

Increasing density leads to generalization in both coarse-grained habitat selection and fine-grained resource selection in a large mammal

Floris M. van Beest¹, Antonio Uzal², Eric Vander Wal³, Michel P. Laforge²,
Adrienne L. Contasti², David Colville⁴ and Philip D. McLoughlin^{2,*}

¹Department of Animal and Poultry Science, College of Agriculture and Bioresources, University of Saskatchewan, 51 Campus Drive, Saskatoon, SK S7N 5E2, Canada; ²Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, SK S7N 5E2, Canada; ³Département de biologie, Université de Sherbrooke, 2500 boul. de l'université, Sherbrooke, QC J1K 2R1, Canada; and ⁴Applied Geomatics Research Group, Centre of Geographic Sciences, Nova Scotia Community College, Middleton, NS B0S 1P0, Canada

Summary

1. Density is a fundamental driver of many ecological processes including habitat selection. Theory on density-dependent habitat selection predicts that animals should be distributed relative to profitability of habitat, resulting in reduced specialization in selection (i.e. generalization) as density increases and competition intensifies.
2. Despite mounting empirical support for density-dependent habitat selection using isodars to describe coarse-grained (interhabitat) animal movements, we know little of how density affects fine-grained resource selection of animals within habitats [e.g. using resource selection functions (RSFs)].
3. Using isodars and RSFs, we tested whether density simultaneously modified habitat selection and within-habitat resource selection in a rapidly growing population of feral horses (*Equus ferus caballus* Linnaeus; Sable Island, Nova Scotia, Canada; 42% increase in population size from 2008 to 2012).
4. Among three heterogeneous habitat zones on Sable Island describing population clusters distributed along a west–east resource gradient (west–central–east), isodars revealed that horses used available habitat in a density-dependent manner. Intercepts and slopes of isodars demonstrated a pattern of habitat selection that first favoured the west, which generalized to include central and east habitats with increasing population size consistent with our understanding of habitat quality on Sable Island.
5. Resource selection functions revealed that horses selected for vegetation associations similarly at two scales of extent (total island and within-habitat zone). When densities were locally low, horses were able to select for sites of the most productive forage (grasslands) relative to those of poorer quality. However, as local carrying capacity was approached, selection for the best of available forage types weakened while selection for lower-quality vegetation increased (and eventually exceeded that of grasslands).
6. Isodars can effectively describe coarse-grained habitat selection in large mammals. Our study also shows that the main predictions of density-dependent habitat selection are highly relevant to our interpretation of RSFs in space and time. At low but not necessarily high population size, density will be a leading indicator of habitat quality. Fitness maximization from specialist vs. generalist strategies of habitat and resource selection may well be apparent at multiple spatial extents and grains of resolution.

Key-words: density dependence, *Equus ferus caballus*, feral horse, habitat selection, ideal-free distribution, individual-based study, isodar, resource selection function, scale, Sable Island

*Correspondence author. E-mail: philip.mcloughlin@usask.ca

Introduction

The process of habitat selection determines how organisms are distributed in space and time with consequences for population dynamics and interspecific interactions, evolution and eco-evolutionary dynamics (Brown & Rosenzweig 1986; Fortin, Morris & McLoughlin 2008; Morris 2011). Competition for space and resources has been shown to be an important driver of habitat selection at both the coarse (dispersal) and fine (foraging) grain (Morris 1992; McLoughlin *et al.* 2006; Fortin, Morris & McLoughlin 2008), which amplifies as population density increases. Considerable effort has been devoted to developing general theories of ‘density-dependent habitat selection’ to test and explain observed spatial heterogeneity in population densities and associated fitness consequences (Rosenzweig 1981, 1991; Morris 1987a, 2003; Morris & MacEachern 2010).

Strategies of habitat selection and their effects on fitness can be revealed by plots of density in contrasting habitats (i.e. using isolegs or isodars *sensu* Rosenzweig 1986; and Morris 1988; respectively). Within this framework, habitat is typically coarse-grained (Fortin, Morris & McLoughlin 2008) and is functionally defined as follows: ‘a spatially bounded area, with a subset of physical and biotic conditions, within which the density of interacting individuals, and at least one of the parameters of population growth, is different than in adjacent subsets (Morris 2003)’. Empirical constructs of isodars can be based on longitudinal observations of changes in densities between habitats (Haugen *et al.* 2006). Evidence supporting density-dependent habitat selection based on isoleg and isodar models has been found in insects (Krasnov, Khokhlova & Shenbrot 2003), fish (Rodríguez 1995; Haugen *et al.* 2006), birds (Shochat *et al.* 2005), mammals (Ramp & Coulson 2002; Ale *et al.* 2011) and plants (Gersani, Abramsky & Falik 1998).

An alternate and increasingly popular approach to quantifying spatial and temporal variation in the distribution of species is the resource selection function (RSF), which models the disproportionality between use and availability of a resource unit (Boyce & McDonald 1999; Manly *et al.* 2002; Aarts *et al.* 2008). Within the RSF framework, use of habitat is almost always fine-grained (Fortin, Morris & McLoughlin 2008; McLoughlin *et al.* 2010) as most studies are based on fine-resolution data such as that collected with Global Positioning System (GPS)-tracking devices (Moorcroft & Barnett 2008; Mobæk *et al.* 2009; van Beest *et al.* 2010). Here, we are interested in how individual survival and reproduction respond to the subsets of biotic and abiotic conditions within habitats that are directly used, and competed for, by a group of individuals (Morrison & Hall 2002; Prins, de Boer, & van Langevelde 2008). That is, RSF studies generally entail selection for resources (e.g. vegetation association, foraging patch) and/or resource modifiers (e.g. distance to water, elevation) that occur at sites

(points or pixels in space) embedded within a habitat [as defined by Morris (2003)].

Irrespective of grain, RSFs may be quantified across a range of spatial scales or extents of study (Wiens 1989; Kotliar & Wiens 1990; Dungan *et al.* 2002). RSFs are powerful tools to study scale-dependent ecological processes related to habitat selection, including species interactions (Johnson *et al.* 2000), sexual segregation (Loe *et al.* 2006) and foraging strategies (Bastille-Rousseau, Fortin & Dussault 2010). Recently, RSFs have also been used to infer fitness consequences of habitat use (McLoughlin *et al.* 2006), termed fitness–habitat or habitat–performance relationships (McLoughlin *et al.* 2007; Gaillard *et al.* 2010). Rarely, however, are RSFs used to explicitly incorporate or test for effects of competition on selection patterns (McLoughlin *et al.* 2010). The few RSF-based studies that have addressed the influence of density on resource selection provide contrasting results with evidence in favour [e.g. domestic sheep (*Ovis aries* Linnaeus), Mobæk *et al.* 2009] and against [e.g. woodland caribou (*Rangifer tarandus caribou* Banfield), Johnson & Seip 2008; moose (*Alces alces* Linnaeus), Herfindal *et al.* 2009] the general expectations of competition on how habitat is used (Rosenzweig 1981, 1991; Morris 1996, 2003).

Due to its central position in ecology and evolution, theory on density-dependent habitat selection would benefit from additional tests using free-ranging populations (Morris & MacEachern 2010). Here we test the primary theoretical prediction that because organisms should distribute themselves relative to the profitability (i.e. fitness return) of habitat, we should observe more even use of habitats and/or their resources when population density increases due to the inclusion of habitat and resources of lower quality (Rosenzweig 1981, 1991; Morris 1988, 2003). Our main interest is in determining the extent to which increasing population density can simultaneously modify habitat selection and multivariable resource selection within habitats. To do so, we constructed both coarse-grained isodars and fine-grained RSF models for a population of free-ranging feral horses on Sable Island, Canada, during a period of rapid population growth (42% increase in island density from 2008–2012).

We considered both extent (size of area surveyed) and grain (size of the sample unit) in our analyses. First, we tested whether coarse-grained habitat selection was evident across three habitat regions or zones present on the island. These habitat zones were characterized by an underlying resource gradient of water availability and vegetation that also reflected subpopulation clustering (Contasti *et al.* 2012) with differences between the west, central and east regions of Sable Island (Fig. 1), and among which density and population growth varied. If density influences coarse-grained habitat selection, we expected that at lower population density, individuals would first occupy the high-quality west before dispersing to lower-quality habitat in the central and east zones, as

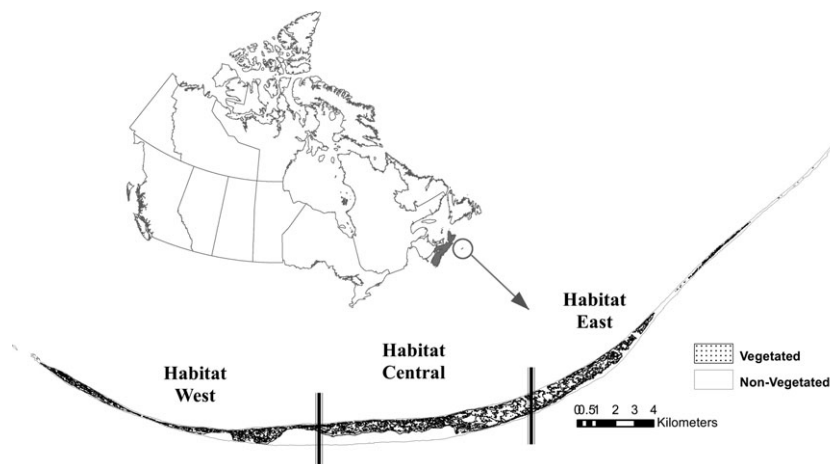


Fig. 1. Map of Sable Island National Park Reserve and its geographical position relative to Nova Scotia, Canada. Horizontal lines delineate three habitat zones distributed along a west–east gradient in water and forage availability that also reflect three subpopulation clusters of feral horses as identified by Contasti *et al.* (2012).

revealed by population growth rates (distance to local carrying capacity) and plots of changes in densities among habitat zones through time, that is, using habitat isodars (Prediction 1). If isodars suggest density dependence, we might also observe density effects in fine-grained RSFs estimated with GPS-referenced locations of individual horses. We therefore expected the relative probability of selection for good foraging resources (vegetation communities such as grasslands) to be highest where population growth rate remained greatest (for animals farthest from local carrying capacity) and selection to become more generalized (i.e. reduced selection for higher-quality vegetation communities and greater selection for lower-quality vegetation communities) where population growth rate was lowest (Prediction 2). We also expected that density effects would be evident across time (years of progressive population growth) at two extents: (i) the island-wide scale; and (ii) the within-habitat (zone) scale. That is, horses would reduce their selection for the best of available resources as local density increased (Prediction 3).

Materials and methods

STUDY AREA

Sable Island National Park Reserve (43°55'N, 60°00'W) is a crescent-shaped sand bar located approximately 275 km east of Halifax, Nova Scotia, Canada (Fig. 1). It is 49 km long and 1–25 km at its widest point. The island's climate is temperate oceanic with cool summers and wet winters. The island is comprised of wide, sandy beaches and vegetated and bare sand dunes up to 30 m in height. Sable Island is treeless, and the vegetation community is dominated by American beach grass, or marram (*Ammophila breviligulata* Fernald), which occurs throughout most of the vegetated parts of the island. Shrub-dominated heath (*Empetrum nigrum* Linnaeus, *Juniperus communis* Linnaeus, *Myrica pensylvanica* Mirbel, *Rosa virginiana* Miller, *Vaccinium angustifolium* Aiton) is the climax vegetation association found on

Sable Island. The west side of the island also contains high-quality patches of sandwort (*Honckenya peploides* Linnaeus) and beach pea (*Lathyrus japonicus* Willdenow var. *maritimus*) which are not as abundant in other regions. In addition, the west contains permanent water ponds and their associated emergent plants that are less common in the centre of the island and absent in the east, where horses must excavate wells to obtain water in summer (Lucas *et al.* 2009; Contasti *et al.* 2012).

Originally introduced to Sable Island in the mid-1700s, the horses have always been free-ranging with minimal interference by humans. The Sable Island horse presents a markedly distinct genetic structure from other horse breeds and is most closely related to the Nordic breeds of horses and ponies (Plante *et al.* 2007; Prystupa *et al.* 2012). Feral horses exhibit a mating system characterized by female-defence polygyny with persistent, non-territorial breeding groups (bands) and transitory mixed adolescent or bachelor groups (Linklater *et al.* 2000). Aside from a small human presence (researchers and tourists), the horses are the only terrestrial mammals on the island.

SAMPLING

We obtained direct observations ($n = 10249$) of individual horses [375, 425, 484, 450 and 534 individuals in years 2008 through 2012, respectively (42% increase in total population size)] via systematic ground censuses of the entire horse population on Sable Island (weekly observations from July–September). During censuses, we approached horses, which were largely ambivalent to humans, to within a few meters and recorded the location of each individual using a hand-held GPS with location error to within 5 m, the horse's identity (verified using digital photographs), sex, reproductive status and group membership. We assumed the absence of a horse from the island between years as evidence of mortality. We evaluated whether censuses were adequate (i.e. if we sampled all horses present on the island) by comparing, for 2010 data, our summer counts of nonfoals (yearlings and older) with that obtained from high-resolution aerial photography in April 2010 (prior to the season of births). This confirmed that our summer census in 2010 accounted for >99% of the horses present in April. Because field procedures were standardized

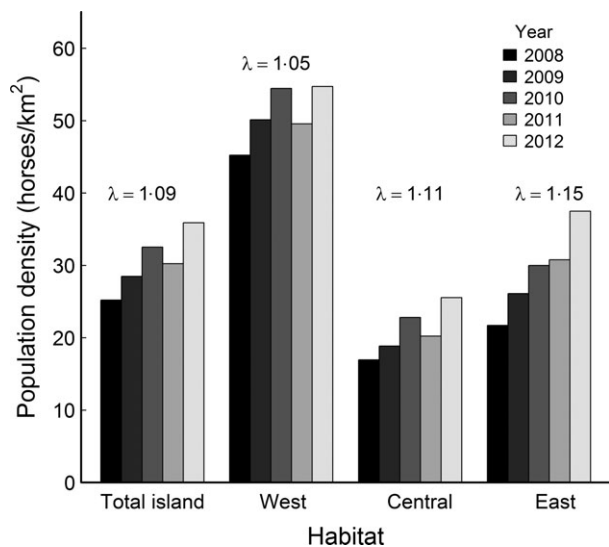


Fig. 2. Annual densities and annualized finite rate of population increase (λ) for the total island and three habitat zones (west, central and east) for feral horses on Sable Island, Canada, 2008–2012.

across years, we assumed that the censuses in other years were equally adequate.

In each year, we determined the island-wide population density (Fig. 2) as the total number of horses per km² of vegetated area (size of vegetated area did not change over time). We also estimated the finite rate of population increase (λ) by dividing the population size at year $t + 1$ by that of the year previous (N_{t+1}/N_t) and calculated the geometric mean across years, where values of $\lambda > 1.0$ indicate population growth, $\lambda < 1.0$ indicate population decrease, and $\lambda = 1.0$ indicate population stability (Caswell 2001). In addition to an island-wide analysis, we computed densities and rate of population increase for the three habitat zones: west, central and east (Fig. 1). These zones were delineated based on a hierarchical cluster analysis of surface water availability and a vegetation indicator–species analysis (presented in Contasti *et al.* 2012), as both water availability and forage are known to influence movements of horses (Rubenstein 1981; Berger 1986). Zones exclusively contained within-summer movements of monitored females (Contasti *et al.* 2012). However, over-winter movements by feral horses between habitat zones occurred following temporal changes in local population density (see Table 3 of Contasti *et al.* 2012), which is an important underlying assumption of density-dependent habitat selection (Rosenzweig 1981; Morris 1987b). For example, among habitat zones, immigration of females added 0.038–0.24 to the finite rate of population increase (λ) determined by resident birth and death rates alone (females only 2008–2010; Contasti 2011), with immigrants numbering 2–15 females per zone and emigrants ranging from 3–10 (Contasti *et al.* 2012).

ISODARS

The application of isodars to habitat selection fundamentally adopts a coarse-grained picture of habitat (Fortin, Morris & McLoughlin 2008). Habitat isodars (i.e. lines depicting response of density in one habitat vs. another) can apply in several instances, including ideal-free habitat selection for diverging fitness functions; ideal-free habitat selection for converging fitness

functions; and ideal-despotic habitat selection where territorial individuals depress the expected fitness of individuals in each habitat (McLoughlin *et al.* 2010). The isodar for a population distributed across two habitats, A and B, is plotted as the density in A (y-axis) vs. density in B (x-axis). If A and B are in all respects identical, with no cost to move between them, the isodar will have an intercept of zero and a slope of unity (Morris 1987b, 1988). When growth occurs first in one habitat over another, the habitat isodar will have a nonzero intercept and the habitat selection process is considered density dependent; the intercept is proportional to the basic differences in average fitness between the two habitats at low density (Morris 1992). If the slope remains at 1.0, there are no density-related costs between moving from habitats A and B to minimize competition (Morris 1987b, 1988), that is, conventional ideal-free distribution (Fretwell & Lucas 1969). A slope < 1.0 implies that an equal increase in density between habitats will have greater fitness costs in habitat (A) than habitat (B). If the slope is > 1.0 , the fitness costs are less severe (Morris 1987b, 1988).

We estimated coarse-grained habitat selection by constructing habitat isodars using repeated measures of horse density across five years for paired, western (y-axis) and eastern (x-axis) habitat zones (i.e. west vs. east, west vs. central, and central vs. east). Our isodars (simple linear regressions) were constructed with little measurement error as densities were based on census counts; they thus reflect effects of only process variation on densities and population growth rates of horses across the length of Sable Island.

RESOURCE SELECTION FUNCTIONS

We estimated fine-grained RSFs as a function of vegetation associations and population density. We used vegetation data derived from 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, Canada. We integrated the map into a Geographical Information System (GIS) and re-classified the vegetation into three major vegetation associations (types) according to the value of forage for horses on Sable Island following Welsh (1975). These included the following: (i) grasslands of marram and other forage species, containing sandwort and beach pea where present (forage production: 800–1566 g m⁻²); (ii) heathlands of woody shrubs and some grasses (forage production: 53–529 g m⁻²); and (iii) ‘nonvegetated’ areas which included sand dunes and beaches with minimal coverage of plants. 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. As such, we did not consider functional responses in resource selection in our RSFs (*sensu* Mysterud & Ims 1998), or explicit effects of rare vegetation types such as sandwort or beach pea, or continuous variables such as elevation or distance to water.

We first constructed an RSF considering the total population on the island (i.e. a population-scale RSF). Here, resource (vegetation) availability was estimated, for each year separately, by drawing a random sample of points from the total island. The number of available points equalled the number of points used by all individuals on the island. Numbers of used points at this scale were 880, 2169, 2258, 1262 and 3664 for years 2008 through 2012, respectively. We also constructed separate RSFs for each of the three habitat zones as described above. Here, resource avail-

ability was estimated for each year separately by drawing a random sample of points from within each habitat zone (Fig. 1), and again the number of available points selected equalled the number of points used. Sample sizes of used points (for 2008 through 2012, respectively) for horses in the west were as follows: 481, 1314, 1004, 551 and 1918; for central: 315, 593, 1038, 501, 1417; and for east: 171, 262, 547, 352 and 721. Our RSF analyses corresponded most closely to that of second-order selection (Johnson 1980). The dependent variable in our RSF models consisted of a binomial variable with used (1) and available (0) locations, and the independent variables consisted of (i) vegetation association (a three-level factor as described above); (ii) density (a continuous variable); and (iii) the interaction between vegetation association and density. Because our RSFs were based on use–availability sampling designs (design III data; Thomas & Taylor 2006), we employed mixed-effect logistic regression models and adopted the extension of the fixed effect, exponential RSF by Manly *et al.* (2002), as proposed by Gillies *et al.* (2006) and highlighted by McLoughlin *et al.* (2010). To account for unbalanced data across years and within-habitat zones, we used habitat zone nested within year as a random intercept for the island-wide RSF, while the habitat zone-specific RSFs included a random intercept for year only. We evaluated predictive success of all 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 five test-training sets. We repeated this procedure 100 times to determine whether the r_s was significantly different from random. We performed all analyses in R (R Development Core Team 2012).

Results

ISLAND-WIDE AND WITHIN-HABITAT POPULATION GROWTH

Population growth (all sex and age classes combined) on the island was rapid, increasing on an annualized basis as $\lambda = 1.09$ from 2008 to 2012. Annual growth was heterogeneous between regional habitat zones, being lower in the high-density habitat in the west ($\lambda = 1.05$) compared with central ($\lambda = 1.11$) and east ($\lambda = 1.15$) zones over the five years of study (Fig. 2). This result satisfied the underlying assumption for coarse-grained habitat selection that at least one of the parameters of population growth should differ from adjacent habitats.

COARSE-GRAINED HABITAT SELECTION

Isodars with western- and eastern-habitat pairings (Fig. 3) indicated that at low density, individuals should first occupy the west habitat; however, as density increases, individuals should increasingly move and/or recruit into the central and east regions of Sable Island. The initial preference of horses to occupy the west is suggested because when it is included as the *y*-variable, the isodar intercept is always substantially greater than zero [isodar intercept (SE) for west vs. central: 27.90 (5.30), $P = 0.014$, $R^2 = 0.86$; and west vs. east: 34.47 (6.66), $P = 0.014$, $R^2 = 0.67$]. Hence, at low island-wide density, individuals

are predicted to select almost exclusively for the western habitat. The habitat isodar for central–east suggests that the central habitat must be selected first before east; however, the intercept did not differ from 0 [isodar intercept (SE) for central vs. east: 4.94 (3.13), $P = 0.218$, $R^2 = 0.90$]. The slope of the west–central habitat isodar did not differ from 1.0 [β (CI) = 1.093 (1.587, 0.598)], suggesting that density-related fitness costs in selecting for west over central habitat was relatively low. In contrast, the slopes of the west–east and central–east habitat isodars were both <1.0 [β (CI) = 0.556 (0.995, 0.332) and 0.546 (0.755, 0.366)], indicating that density-dependent fitness costs are greater in west and central habitat zones relative to the east (i.e. horses are not classically ideal-free distributed on Sable Island).

FINE-GRAINED RESOURCE SELECTION

The island-wide RSF revealed that the relative probability of selection for grassland and poorer-quality heathland changed with increasing population density, while selection for nonvegetated areas was low and remained stable, irrespective of changes in population density (Table 1; Fig. 4). At the lowest observed population density, selection favoured grasslands over poorer-quality heathland ($\beta_{\text{heathland}} = -1.676 \pm 0.376$ [SE], $P < 0.001$; Table 1). However, when population density increased, selection for grassland was reduced (though not significantly; $\beta_{\text{grassland} \times \text{density}} = -0.016 \pm 0.009$, $P = 0.095$), while selec-

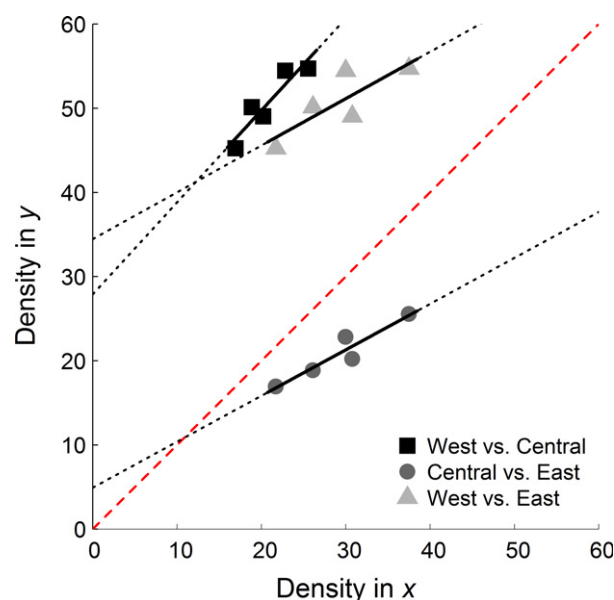


Fig. 3. Habitat isodar regression lines (slope and intercept with SE in brackets) from pairwise east (*x*) and west (*y*) combinations of habitat densities of feral horses on Sable Island, Canada, 2008–2012. Dashed line through the origin represents a habitat isodar with a slope of 1.0. See text for interpretation of slopes and intercepts described by isodar linear equations. Regression lines were fitted as simple linear models.

Table 1. Summary of the population-level RSF model predicting feral horse resource selection during summer as a function of vegetation association and density on Sable Island, Canada, 2008–2012. Habitat zone is nested within year as a random intercept to account for unbalanced data across years and regional habitat differences along the length of Sable Island (Fig. 1)

RSF variable	β	SE	z -value	P -value
Vegetation association				
Grassland (Intercept)	0.896	0.304	2.949	0.003
Heathland	-1.676	0.376	-4.464	<0.001
Nonvegetated	-1.901	0.299	-6.340	<0.001
Density	-0.016	0.009	-1.669	0.095
Vegetation association \times Density ^a				
Heathland \times Density	0.058	0.012	4.991	<0.001
Nonvegetated \times Density	0.016	0.009	1.718	0.086
Random effects				
Year Habitat zone	Var	SD		
	0.011	0.106		

^aReference category is Grassland. RSF, resource selection functions.

tion for heathland strongly increased ($\beta_{\text{heathland} \times \text{density}} = 0.058 \pm 0.012$) and was selected most at highest observed population size (Fig. 4). The population-scale RSF had good predictive performance (Spearman rank correlation across five cross-validation sets was $r_s = 0.770$, $P < 0.001$).

In general, the within-habitat zone RSFs revealed similar patterns in vegetation selection compared with the island-wide RSF. For example, at the lowest observed local densities, selection was always higher for grassland than for poorer-quality heathland, and selection for non-vegetated areas was typically lowest in all habitats and densities (Table 2; Fig. 4). However, as densities increased within habitats, subtle differences in resource (i.e. vegetation association) selection patterns became evident. Selection for grassland decreased strongly with increasing density, but only in the west ($\beta_{\text{grassland} \times \text{density}} = -0.040 \pm 0.011$ SE, $P < 0.001$) where population densities were highest and growth rates slowest (Fig 2). In central Sable Island, where local density was lower and population growth higher (Fig. 2), selection for grassland decreased slightly with increasing density though not significantly ($\beta_{\text{grassland} \times \text{density}} = -0.014 \pm 0.011$ SE, $P = 0.211$). In the east, where local density was also low and population growth fastest (Fig. 2), selection for grassland remained stable and high irrespective of increasing local density (Fig. 4). Selection for heathland typically increased with increasing local densities (west: $\beta_{\text{heathland} \times \text{density}} = 0.076 \pm 0.018$, $P < 0.001$; central: $\beta_{\text{heathland} \times \text{density}} = 0.047 \pm 0.022$, $P = 0.029$) although

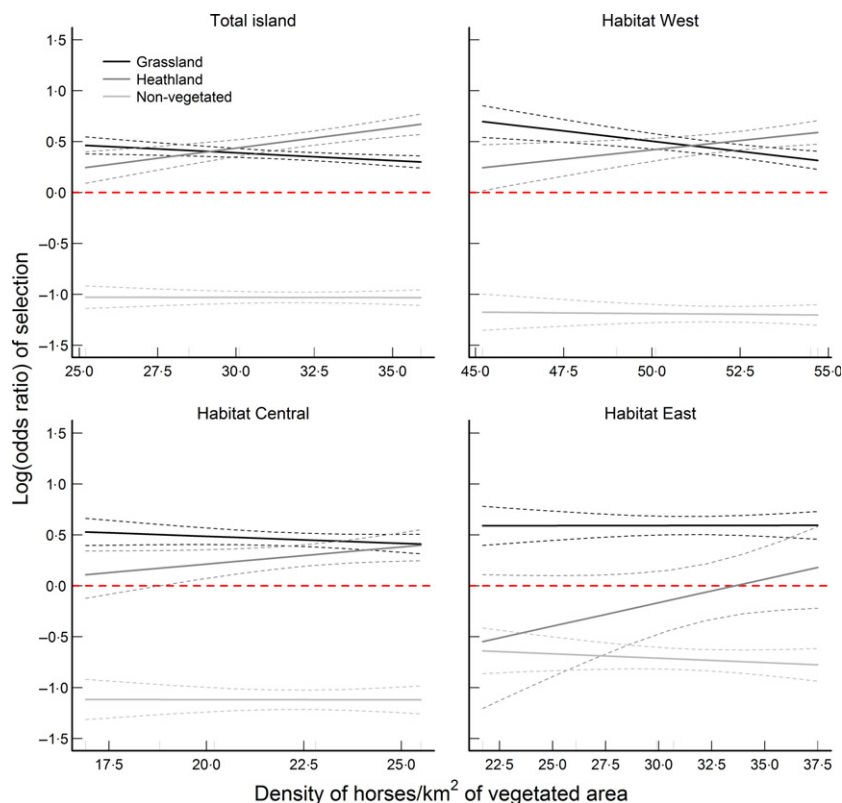


Fig. 4. Estimates of resource selection functions (log odds ratio \pm 95% confidence intervals) for two extents: total island and within-habitat zone (west, central and east) over five consecutive years with increasing population densities of feral horses on Sable Island, Canada, 2008–2012. Estimates overlapping 0 (dashed line) indicate that proportional use of a vegetation association is relative to its availability, whereas estimates higher than 0 indicate higher selection of a vegetation association relative to its availability, and values below 0 indicate lower selection of a vegetation association relative to its availability. Observed densities are indicated in grey lines on the x-axis.

Table 2. Summary of the within-habitat zone RSF models (west, central and east; Fig. 1), predicting feral horse resource selection during summer as a function of vegetation association and density on Sable Island, Canada, 2008–2012

Habitat	RSF variable	β	SE	z-value	P-value
West	Vegetation association				
	Grassland (Intercept)	2.518	0.582	4.328	< 0.001
	Heathland	-3.904	0.964	-4.049	< 0.001
	Nonvegetated	-3.555	0.848	-4.018	< 0.001
	Density	-0.040	0.011	-3.593	< 0.001
	Vegetation association \times Density ^a				
	Heathland \times Density	0.076	0.018	4.135	< 0.001
	Nonvegetated \times Density	0.037	0.016	2.282	0.022
	Random effects	Var	SD		
	Year	0.001	0.019		
Central	Vegetation association				
	Grassland (Intercept)	0.764	0.249	3.060	0.002
	Heathland	-1.222	0.495	-2.473	0.013
	Nonvegetated	-1.874	0.443	-4.232	< 0.001
	Density	-0.014	0.011	-1.249	0.211
	Vegetation association \times Density ^a				
	Heathland \times Density	0.047	0.022	2.174	0.029
	Nonvegetated \times Density	0.013	0.019	0.686	0.493
	Random effects	Var	SD		
	Year	0.024	0.037		
East	Vegetation association				
	Grassland (Intercept)	0.581	0.291	2.000	0.045
	Heathland	-2.142	0.976	-2.195	0.028
	Nonvegetated	-1.039	0.437	-2.379	0.017
	Density	0.0003	0.009	0.037	0.971
	Vegetation association \times Density ^a				
	Heathland \times Density	0.046	0.029	1.542	0.123
	Nonvegetated \times Density	-0.008	0.013	-0.642	0.521
	Random effects	Var	SD		
	Year	0.009	0.022		

^aReference category is Grassland. RSF, resource selection functions.

the relative probability of selection for heathland in the east habitat zone did not differ from availability as local density increased ($\beta_{\text{heathland} \times \text{density}} = 0.046 \pm 0.029$, $P = 0.123$). Predictive performance of the within-habitat RSFs was good [$r_s = 0.827$, $P < 0.001$ (west); $r_s = 0.857$, $P < 0.001$ (central); and $r_s = 0.781$, $P < 0.001$ (east)].

Discussion

Heterogeneity in density and population growth for horses on Sable Island resulted in habitat isodars consistent with the hypothesis that competition influences coarse-grained habitat selection (Prediction 1). Isodar intercepts and slopes were indicative of processes other than density-independent movements across the island. Horses clearly selected for the west habitat zone followed by the central and east habitats. Observed patterns imply that the west contains more resources to sustain higher densities compared with other regions of the island. This is supported by the finding that most available fresh water (and emergent pond vegetation) occurs in western Sable Island, in addition to high-quality patches of sandwort and beach pea (Contasti *et al.* 2012). Our results also sug-

gest that as density increases, horses are not entirely free to move among habitats. Observed patterns are more indicative of a 'spill-over' pattern of source-sink theory (Holt 1985; Pulliam 1988), as individuals are expected to first populate the west (source) habitat prior to dispersing to poorer-quality habitat in the centre and east of Sable Island. Deviations from classical ideal-free distribution are not uncommon in large herbivore populations and should perhaps be expected as large-scale movements for herbivores are not likely to be free of cost (Coulson *et al.* 1997; Pettoelli *et al.* 2003; McLoughlin *et al.* 2006).

Fine-grained RSF models also suggested that relative use of available vegetation was influenced by density at both the island-wide and within-habitat scales of analysis. Supporting Prediction 2, when densities were low, horses selected the most productive vegetation association available (i.e. grasslands; Fig. 4). The ability of horses to select grassland over all other associations was also strongest where population growth was fastest (i.e. density farthest from local carrying capacity) in the east (Fig. 4). In addition, we were able to detect strong effects of temporal increases in density on fine-grained selection patterns. For example, as densities increased over time, selection for high-quality grasslands decreased at the scale of the total

island and in the west zone. In contrast, selection for lower-quality heathland typically increased across the island and within all habitat zones with increasing population density.

We considered that it was possible temporal changes other than density might have influenced this result, such as stochasticity in forage availability or carry-over depletion in forage. However, in contrasting RSFs built using data only from years of higher vs. lower (2010 vs. 2011) and equal density (2009 vs. 2011), we could not detect patterns inconsistent with density-dependent resource selection (Fig. S1, Supporting information). Although forage depletion can be a major factor in resource selection when population densities increase, its effect on resource selection is most pronounced during winter and less in summer (as in this study), when forage resources are continuously replenished after consumption (van Beest *et al.* 2010). Only in the lower-density central and eastern areas was strong selection for grassland still possible at the highest observed local densities (and, in the east, heathland not selected). These patterns indicate that horses reduce selection for the best of available resources as (local) density increases (supporting Prediction 3), while at the same time, selection for lower-quality forage resources increases. We conclude that increases in local density (i.e. competition) led to a generalization in resource selection, as expected from density-dependent habitat selection (Rosenzweig 1981, 1991; Morris 1987b, 2003).

Our confirmation of density-dependent habitat/resource selection in a large mammal, at multiple scales and extents, and across time, has important implications for species conservation and management. Of foremost concern is the strong effect of density on the generalization of resource selection. For example, our results suggest that RSFs for populations close to local carrying capacity may lead researchers and managers to erroneously draw conclusions about resource preference and habitat quality (if density effects are not explicitly taken into account). Indeed, resources that are selected most strongly are often considered to be of highest quality. However, selection reflects quality of a resource, or an organism's 'first choice', only when all other conditions are equal (Thomas & Taylor 2006). As such, without knowledge of density effects on selection, low-quality resources may be interpreted to be of higher value for a species than they really are. In our case, grasslands are clearly the preferred resource when local density was lowest. But if we were to only examine resource selection at high density, we could easily conclude that the poorer-quality resource (heathlands) is the preferred resource for horses (e.g. if we took a snapshot view of the west RSF at highest density). Further, only by assessing habitat selection at both the fine and coarse grains is it apparent that the most valuable habitat for Sable Island horses is likely found in the west, which supports densities twice that of the central and east areas. With knowledge of distance from carrying capacity, density appears to be the leading indicator of habitat quality as opposed to the misleading indicator it is referenced so

often (e.g. after Van Horne 1983). Our results also have implications for understanding of the evolution of generalists and specialists in heterogeneous environments, as our data suggest that generalizing strategies of coarse-grained habitat selection and fine-grained resource selection should be favoured concomitantly as density increases. We note that the fitness-maximizing result of abandoning preferred grasslands at high density for female red deer (*Cervus elaphus* Linnaeus) of the Isle of Rum (McLoughlin *et al.* 2006; Fortin, Morris & McLoughlin 2008) is supported by our finding that horses reduced selection for high-quality grasslands at high density on Sable Island.

Our study clearly demonstrates density dependence in fine-grained models of resource selection for a free-ranging large mammal. Other researchers working with density effects on RSFs have failed to detect responses (Johnson & Seip 2008; Herfindal *et al.* 2009); however, we note that we would not have detected density dependence in our RSF if we had three or less years of data. A lack of density effects in RSFs may be the result of several factors, including too short a study period or lack of large enough change in (local) population density, or because effects of density on fine-grained resource selection are modified by density-independent factors, such as weather (Mobæk *et al.* 2009). One of the few published studies that tested for density-dependent resource selection patterns at a comparable extent of analysis to our study was carried out for an island-based population of moose in Norway (Herfindal *et al.* 2009). Here, the authors attributed the lack of density dependence in RSF patterns to favourable environmental conditions and high population growth rates (Sæther *et al.* 2007; Herfindal *et al.* 2009).

We show that density affected horse movements at both the coarse and fine grain, and in a similar manner, whereby generalization of habitat and resource selection is the consequence of increasing density. What is notable about this finding is that theory on density-dependent habitat selection has almost exclusively been supported with empirical data under constructs of the original models of density-dependent habitat selection, using isodars as opposed to RSFs. We show that density dependence can and does apply to the fine-grained world of the multivariable RSF in a manner similar to what is expected from coarse-grained models of habitat selection. Our results have implications for understanding when and where density might accurately reflect habitat quality for species, and how density might influence selection for specialist vs. generalist strategies of both habitat and resource use.

Acknowledgements

We thank S. Medill, S. Simpson, J. Weisgerber, P. Marjamaki, E. Tissier, K. Lysak, A. Sovie, J. McMillan, D. Bowen, N. den Heyer, S. Smith, G. Forbes and Z. Lucas for assisting in the fieldwork and/or providing logistics for this project. All work was carried out following University of Saskatchewan Animal Care Protocol 20090032 and under guidance of the Canadian Council on Animal Care. The project was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC), the Canada Foundation for Innovation, PrioNet Canada, the University of

Saskatchewan and donations in memory of A. Eisler to the Friends of Sable Island Society. In-kind and logistical support was provided by Parks Canada Agency and Fisheries and Oceans Canada including Canada Coast Guard and the Bedford Institute of Oceanography (DFO Science), Environment Canada, Maritime Air Charters Limited and Sable Island Station (Meteorological Service of Canada). Mapping was provided with assistance of A. Muise and the Sable Island Preservation Trust. We also thank D. W. Morris and B. Kotler for helpful discussions on the intricacies of density-dependent habitat selection and two anonymous referees for helpful comments that greatly improved a previous version of the manuscript.

References

- Aarts, G., MacKenzie, M., McConnell, B., Fedak, M. & Matthiopoulos, J. (2008) Estimating space-use and habitat preference from wildlife telemetry data. *Ecography*, **31**, 140–160.
- Ale, S.B., Morris, D.W., Dupuch, A. & Moore, D.E. (2011) Habitat selection and the scale of ghostly coexistence among Arctic rodents. *Oikos*, **120**, 1191–1200.
- Bastille-Rousseau, G., Fortin, D. & Dussault, C. (2010) Inference from habitat-selection analysis depends on foraging strategies. *Journal of Animal Ecology*, **79**, 1157–1163.
- van Beest, F.M., Myrsterud, A., Loe, L.E. & Milner, J.M. (2010) Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. *Journal of Animal Ecology*, **79**, 910–922.
- Berger, J. (1986) *Wild Horses of the Great Basin: Social Competition and Population Size*. University of Chicago Press, Chicago, Illinois, USA.
- Boyce, M.S. & McDonald, L.L. (1999) Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution*, **14**, 268–272.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002) Evaluating resource selection functions. *Ecological Modelling*, **157**, 281–300.
- Brown, J.S. & Rosenzweig, M.L. (1986) Habitat selection in slowly regenerating environments. *Journal of Theoretical Biology*, **123**, 151–171.
- Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Contasti, A.L. (2011) *Structure in vital rates, internal source-sink dynamics, and their influence on current population expansion for the feral horses (Equus Ferus Caballus) of Sable Island, Nova Scotia*. MSc thesis, Department of Biology, University of Saskatchewan, SK.
- Contasti, A.L., Tissier, E.J., Johnstone, J.F. & McLoughlin, P.D. (2012) Explaining spatial heterogeneity in population dynamics and genetics from spatial variation in resources for a large herbivore. *PLoS One*, **7**, e47858.
- Coulson, T., Albon, S., Guinness, F., Pemberton, J. & Clutton-Brock, T. (1997) Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus*). *Ecology*, **78**, 852–863.
- Dungan, J.L., Perry, J.N., Dale, M.R.T., Legendre, P., Citron-Pousty, S., Fortin, M.J. *et al.* (2002) A balanced view of scale in spatial statistical analysis. *Ecography*, **25**, 626–640.
- Fortin, D., Morris, D.W. & McLoughlin, P.D. (2008) Habitat selection and the evolution of specialists in heterogeneous environments. *Israel Journal of Ecology & Evolution*, **54**, 311–328.
- Fretwell, D.S. & Lucas, H.L. (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, **19**, 16–32.
- Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M. *et al.* (2010) Habitat-performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2255–2265.
- Gersani, M., Abramsky, Z. & Falik, O. (1998) Density-dependent habitat selection in plants. *Evolutionary Ecology*, **12**, 223–234.
- Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L. *et al.* (2006) Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, **75**, 887–898.
- Haugen, T.O., Winfield, I.J., Vollestad, L.A., Fletcher, J.M., James, J.B. & Stenseth, N.C. (2006) The ideal free pike: 50 years of fitness-maximizing dispersal in Windermere. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 2917–2924.
- Herfindal, I., Tremblay, J.P., Hansen, B.B., Solberg, E.J., Heim, M. & Saether, B.E. (2009) Scale dependency and functional response in moose habitat selection. *Ecography*, **32**, 849–859.
- Holt, R.D. (1985) Population-dynamics in 2-patch environments – some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology*, **28**, 181–208.
- Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65–71.
- Johnson, C.J. & Seip, D.R. (2008) Relationship between resource selection, distribution, and abundance: a test with implications to theory and conservation. *Population Ecology*, **50**, 145–157.
- Johnson, B.K., Kern, J.W., Wisdom, M.J., Findholt, S.L. & Kie, J.G. (2000) Resource selection and spatial separation of mule deer and elk during spring. *Journal of Wildlife Management*, **64**, 685–697.
- Kotliar, N.B. & Wiens, J.A. (1990) Multiple scales of patchiness and patch structure – a hierarchical framework for the study of heterogeneity. *Oikos*, **59**, 253–260.
- Krasnov, B., Khokhlova, I. & Shenbrot, G. (2003) Density-dependent host selection in ectoparasites: an application of isodar theory to fleas parasitizing rodents. *Oecologia*, **134**, 365–372.
- Linklater, W.L., Cameron, E.Z., Stafford, K.J. & Veltman, C.J. (2000) Social and spatial structure and range use by Kaimanawa wild horses (*Equus caballus*: Equidae). *New Zealand Journal of Ecology*, **24**, 139–152.
- Loe, L.E., Irvine, R.J., Bonenfant, C., Stien, A., Langvatn, R., Albon, S.D. *et al.* (2006) Testing five hypotheses of sexual segregation in an arctic ungulate. *Journal of Animal Ecology*, **75**, 485–496.
- Lucas, Z.L., McLoughlin, P.D., Coltman, D.W. & Barber, C. (2009) Multiscale analysis reveals restricted gene flow and a linear gradient in heterozygosity for an island population of feral horses. *Canadian Journal of Zoology*, **87**, 310–316.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002) *Resource Selection by Animals: Statistical Analysis and Design for Field Studies*. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- McLoughlin, P.D., Boyce, M.S., Coulson, T. & Clutton-Brock, T. (2006) Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 1449–1454.
- McLoughlin, P.D., Gaillard, J.M., Boyce, M.S., Bonenfant, C., Messier, F., Duncan, P. *et al.* (2007) Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology*, **88**, 3192–3201.
- McLoughlin, P.D., Morris, D.W., Fortin, D., Vander Wal, E. & Contasti, A.L. (2010) Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology*, **79**, 4–12.
- Mobæk, R., Myrsterud, A., Loe, L.E., Holand, O. & Austrheim, G. (2009) Density dependent and temporal variability in habitat selection by a large herbivore; an experimental approach. *Oikos*, **118**, 209–218.
- Moorcroft, P.R. & Barnett, A. (2008) Mechanistic home range models and resource selection analysis: a reconciliation and unification. *Ecology*, **89**, 1112–1119.
- Morris, D.W. (1987a) Ecological scale and habitat use. *Ecology*, **68**, 362–369.
- Morris, D.W. (1987b) Tests of density-dependent habitat selection in a patchy environment. *Ecological Monographs*, **57**, 270–281.
- Morris, D.W. (1988) Habitat-dependent population regulation and community structure. *Evolutionary Ecology*, **2**, 253–269.
- Morris, D.W. (1992) Scales and costs of habitat selection in heterogeneous landscapes. *Evolutionary Ecology*, **6**, 412–432.
- Morris, D.W. (1996) Temporal and spatial population dynamics among patches connected by habitat selection. *Oikos*, **75**, 207–219.
- Morris, D.W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia*, **136**, 1–13.
- Morris, D.W. (2011) Adaptation and habitat selection in the eco-evolutionary process. *Proceedings of the Royal Society B-Biological Sciences*, **278**, 2401–2411.
- Morris, D.W. & MacEachern, J.T. (2010) Active density-dependent habitat selection in a controlled population of small mammals. *Ecology*, **91**, 3131–3137.
- Morrison, M.L. & Hall, L.S. (2002) *Standard Terminology: Toward a Common Language to Advance Ecological Understanding and Application* (ed. J.M. Scott). Island Press, Washington, USA.
- Myrsterud, A. & Ims, R.A. (1998) Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology*, **79**, 1435–1441.

- Pettorelli, N., Gaillard, J.M., Duncan, P., Maillard, D., Van Laere, G. & Delorme, D. (2003) Age and density modify the effects of habitat quality on survival and movements of roe deer. *Ecology*, **84**, 3307–3316.
- Plante, Y., Vega-Pla, J.L., Lucas, Z., Colling, D., De March, B. & Buchanan, F. (2007) Genetic diversity in a feral horse population from Sable Island, Canada. *Journal of Heredity*, **98**, 594–602.
- Prins, H.H., de Boer, W.F. & van Langevelde, F. (2008) Comments on 'Resource distribution and dynamics: mapping herbivore resources.' *Resource Ecology: Spatial and Temporal Dynamics of Foraging* (eds H.H. Prins & F. van Langevelde), pp. 79–80. Springer, Dordrecht, The Netherlands.
- Prystupa, J.M., Juras, R., Cothran, E.G., Buchanan, F.C. & Plante, Y. (2012) Genetic diversity and admixture among Canadian, Mountain and Moorland and Nordic pony populations. *Animal*, **6**, 19–30.
- Pulliam, H. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652–661.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ramp, D. & Coulson, G. (2002) Density dependence in foraging habitat preference of eastern grey kangaroos. *Oikos*, **98**, 393–402.
- Rodriguez, M.A. (1995) Habitat-specific estimates of competition in stream salmonids – a field-test of the isodar model of habitat selection. *Evolutionary Ecology*, **9**, 169–184.
- Rosenzweig, M.L. (1981) A theory of habitat selection. *Ecology*, **62**, 327–335.
- Rosenzweig, M.L. (1986) Hummingbird isolegs in an experimental system. *Behavioral Ecology and Sociobiology*, **19**, 313–322.
- Rosenzweig, M.L. (1991) Habitat selection and population interactions – the search for mechanism. *American Naturalist*, **137**, S5–S28.
- Rubenstein, D.I. (1981) Behavioural ecology of island feral horses. *Equine Veterinary Journal*, **13**, 27–34.
- Sæther, B.E., Engen, S., Solberg, E.J. & Heim, M. (2007) Estimating the growth of a newly established moose population using reproductive value. *Ecography*, **30**, 417–421.
- Shochat, E., Patten, M.A., Morris, D.W., Reinking, D.L., Wolfe, D.H. & Sherrod, S.K. (2005) Ecological traps in isodars: effects of tallgrass prairie management on bird nest success. *Oikos*, **111**, 159–169.
- Thomas, D.L. & Taylor, E.J. (2006) Study designs and tests for comparing resource use and availability II. *Journal of Wildlife Management*, **70**, 324–336.
- Van Horne, B. (1983) Density as a misleading indicator of habitat quality. *Journal of Wildlife Management*, **47**, 893–901.
- Welsh, D.A. (1975) *Population, behavioural, and grazing ecology of the horses of Sable Island, Nova Scotia*. PhD thesis, Dalhousie University, Halifax, Canada.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.

Received 2 October 2012; accepted 15 June 2013

Handling Editor: Stan Boutin

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1 Estimates of resource selection functions (log odds ratio \pm 95% confidence intervals) predicting annual selection of vegetation associations by feral horses in the western habitat zone on Sable Island, Canada, using data only for 2010 and 2011 (left panel) and only for 2009 and 2011 (right panel).