Density-dependent, central-place foraging in a grazing herbivore: competition and tradeoffs in time allocation near water

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

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

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

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

There remains a need for empirical studies that go beyond testing assumptions of single models of classical foraging theory (Chudzinska et al. 2015). Here we seek to highlight common links between central-place foraging and density-dependent habitat selection. Specifically, we test the general prediction that habitat or resource selection by animals around points of attraction on a landscape (like water holes) will be a fundamentally density-dependent process shaped by time constraints reminiscent of central-place foraging. For our analysis, we use six years of movement data from the individual-based study of an island population of feral horses *Equus ferus caballus* (Sable Island, Nova Scotia,

Canada, 2008–2013). Sable Island presents an idealized system as horses are known to compete for space and forage resources (van Beest et al. 2014) yet live in a natural though simplified system without predation, human interference or interspecific competition (they are the island's only terrestrial mammal). The population is subject to an individual-based monitoring program of movements, behavior, and life history, where all members of the population (n = 559 horses in 2013) are identified and followed (801 life histories from 2008–2013; see van Beest et al. 2014). The whole-island system allows us to meaningfully test ecological theory at larger scales than most researchers of optimal foraging are accustomed (Owen-Smith et al. 2010). Although central-place foraging has the potential to shape movement and habitat selection patterns, few studies have addressed the mechanisms underlying habitat use at the landscape scale (Shrader et al. 2012, Patenaude-Monette et al. 2014).

A unique feature of Sable Island, which is a long (49 km) and narrow (1.25 km at its widest) vegetated sand bar (Fig. 1), is a longitudinal gradient in water availability (Contasti et al. 2013). Horses occupying west–central Sable Island can drink at permanent ponds where freshwater is abundant, while in eastern Sable Island horses must obtain water from self-excavated holes or wells (Contasti et al. 2012). Home ranges on Sable Island are relatively small (2.79 ± 1.17 km² [$\bar{x}$ ± SD]; Welsh 1975), and our observations suggest most individuals specialize on either drinking from ponds or excavated holes. If water acts as a point of attraction, and ponds versus excavated holes present horses with different time budgets for obtaining daily water requirements (and thus time to forage), we expect foraging decisions of horses around water to be constrained by distance to water, local density, and/or quality of water source. In particular, we can predict a shift in selectivity away from higher-quality (in terms of forage productivity) vegetation associations (grasslands) toward poorer-quality habitat (heathlands) as density increases closer to water, following core expectations of density-dependent habitat selection (Rosenzweig 1981, 1991). That is, the ability for horses to select for
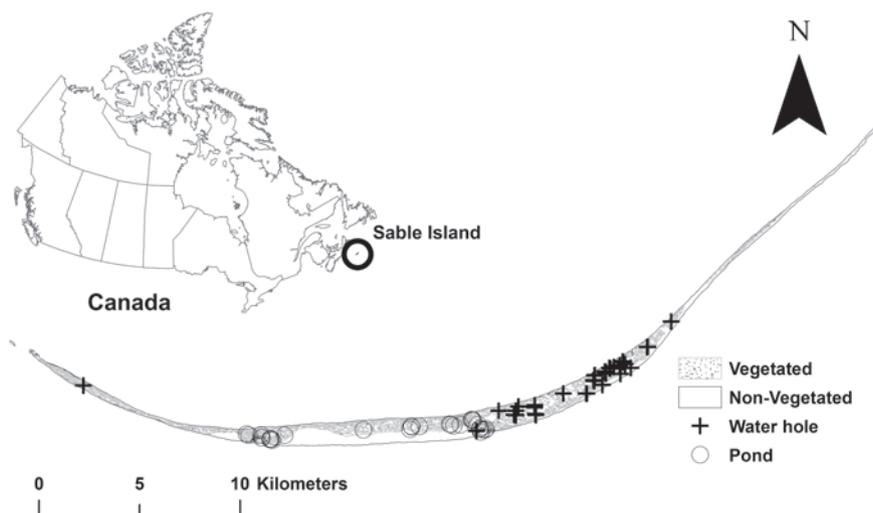
Figure 1. Sable Island, Nova Scotia, Canada, and location of different water sources available to feral horses (2008–2013). Crosses indicate locations of wells excavated by horses (water holes) and circles indicate locations of freshwater ponds on the island. Grey zones indicate locations of vegetated areas.

grasslands should erode (and use of heathlands increase) where density effects (crowding and the depletion of high-quality forage) increase (prediction 1). Horses should also demonstrate selection for higher quality grasslands as the energetic cost of travelling increases with distance from water (prediction 2), following principles of central-place foraging (Orians and Pearson 1979). Extending upon these predictions we can add the hypothesis that the quality of the water source (resource defining the central place) will lead to differences in where on the distance gradient selection patterns switch because of differential time constraints on how individuals access water. For example, the constraint of being away from large, permanent ponds where water may not be as limiting should be less compared to where horses must queue and dig for water at wells. The daily time constraints presented by having to obtain water at self-excavated holes may not exist (or is reduced substantially) where horses obtain water from ponds; hence, any switch in selection between low and high quality vegetation associations should occur at a relatively greater distance from ponds compared to holes (prediction 3).

Material and methods

Study area

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

1995). The horses are the only terrestrial mammal on the island and are protected and unmanaged.

Horse location data

We obtained location data from horses through direct observations of individuals via systematic ground censuses on Sable Island (weekly observations from July–September between 2008 and 2013). This includes whole-island censuses (n = 380, 437, 503, 448, 534 and 559 individuals known to be alive at 1 September for years 2008 through 2013, respectively). During each daily sampling effort (in one of seven sections of the island, stratified to allow complete coverage of a section in one day and roughly complete coverage of the island in one week), we approached horses on foot (which largely ignored our presence) and recorded the location of an individual using a hand-held GPS with location error to within 5 m, the horse's identity from facial features and other distinguishing marks (verified using digital photographs at every sampling event), sex, field age, reproductive status and group membership. On average, each horse was observed 5 ± 2 times ($\overline{x} \pm$ SD) a year, with a maximum of 17 times a summer. In total, we collected 16 120 locations of horses (2008 = 1005; 2009 = 2429; 2010 = 2702; 2011 = 1402; 2012 = 4048; 2013 = 4534). We evaluated whether our censuses were accurate by comparing summer count data of non-foals in 2010 with data obtained from high-resolution aerial photography in January 2010 (prior to births). This procedure confirmed that our 2010 census accounted for > 99% of the horses expected to be present (Contasti et al. 2013). Using mark–recapture analysis, we also observed that resighting probability was very high across the period of study (0.99 for each sex). All collection and sampling methods (strictly observation) were approved by the Univ. of Saskatchewan's Animal Research and Ethics Board, under Univ. of Saskatchewan Animal Care Protocol 20090032 and guidance of the Canada Council on Animal Care.

Use of vegetation

Vegetation data for the island were obtained using high-resolution aerial photography and a Light Detection and Ranging (LIDAR) map (2009) classified and ground-truthed by the Applied Geomatics Research Group (AGRG) at Nova Scotia Community College, Middleton, Nova Scotia,

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

Canada. This included locations of dense and sparse grasslands of marram; dense and sparse patches of sandwort *Honckenya peploides*; dense and sparse heathlands; patches of beach pea *Lathyrus japonicus* var. *maritimus*; non-vegetated areas (dunes, beaches); buildings and fenced areas; and permanent water ponds. We merged vegetation types into three categories (following van Beest et al. 2014), including: a) grasslands of marram and other forage species, containing sandwort and beach pea where present (total annual forage [non-woody plant] production: 549–1566 g m^{-2}, Welsh 1975); b) heathlands of shrubs and some grasses (forage production: 53–529 g m^{-2}, Welsh 1975), and c) 'non-vegetated' areas which included sand dunes and beaches with minimal coverage of plants. These vegetation classes have previously been shown to influence resource selection patterns of horses on Sable Island (van Beest et al. 2014), with horses showing a strong preference for grasslands compared to heathland when effects of density (competition) are controlled. For all spatial analyses here and below we used a geographical information system (ArcGIS 10.1, ESRI, USA).

Use of water

In addition to having mapped water ponds, each year we recorded the locations of excavated water holes, which were typically located in depressions (e.g. valleys and sand dune blow-outs) and were accessed and re-excavated over multiple years (Fig. 1, 2). We computed the mean distance in meters (m) of both water ponds and holes from vegetation associations. We quantified time costs for individual horses drinking at excavated water holes on Sable Island compared to horses drinking at permanent ponds (Fig. 2), as our conceptual model assumed that drinking from excavated holes would be more costly than drinking from ponds. To confirm this, we collected data on the duration of time spent drinking at either ponds or water holes for a series of focal observations in summer 2012 (93 drinking bouts from 55 horses: 32 at holes and 23 at ponds). We defined start of time spent drinking when a horse approached water and lowered its head to drink, and end of each drinking bout by a horse walking away or being forced away from the water by another individual. A complete start-end drinking cycle was considered a drinking bout, excluding instances of feeding on submerged vegetation. We compared individual times to finish drinking water (all bouts) at holes versus ponds using a *t*-test assuming unequal variances (square root-transformed data); and a Wilcoxon rank sum test for group drinking times, as the data could not be transformed to a normal distribution.

Resource selection functions (RSFs)

A powerful analytical approach to quantifying how animals select habitat and resources therein is the resource selection function (RSF; Manly et al. 2002). An RSF is typically defined as any function describing habitat or resource use that is proportional to the probability of use by an organism (Manly et al. 2002). A particular strength of the RSF modelling approach is that multiple continuous and categorical variables that influence selection can be incorporated simultaneously. We estimated RSFs for Sable Island horses

as a function of vegetation associations and distance to water sources (ponds, holes and both).

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

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

Because our RSFs were based on use-availability sampling designs (design III data; Thomas and Taylor 2006), we employed mixed-effect logistic regression to estimate coefficients (Gillies et al. 2006). For this, we used the 'lme4' package (Bates et al. 2014) in R (<www.r-project.org>). Our RSF analyses corresponded most closely to that of second-order selection (Johnson 1980). The application of distance-based models is preferred when analyzing resource selection for animals for which a central place can be identified because they incorporate potential spatial clustering of habitats surrounding the central place and, therefore, account for potential bias in selection estimates (Rosenberg and McKelvey 1999). To account for unbalanced data across years, we used year as a random intercept in each RSF (Gillies et al. 2006). We did not include Group ID as an additional random intercept or nesting within year as neither resulted in better models as determined by AIC. We evaluated predictive success of RSFs using the *k*-fold cross-validation procedure as proposed by Boyce et al. (2002). For this we calculated cross-validated Spearman rank correlations (r_s) between ten RSF-bin ranks and 10 test-training sets. We repeated this procedure

100 times to determine if the r_s was significantly different from random (*t*-test).

Horse density and distance to water

An assumption underlying our predictions is that water sources act as points of attraction (i.e. central places) in the landscape and that local density should decrease as distance from water increases. To confirm this, we calculated for each of the random points created for the RSF analysis (estimation of the available resources) distance to nearest water source and the type of water source (water hole, water pond, or both), and the local density of horses associated with each random point. We defined this local density from the count of horse centroids for the year associated with a random location contained within the 4000 m-radius buffer centered on that location, divided by the area of the buffer (horses km⁻²). To quantify relationships between local density and distance to water we computed a general additive mixed model using the 'mgcv' package (Wood 2006) in R. We used local density as the response variable and included class of water availability as a 3-level factor. In addition, distance to water was included as the smoothing parameter (i.e. the non-linear effect following a natural cubic spline relationship). We estimated the number of knots (k) using cross-validation. Here, k refers to the number of points by which the non-linear function is bent to pass, meaning that $k + 1$ is the number of intervals in the distance to water range where density is described by a different polynomial function. If $k = 1$ the relation is considered linear and no smoothing is applied. We used the year associated with the random location to estimate a random intercept.

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.rb3jp > (Rosen-Rechels et al. 2015).

Results

Focal horses (n = 23) drinking at ponds on Sable Island typically drank water in a single bout, with bouts lasting on average 135 ± 23 s ($\bar{x}$ ± SE) and most horses of a group drinking at or near the same time (Fig. 2). Focal horses (n = 32) drinking at excavated holes, however, typically queued to drink (Fig. 2) and often drank in multiple bouts (range 1–5). Mean (total) drinking time for a horse using an excavated hole was 633 ± 89 s. The difference in time spent drinking from holes versus ponds was significant among individuals ($t = -5.34$, DF = 35, p < 0.0001). Drinking bouts were ended by conspecifics in 23% of the observations at ponds but 45% of the observations at water holes. Focal horses drinking at holes were in groups of 2–6 horses ($\bar{x}$ = 3.8 individuals), and mean drinking time for a group was > 25 minutes 1510 ± 255 s [$\bar{x}$ ± SE]; median 1523 s). Focal horses at ponds were in 7 groups of 2–7 horses ($\bar{x}$ = 5.1 individuals). Average time for 9 groups to drink at ponds was less than 8 minutes (439 ± 132 s; median 420 s). Drinking times for groups at holes and ponds were significantly different (Wilcoxon rank sum test; $W = 10$, p = 0.026).

Horses only accessing excavated holes were, on average, located 754 ± 15 m ($\bar{x}$ ± SE) from water (SD = 844

m, range 0–4678 m, n = 5598 locations). Horses drinking from ponds only were located 879 m ± 16 m from water (SD = 1087 m, range to 4205 m, n = 5046 locations). Horses that were able to access both ponds and holes were located 281 ± 11 m from water (SD = 223 m, range 0–1664 m, n = 5266 locations). Local density (horses km⁻²) was greatest in areas with both holes and ponds (Fig. 3a), and declined in a linear fashion as distance from water increased ($k = 1$, $F = 74.2$, p < 0.001). Local density around water holes decreased non-linearly but steadily (Fig. 3b) as distance from water increased ($k = 2$, $F = 272.7$, p < 0.001). Local density around ponds showed a strong non-linear relation (Fig. 3c) with distance from the source ($k = 4$, $F = 635.4$, p < 0.001). Here, density decreased to just under 1000 m from ponds (2.4 to 1.5 horses km⁻², respectively), beyond which density increased, peaking at approximately 2500 m from water with densities slightly higher (2.7 horses km⁻²) than observed at ponds. The model explained 65.4% of the observed variation in local density of horses.

Irrespective of the water source, horses were found in heathland in the immediate vicinity of water more than expected from random and greater than that observed for the selection of grasslands (Fig. 4, Table 1). This was despite relatively close proximity of grasslands to both holes and ponds. Water holes (n = 45) were predominately excavated within or adjacent to grasslands (mean distance to nearest grassland 11 ± 4 m [$\bar{x}$ ± SE], 95% CI 4–18 m), though ponds (n = 30) were located farther (69 ± 9 m, 95% CI 49–88 m) from grasslands than were excavated holes.

The RSF for horses with access to water holes only (Table 1, Fig. 4a) showed that in the immediate vicinity of water, horses selected strongly for heathland while grasslands
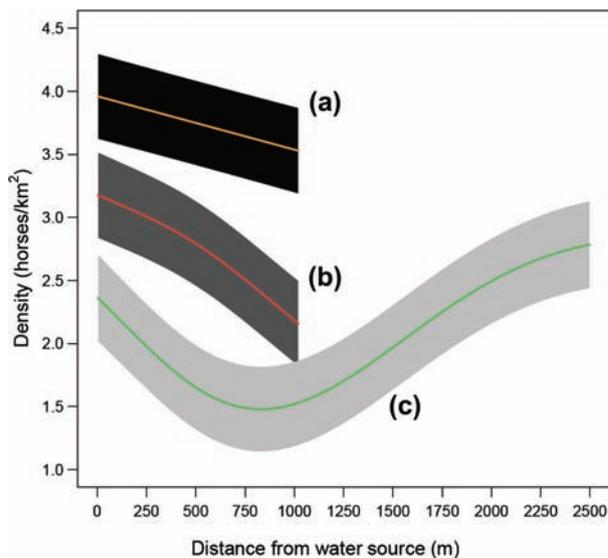
Figure 3. Predicted density of horses on Sable Island, Nova Scotia (horses per km² in a 4000 m buffer at a sampling point; years 2008–2013) as a function of distance to water source for horses with access to (a) both freshwater ponds and excavated holes; (b) water holes only; and (c) ponds only. Functions are plotted out along the *x*-axis to follow the 90th percentile of all horse observations with distance from water for each class of water availability. Lines are fitted means (± 95% confidence interval) of densities estimated with a generalized additive mixed model.
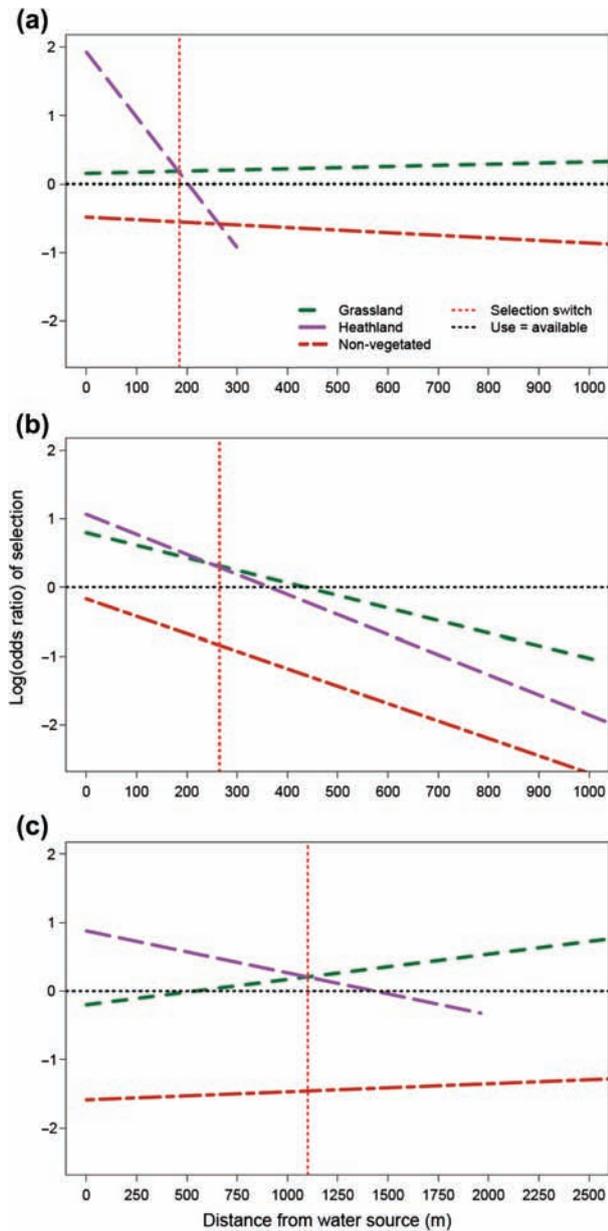
Figure 4. Estimates of resource selection functions (log odds ratio) for three vegetation associations used by Sable Island horses, 2008–2013, where horses accessed: (a) self-excavated water holes only; (b) water holes and ponds; and (c) ponds only. Estimates overlapping 0 (black dotted line) indicate that use of a vegetation association is proportional to its availability, whereas estimates higher than 0 indicate selection of a vegetation association relative to its availability; values below 0 indicate reduced selection of a vegetation association relative to its availability. The red-dotted, vertical line indicates the distance from a water source where a switch in selection occurs. Note the difference in scale on the *x*-axis between panels, which follows the 90th percentile of all horse observations with distance from water for each type of source (as in Fig. 3). Confidence intervals (95%) around regression lines were not drawn to facilitate plot interpretation but these are presented in Supplementary material Appendix 1 Fig. A1.

and non-vegetated areas were used in proportion to availability (95% CI of selection estimates overlapped with 0; Supplementary material Appendix 1 Fig. A1). A switch in selection from heathland to grassland was evident at approxi-

mately 165 m from water beyond which heathland was used less than available, while selection for grasslands increased (Fig. 4a). Selection for non-vegetated sites decreased as distance from water holes increased. The RSF showed good predictive performance (Spearman-rank correlation across 10 cross-validation sets was $r_s = 0.765$, p < 0.001).

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

The RSF for horses only accessing permanent ponds revealed that selection for grassland and heathland also changed with increasing distance from water, while selection for non-vegetated areas was low and remained stable, irrespective of changes in distance from water (Table 1, Fig. 4c, Supplementary material Appendix 1 Fig. A1). Similar to patterns found around water holes, horses selected for heathland in the direct vicinity of ponds whereas grasslands were used in proportion to availability. As distance from ponds increased the relative probability of using grasslands increased and use of heathland became proportional to availability. The switch in selection from heathland to grassland occurred at 1100 m from ponds, which is almost seven times farther than the observed selection switch point for horses using only water holes and four times farther than the observed selection switch point for horses using water holes and ponds. The pond-only RSF also had good predictive performance ($r_s = 0.763$, p < 0.001).

Discussion

Resource selection in the vicinity of water by feral horses on Sable Island showed signatures of both density-dependent habitat selection and central-place foraging. As predicted, horses concentrated the majority of their summer movements close to water, confirming that ponds and water holes act as points of attraction on the landscape. Our data suggest that local density and hence competition for food resources declined as distance from water increased, in all cases, for approximately the first 1000 m around the water source (Fig. 3). Although this is an important assumption of classical central-place foraging theory, which relies on exploitation of a resource around the central place prior to moving on to the next site, the pattern has rarely been quantified using empirical data on animal densities and resource selectivity. Consistent with our predictions, horses selected primarily for lower-quality heathland when in the vicinity of water where density constrained selection for higher-quality grassland and depletion of forage was likely (prediction 1).

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 × DW	0.0002	0.0002	−0.0002, 0.00059	0.258
	H × DW	−0.009	0.0007	−0.0104, −0.0076	<0.001
	N × 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 × DW	0.0005	0.0001	0.0003, 0.0008	<0.001
	H × DW	−0.0005	0.0002	−0.0008, −0.0002	0.007
	N × 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
	Hathland (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		

When horses moved away from water their selection patterns gradually shifted towards grassland, which we expected as the energetic costs of moving away from the central place increases while at the same time constraints presented by local density generally declines (supporting prediction 2). What is especially notable about our study, however, is that we also demonstrate how the shift in selection varied with the quality of the non-food resource defining the central place (freshwater pond versus excavated hole). Horses, and by extension groups, required much longer times to drink at water holes compared to ponds. The switch in selection from use of lower quality to higher quality vegetation as a function of distance to water occurred closer to water for horses drinking at self-excavated holes compared to ponds, with horses drinking at both water sources as an intermediate along this gradient (supporting prediction 3). Ours is the first study to our knowledge that explicitly accounts for density-dependent habitat selection by a grazing herbivore as it may be constrained by use of a centrally-placed, non-food resource (water).

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

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

gradient in water and vegetation on Sable Island (Contasti et al. 2012), we expected differences in vegetation among the three regions of water availability we mapped. Indeed, heathlands were more common where horses drank from ponds only (14.1%) and both holes and ponds (13.1%), compared to holes only (7.7%); and proportional availability of grasslands was inversely related to these values (30.2%, 43.5% and 50.2%, respectively). This likely influenced the elevation of slopes of the lines presented in Fig. 4; however, we do not believe that the shift in selection as a function of distance to water (and hence density) was spurious (our main conclusion). The mean distance of patches of heathland to water was 375 ± 663 m ($\bar{x} \pm$ SD) for horses drinking from ponds only, 396 ± 361 m from horses using both ponds and holes, and 379 ± 215 m for horses drinking from holes only – values too similar for a functional response to account for the striking shift in selectivity patterns with distance from water we observed (Fig. 4). The more likely explanation for our observation is a tradeoff in time available for horses to move and forage versus acquire water in each region. This shift seems to be apparent as the region of the island where both ponds and holes were available to horses (central Sable Island) produced results that were intermediate between regions where access to water was from ponds or holes only.

Central-place foraging is, at its core, a process of time management (Charnov 1976, Orians and Pearson 1979). Maximizing energy intake per unit foraging time as a currency of fitness is often assumed for central-place foragers (Lewison and Carter 2004). In this context, we believe the contrasting time budgets observed for horses drinking at different water sources are biologically important and may be conservative. Indeed, we did not measure group wait times prior to initiation of timed drinking sequences. We suspect these wait times at the periphery of active water holes (queuing) add considerably to time spent away from foraging, and so would exacerbate differences in time budgets for hole- versus pond-drinking horses. It may thus be that where horses are accessing water from holes versus ponds, acquisition of water, rather than energy, becomes the currency that horses must maximize on a daily basis to optimize fitness. This may be particularly true in summer (our sampling season) where lactating females must have regular access to water to provide for offspring (Berger 1986). The implications of this to the population dynamics of Sable Island horses are beyond the scope of this study, but different densities, sex ratios, and population dynamics across the length of Sable Island from west to east associated with the observed gradient in water availability have already been documented (Contasti et al. 2012, 2013, van Beest et al. 2014).

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

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

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