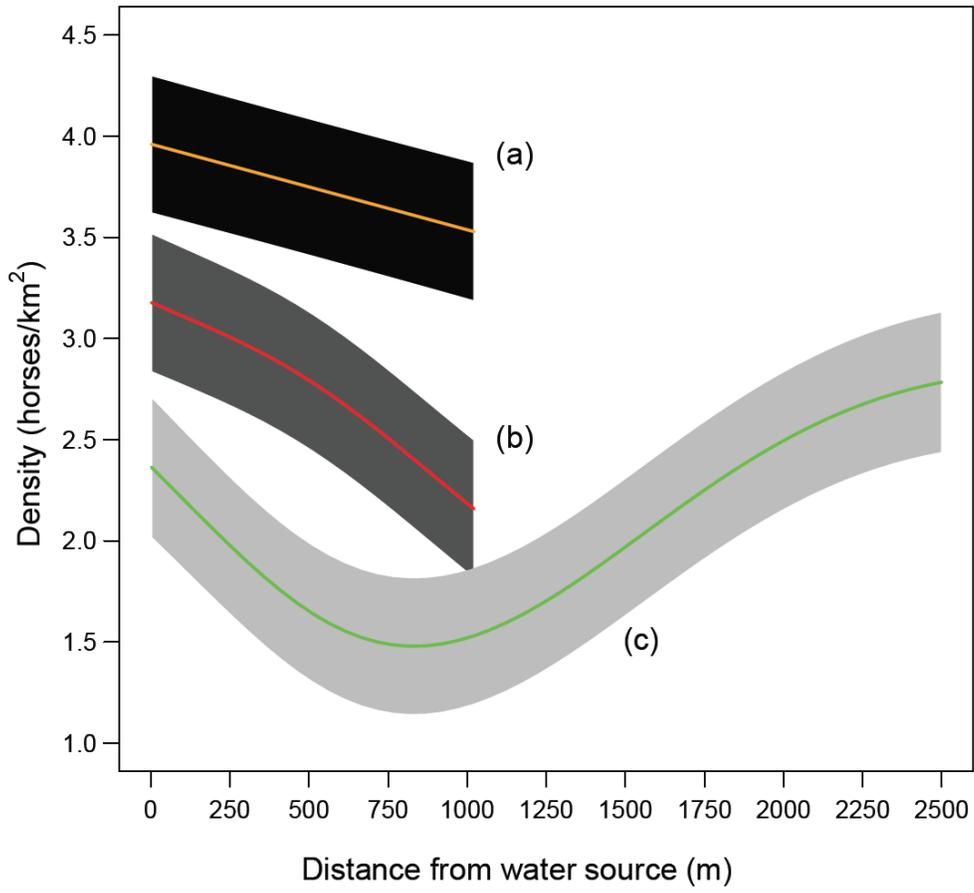


Figure 3.

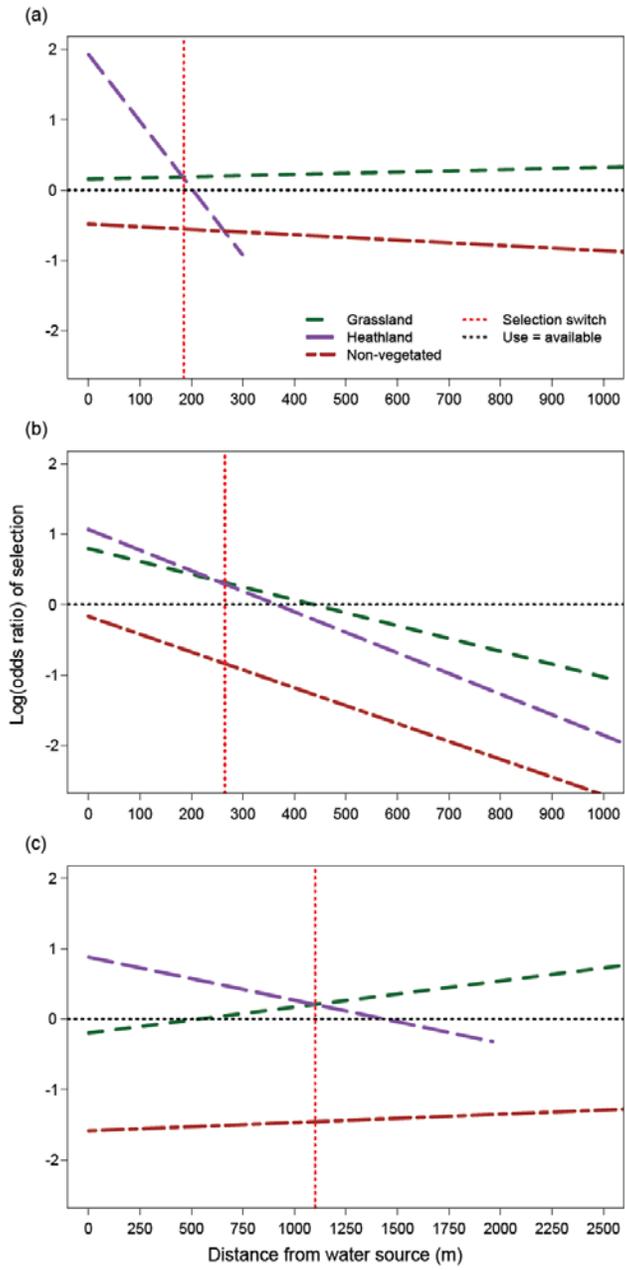


Figure 4.

550 **Supplementary Material Appendix 1**

551

552 **Density-dependent, central-place foraging in a grazing herbivore:**
553 **competition and trade-offs in time allocation near water**

554

555 David Rozen-Rechels, Floris M. van Beest, Emmanuelle Richard, Antonio Uzal,
556 Sarah A. Medill, and Philip D. McLoughlin

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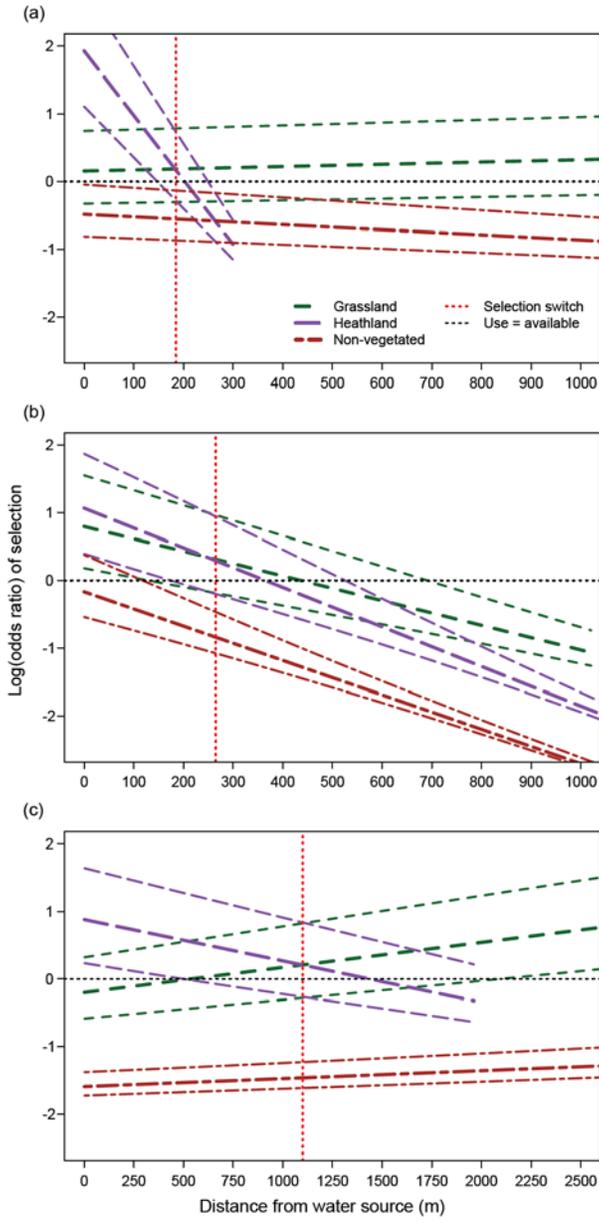
559 Figure A1. Estimates of resource selection functions (log odds ratio) for three vegetation associations
560 for Sable Island horses, 2008–2013, where horses accessed: (a) self-excavated water holes
561 only; (b) water holes and ponds; and (c) ponds only. Estimates overlapping 0 (black dotted
562 line) indicate that use of a vegetation association is proportional to its availability, whereas
563 estimates higher than 0 indicate selection of a vegetation association relative to its
564 availability; values below 0 indicate reduced selection of a vegetation association relative
565 to its availability. The red-dotted, vertical line indicates the distance from a water source
566 where a switch in selection occurs. Note the difference in scale on the *x*-axis between
567 panels, which follows the 90th percentile of all horse observations with distance from water
568 for each type of source (as in Figs. 3 and 4 of the main article). Confidence intervals (95%)
569 around regression lines are presented as thinner dashed lines of the same pattern and color
570 as the regression lines (bands).

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575

576

577 Figure A1.

