

Density-dependent habitat selection and partitioning between two sympatric ungulates

Floris M. van Beest · Philip D. McLoughlin ·
Eric Vander Wal · Ryan K. Brook

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Abstract Theory on density-dependent habitat selection predicts that as population density of a species increases, use of higher quality (primary) habitat by individuals declines while use of lower quality (secondary) habitat rises. Habitat partitioning is often considered the primary mechanism for coexistence between similar species, but how this process evolves with changes in population density remains to be empirically tested for free-ranging ungulates. We used resource-selection functions to quantify density effects on landscape-scale habitat selection of two sympatric species of ungulates [moose (*Alces alces*) and elk (*Cervus canadensis manitobensis*)] in Riding Mountain National Park, Manitoba, Canada (2000–2011). The density of elk was actively reduced from 1.2 to 0.4 elk km⁻² through increased hunting effort during the period of study, while moose density

decreased without additional human influence from 1.6–0.7 moose km⁻². Patterns of habitat selection during winter by both species changed in accordance to expectations from density-dependent habitat-selection theory. At low intraspecific density, moose and elk did not partition habitat, as both species selected strongly for mixed forest (primary habitat providing both food and cover), but did so in different areas segregated across an elevational gradient. As intraspecific density increased, selection for primary habitat by both species decreased, while selection for secondary, lower quality habitat such as agricultural fields (for elk) and built-up areas (for moose) increased. We show that habitat-selection strategies during winter for moose and elk, and subsequent effects on habitat partitioning, depend heavily on the position in state space (density) of both species.

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F. M. van Beest · R. K. Brook
Department of Animal and Poultry Science, College
of Agriculture and Bioresources, University of Saskatchewan,
51 Campus Drive, Saskatoon, SK S7N 5E2, Canada

F. M. van Beest (✉)
Department of Bioscience, Aarhus University,
Frederiksborgvej 399, 4000 Roskilde, Denmark
e-mail: flbe@dmu.dk

P. D. McLoughlin
Department of Biology, University of Saskatchewan, 112 Science
Place, Saskatoon, SK S7N 5E2, Canada

E. Vander Wal
Department of Biology, Université de Sherbrooke,
2500 boulevard de l'université, Sherbrooke, QC J1K 2R1, Canada

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Introduction

The process of habitat selection influences the abundance and distribution of species (Johnson 1980; Rosenzweig 1981; Morris 2003) and constitutes an integral part of effective management and conservation (Boyce and McDonald 1999). Understanding how population density influences habitat selection (i.e. density-dependent habitat selection) is a prerequisite to inferring patterns of competition both within and between species (Schroder and Rosenzweig 1975; Rosenzweig 1991). Intraspecific and interspecific competition can occur by interference (direct competition) or by exploitation of the same habitat (indirect competition). Quantifying habitat-selection patterns of

similar species occupying the same landscape may provide insight into the mechanisms that eventually lead to coexistence, which remains one of the oldest and most persistent problems in ecology (Hutchinson 1959; McPeck 2012).

Habitat selection occurs at very small spatial scales (e.g. warblers in a tree: MacArthur 1958) but also over large areas when we consider higher order scales of selection (Johnson 1980; Kittle et al. 2008; Peters et al. 2013). Similarly, habitat selection can vary over time (e.g. seasons) with habitat use in winter (or the dry season in tropical areas) being most sensitive to competitive interactions within and between species (Singer 1979; Jenkins and Wright 1988; Macandza et al. 2012) as the forage base progressively depletes (Brown and Rosenzweig 1986; van Beest et al. 2010). Quantifying habitat-selection patterns using simulation models (Guthrie and Moorhead 2002) or experimental manipulation of population densities (Ale et al. 2011; Stewart et al. 2011) are effective approaches to identifying the behavioural mechanisms that facilitate competitive avoidance (e.g. habitat partitioning) and to quantifying how the strength varies across a density gradient.

We tested for density dependence on landscape-scale habitat selection and subsequent habitat overlap between two large ungulates [moose (*Alces alces* L.) and elk (*Cervus canadensis manitobensis* Millais)] co-occurring within Riding Mountain National Park, Manitoba, Canada. Population density of elk was quasi-experimentally manipulated (through increased harvest quotas in the area surrounding the park) between 2000 and 2011 (1.2–0.4 elk km⁻²). Moose density declined simultaneously (1.6–0.7 moose km⁻²) even though hunting pressure remained stable. Moose and elk are sympatric in many areas of their distribution in North America (Kittle et al. 2008) and the potential for competition between the species is expected to be greatest during winter when dietary overlap is highest and forage least accessible (Singer 1979; Jenkins and Wright 1988).

We hypothesized that habitat selection and habitat overlap by elk and moose are dependent on population size and that increasing competition at high density will impede the process of habitat partitioning due to more even use of all available habitat by both species. If habitat-selection patterns of elk and moose are density dependent, we predicted both species to reduce selection for primary high-quality habitat with increasing population density and simultaneously increase selection for secondary lower quality habitat (prediction 1). At high population densities, we predict habitat overlap to be greatest (i.e. low habitat partitioning; prediction 2). Habitat overlap at low population densities (few individuals within and between species co-occurring on the landscape) is largely contingent on the preferred (primary) habitat type selected by both species. If the primary habitat type selected differs between elk and moose,

we would expect habitat overlap to be low as habitat is partitioned (prediction 3a). Alternatively, if the primary habitat types selected were the same, we would expect habitat overlap to be high and as such habitat partitioning to be low (prediction 3b).

Materials and methods

Study area

Riding Mountain National Park (RMNP; 50°51'N, 100°15'W) is located in the Prairie and Boreal Plain ecozones in southwest Manitoba, Canada (Fig. 1a). The area has an elevation gradient which increases by ca. 600 m from east to west. The climate in the region is characterized by warm summers (mean July temperature 16.5 °C) and cold winters (mean January temperature -19.7 °C) with annual snow accumulation often exceeding 1 m and snow cover persisting for several months. Dominant forest types found in RMNP consist of coniferous [*Picea glauca* (Moench) Voss and *Pinus banksiana* Lamb] and mixed coniferous-deciduous [mainly aspen (*Populus tremuloides* Michx.)] stands interspersed with grasslands and wetlands. Most of the area surrounding RMNP is under intensive agriculture (Brook 2010a). Licensed hunting is not permitted within RMNP but does occur outside the park boundaries between 26 August and 11 November and between 2 December and 31 January. As such, the hunting season ended before population densities of elk and moose were estimated using aerial surveys in February as described below.

RMNP is inhabited by a small, stable population of wolves (*Canis lupus*) of around 60–80 individuals (Parks Canada 2012). The diet composition of wolves in RMNP (Paquet 1992) shows that elk are their preferred prey species, followed by beaver (*Castor canadensis*), moose, white-tailed deer (*Odocoileus virginianus*), and snowshoe hare (*Lepus americanus*).

Since 2000, the elk population in RMNP has been actively reduced through a federal and provincial management program, which involves longer hunting seasons and an increased number of elk hunting tags available in the hunting zones immediately adjacent to RMNP. Population reduction was initiated in an attempt to limit agricultural damage during spring and summer, and to reduce the risk of elk transmitting bovine tuberculosis (*Mycobacterium bovis*) to cattle (Brook and McLachlan 2009). The sex ratio (female:male) of hunter harvest during this period was approximately 2:1 for elk and 1:1 for moose (Manitoba Conservation, unpublished data). Through this quasi-experimental approach the elk population was reduced from a high of ca. 3,600 individuals in 2000 to a low of ca. 1,300 individuals in 2011.

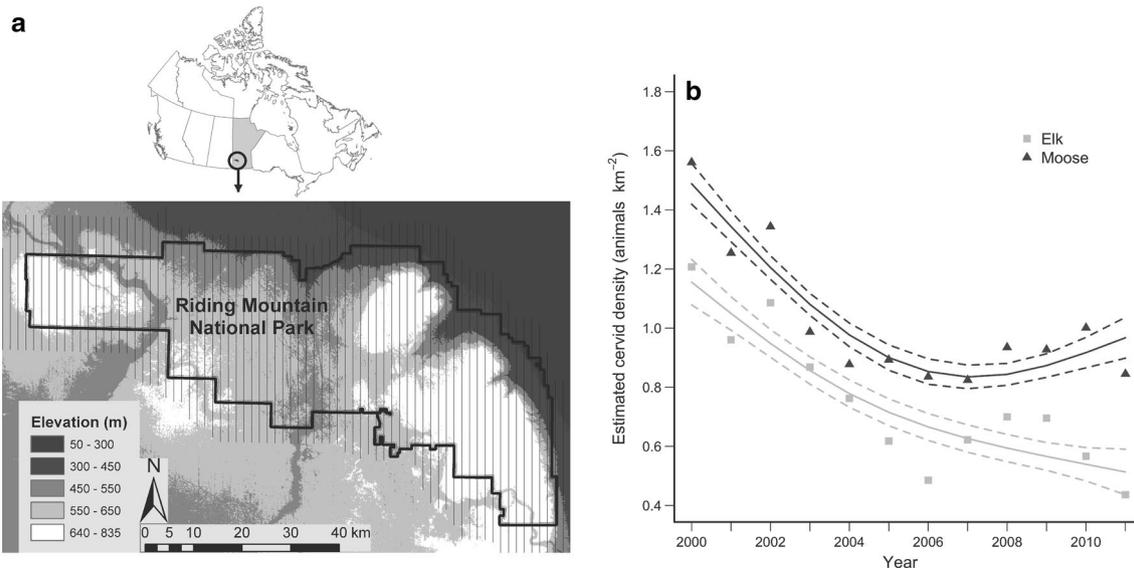


Fig. 1 **a** Study area, transects of annual aerial surveys (*thin black lines*), and elevation (m) of Riding Mountain National Park (RMNP) in southwestern Manitoba, Canada, and **b** population densities of elk and moose, as estimated by annual population surveys during winter

Population-densities and habitat-use validation

Moose and elk population densities (abundance/available habitat km²) were derived from 25 % coverage, standardized aerial surveys conducted annually (2000–2011) by Parks Canada Agency (Vander Wal et al. 2013). During the surveys identically spaced transects (north–south direction) were flown using a fixed-wing aircraft flying at an altitude of 120 m at 120 km h⁻¹. Transects were 200 m wide and extended on average 5 km beyond the RMNP park boundaries (Fig. 1a) to incorporate habitat use of the immediate agricultural fields surrounding the park. The total area surveyed was 745 km² each year. Flights were completed every February when sightability was at an optimum (Vander Wal et al. 2011), with snow cover on the ground and canopy foliage on deciduous trees absent. Two observers seated behind the pilot counted both moose and elk (one observer for the left side and one observer for the right side of the aircraft) and marked their location with a global positioning system (GPS). Group size was also recorded for both species for all observations. Over the complete study period group sizes of elk ranged between one and 49 individuals, with a mean of 2.37 and a median of one individual, while for moose group size ranged between one and nine individuals, with a mean of 1.5 and a median of one individual. Animals did not react strongly or adversely (e.g. by long-distance movements) to the presence or noise of the aircraft, so the likelihood of double counts among transects was low. All surveys were flown using the same pilot and observers to ensure that any observation bias and

(2000–2011). *Lines* are fitted means (\pm SE) of densities estimated with a generalized additive model with the optimal smoothing parameter chosen by generalized cross-validation

location error was consistent and systematic. Hence, annual variation in the precision of population estimates was likely low although, as expected, some variation in accuracy was detected (for more details see Vander Wal et al. 2013). We considered the aerial survey data to be of sufficient quality to reflect large-scale differences in population density of elk and moose over time.

Data derived from aerial surveys are sometimes prone to habitat sightability bias and as such may bias estimates of habitat use, the main topic of this study. To validate the accuracy of the aerial survey data we compared habitat-use estimates derived from the aerial survey data with estimates derived from GPS-collared elk in the same area during the same time period (winter). We were unable to validate habitat-use estimates of moose as GPS-collar data were lacking for this species. To do the habitat-use comparisons for elk we only considered years (winters) with both data collection methods available. As such, we focussed our analysis on winters of 2004, 2005, 2008–2011. During this period a total of 22 elk (seven males and 15 females) were captured with a net-gun fired from a helicopter and fitted with a GPS collar programmed with a 2-h relocation schedule for up to 1 year. All GPS positions collected within 24 h of capture and large positional outliers were excluded from the data and spatial errors associated with the GPS collars were small enough (14 m on average) to not bias fine-scale movement and habitat-use estimates (van Beest et al. 2013a, b). We included all GPS locations collected during winter [defined by season-specific movement rates (van Beest et al. 2013b)] to assess if the aerial survey data (a 1-week

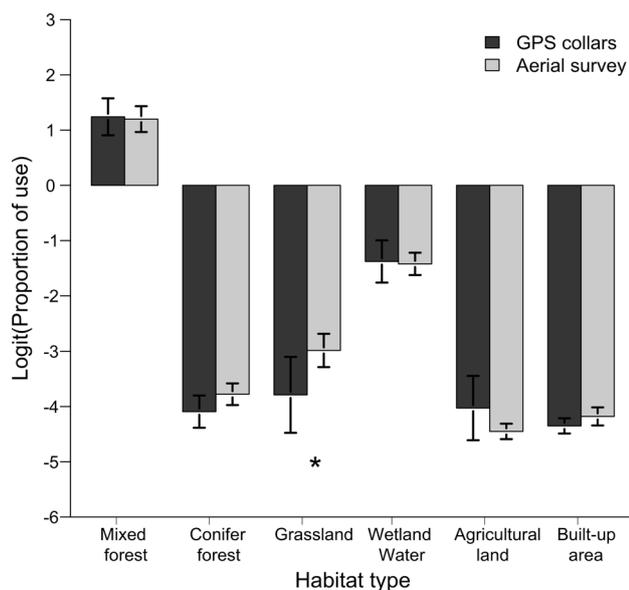


Fig. 2 Comparative habitat-use estimates (logit-transformed mean proportions and 95 % confidence intervals) derived from aerial survey data and global positioning system (GPS)-collared elk during winter in RMNP, Manitoba, Canada. Significant differences in habitat use between data-collection methods ($P < 0.05$) are indicated with an asterisk

snapshot in time each year) would accurately depict habitat use for the complete season. Habitat use was calculated as the proportion of locations in different land-cover types for each data set separately. The proportion of locations in each habitat was logit transformed and subsequently analysed using linear regression to test for differences in habitat use between data-collection methods (two-way interaction, data-collection method \times habitat type). The results showed that habitat-use estimates of both data-collection methods were similar for most habitat types (same strength and direction) with the exception of grassland (Fig. 2), which was overestimated by the survey data compared to the GPS collar data [$\beta_{\text{grassland} \times \text{data-collection method (GPS data as reference category)}} \pm \text{SE} = 0.845 \pm 0.354$; $P = 0.0201$]. Overall, we considered the survey data to accurately reflect habitat use of elk during winter seasons, without major biases introduced due to sightability issues.

Quantifying habitat selection

A powerful analytical approach to quantifying how animals select habitat is the resource-selection function (RSF) (Boyce and McDonald 1999; Manly et al. 2002). The RSF is defined as any function describing habitat or resource use that is proportional to the probability of use by an organism (Manly et al. 2002). Habitat may be defined as an area with different biotic and abiotic conditions, within which at least one of the parameters of population growth is different than

in adjacent areas (Hall et al. 1997; Morris 2003). In contrast, most RSF-based studies refer to distinct land-cover types or vegetation classes as habitat (McLoughlin et al. 2010; Pérez-Barbería et al. 2013; van Beest et al. 2014). Similarly and for our purpose, we defined habitat by six common land-cover types in and around RMNP [mixed forest (both deciduous and coniferous species), coniferous forest, grassland, wetland and water (including lakes and streams), agricultural land, and built-up areas (sites with human influence such as houses or other buildings)], which are known to influence selection patterns of both elk and moose (Kittle et al. 2008; Dugal et al. 2013). Moreover, these land-cover types differ in their availability of forage and cover (van Beest et al. 2013a) and as such vary in quality. We considered habitat types with both abundant forage and cover to be of high quality (mixed forest), while habitat types with either cover (coniferous forest) or forage (grassland, wetland) to be of lower quality. Agricultural land was also considered of low quality as cover is largely absent and any forage present is of poor quality and difficult to access (under snow). Although some hay bales may be found on agricultural fields year round, most are stored within fences before winter (Brook 2010b). We also considered several other environmental features in our RSFs that are known to influence selection patterns of elk and moose, such as elevation, distance to paved and unpaved roads. Whether and how selection for these variables changes in response to altered population densities is highly relevant for the management and conservation of both elk and moose.

RSFs compare environmental conditions at animal locations (e.g. land-cover type, elevation) to the attributes at random (available) points (Boyce and McDonald 1999; Manly et al. 2002). We estimated RSFs for elk and moose separately and points of use were derived from locations of animals observed during the aerial surveys (as described above). We selected available locations for each species by drawing a random sample of points from within the total study area (delineated by a 100 % minimum convex polygon of all used locations). Our analyses, therefore, corresponded most closely to those of second-order selection (Johnson 1980) and were based on population-level use-availability sampling designs [design I (Thomas and Taylor 2006)]. The number of randomly drawn available points equalled the number of used points (1:1 ratio) for each year and for each species. Mean (SD) number of used points per year was 1,021 (393) for moose and 631 (239) for elk.

A particular strength of the RSF modelling approach to test for density dependence is that multiple continuous and categorical variables that influence selection can be incorporated as fixed effects and as interactions with animal density (McLoughlin et al. 2010; van Beest et al. 2014). As such, the independent variables in our species-specific RSFs were: (1) land-cover type, (2) distance to

paved roads, (3) distance to unpaved roads, (4) elevation, (5) species-specific population density, and (6) the interaction between covariates 1–4 and 5. The interaction between land-cover types and density was fitted using a Boolean variable for each land-cover type separately (e.g. land-cover type = mixed forest \times density). Attributes of used and available locations were assigned using ground-truthed land-cover maps and a digital elevation model (50 \times 50-m-pixel resolution). Multi-collinearity between independent variables was low: Spearman correlation (r_s) < 0.5 and variance inflation factor < 3 . We employed mixed-effect logistic regression models with year and group size as random intercepts to account for unbalanced data. 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 r_s between ten RSF-bin ranks and five test-training sets. We repeated this procedure 100 times to determine if the r_s was significantly different from random. We performed all analyses in R (R Development Core Team 2013).

Quantifying habitat overlap

There are many environmental features that can be partitioned by species including space, habitat, and resources (Schoener 1974). The reverse of habitat partitioning is habitat overlap, which is often used to quantify and evaluate competitive interactions between similar species (Schroder and Rosenzweig 1975; Iranzo et al. 2013). Traditionally, measures of habitat or forage resource overlap are based on proportional use data (Lawlot 1980); however, they are increasingly being employed with data that describe habitat or resource choice in a probabilistic fashion (Banta et al. 2012). RSF coefficients have particular merit for quantifying habitat overlap as they are calculated from estimates of habitat abundance and provide a relative probability of habitat or resource use, which is typically missing in traditional overlap indices (Lawlot 1980). We quantified coarse-scale habitat overlap of elk and moose using an adaptation of Pianka's (1974) niche-overlap index based on species-dependent selection coefficients for each fixed effect included in the RSFs (land-cover types, distance to paved and unpaved roads, and elevation) as well as for all fixed effects combined (total habitat overlap). The overlap index ranges between 0 (no habitat overlap) to 1 (complete habitat overlap). We calculated habitat overlap at each 0.1 km⁻² point increment in density within a 0.4–2.0 km⁻² animal density gradient, which is a range at which elk and moose are known to co-occur (e.g. Singer et al. 1994) and includes the range of equal densities between both species observed in our study area and study period (Fig. 1b). At each density point we calculated the mean overlap from a bootstrap procedure using 1,000 permutations. We tested for a statistical relation

between habitat overlap and density using non-linear generalized additive models (Wood 2006) as abrupt changes (non-linearity) in habitat overlap are likely in forage-limited systems (Brown and Rosenzweig 1986; Stewart et al. 2002).

Results

Habitat selection

Habitat-selection patterns were clearly influenced by population density for both species. Selection estimates for mixed forest were highest when animals occurred at the lowest observed density, but decreased as intraspecific density increased, a pattern consistent for both elk and moose (Fig. 3; Tables A1, A2, Online Resource 1). Moose further reduced selection for coniferous forest, wetland and water and agricultural land, while increasing selection for built-up areas as density increased. Selection for grassland did not change as moose density increased ($P > 0.05$). Elk increased selection for coniferous forest and agricultural land as density increased (Fig. 3) but decreased selection for wetland and water. Relative probability of use of grasslands and built-up areas did not change as elk density increased ($P > 0.05$ for both land-cover type \times density interactions).

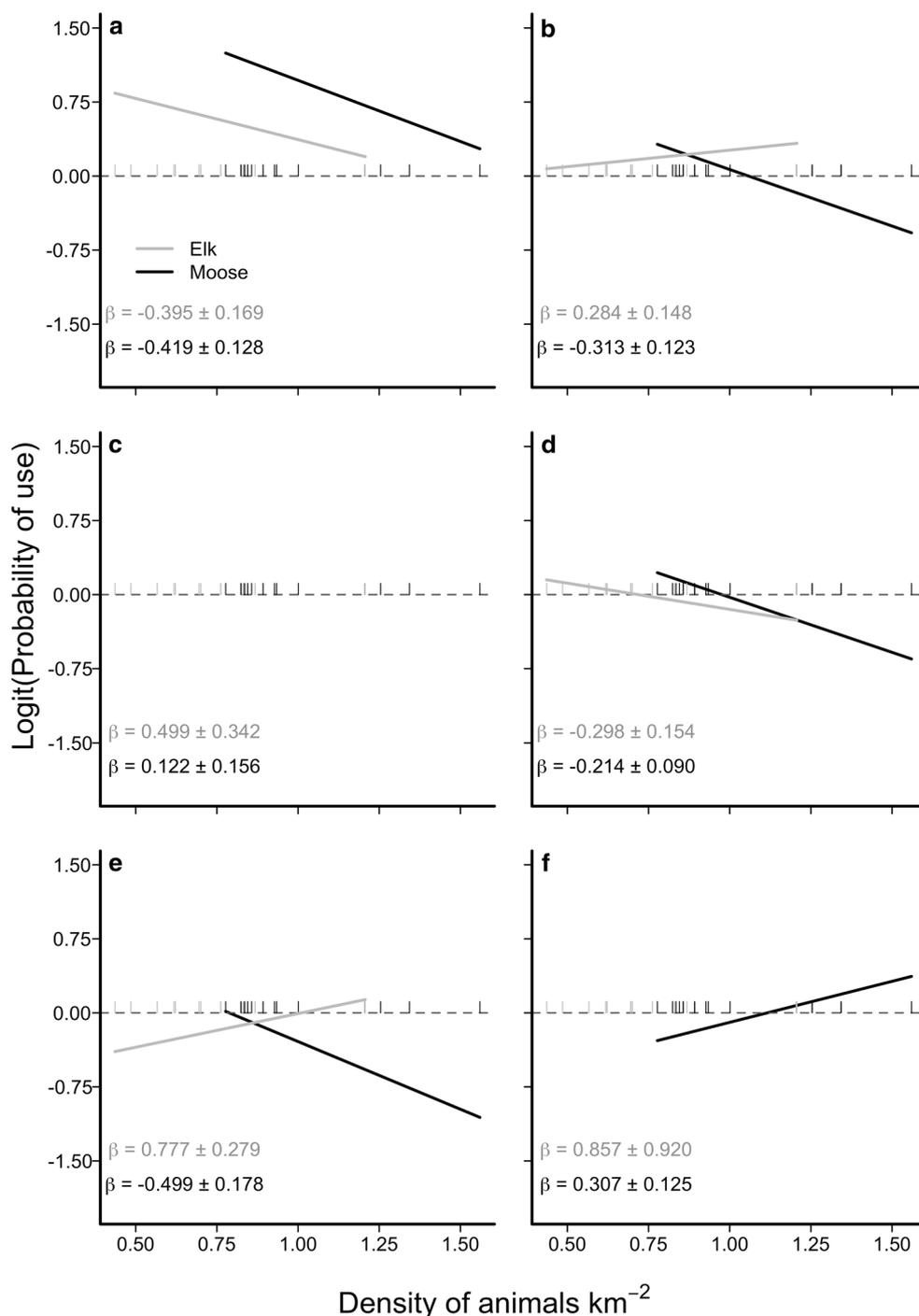
Selection for paved- and unpaved roads by moose did not change significantly as intraspecific density increased ($P = 0.803$ and $P = 0.882$ respectively; Fig. 4). Elk did not change their selection pattern for paved roads with changing density ($P = 0.187$), though selection for unpaved roads was density dependent ($P = 0.018$) with increased selection for areas close to unpaved roads when densities were low, leading to more even use as densities increased (Fig. 4). At low densities, moose selected for high-elevation areas while elk selected for low-elevation areas. However, as densities increased, both species increasingly used sites more evenly across the elevation gradient ($P = 0.032$ and $P = 0.026$ respectively; Fig. 4).

All RSFs had good predictive performance as the Spearman rank correlation across five cross-validation sets was $r_s = 0.806$, $P < 0.001$ and $r_s = 0.812$, $P < 0.001$ for moose and elk, respectively.

Habitat overlap

Total habitat overlap (combining all fixed effects: land-cover types, distance to paved and unpaved roads, and elevation), did not change with increasing density ($F = 0.376$, $P = 0.646$) and remained constant at a mean proportion of 0.55 ± 0.003 SE (Fig. A1, Online Resource 1). Overlap in land-cover types was clearly dependent on the density at which both species were co-occurring (Fig. 5). Proportion of overlap was 0.73 at relatively low interspecific density

Fig. 3 Mean RSF estimates [logit(probability of use)] of elk (*grey*) and moose (*black*) selection for **a** mixed forest, **b** coniferous forest, **c** grassland, **d** wetland and water, **e** agricultural land, and **f** built-up areas in RMNP as a function of species-specific density (2000–2011). Predicted lines are shown only for those variables with a significant ($P < 0.05$) change with species density. Error bars for predicted lines are not shown to improve clarity but all RSF estimates ($\beta \pm SE$) are reported in the figure panels. Predictions for each land-cover type selection estimate were made for within the observed range of densities while keeping the values of additional covariates in the RSFs constant at their mean value. Tick marks on the horizontal line $y = 0$ indicate observed species densities [elk (*grey*) and moose (*black*)]



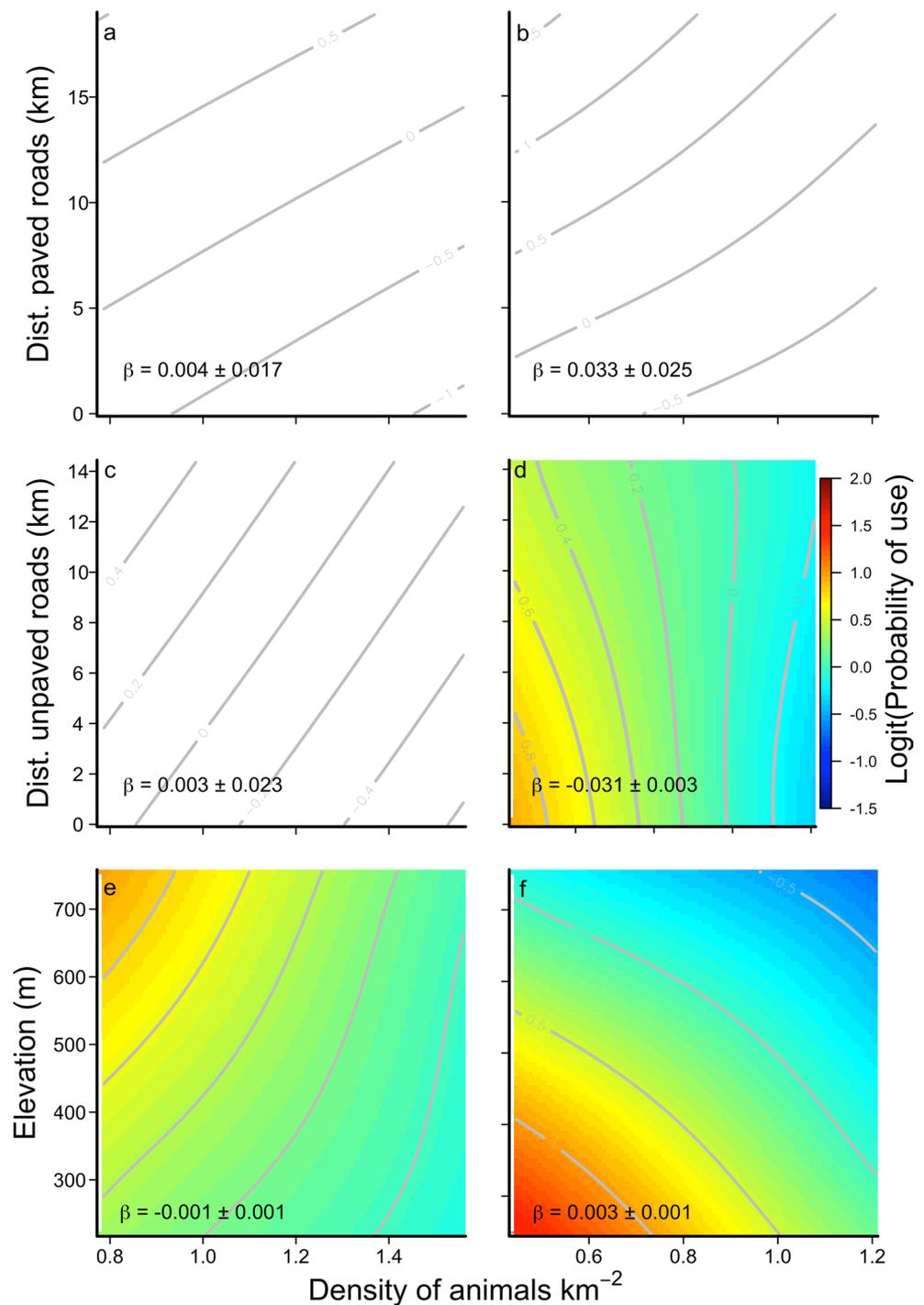
(0.4 animals km⁻²) and decreased ($F = 43.67$, $P < 0.001$) to 0.53 at relatively high interspecific density (2.0 animals km⁻²). Overlap as determined from selection for distance to paved and unpaved roads did not change as a function of density ($F = 0.534$, $P = 0.748$ and $F = 1.152$, $P = 0.435$, respectively) and remained constant at a proportion of ca. 0.5 (Fig. 5). Overlap as determined from selection for elevation increased as both species increased in density across the landscape ($F = 42.863$, $P < 0.001$) as

the proportion of overlap was 0.41 at relatively low interspecific density (0.4 animals km⁻²) and 0.55 at relatively high interspecific density (2.0 animals km⁻²).

Discussion

Coexistence of similar species in ecological communities can be achieved through differential use of space, habitat

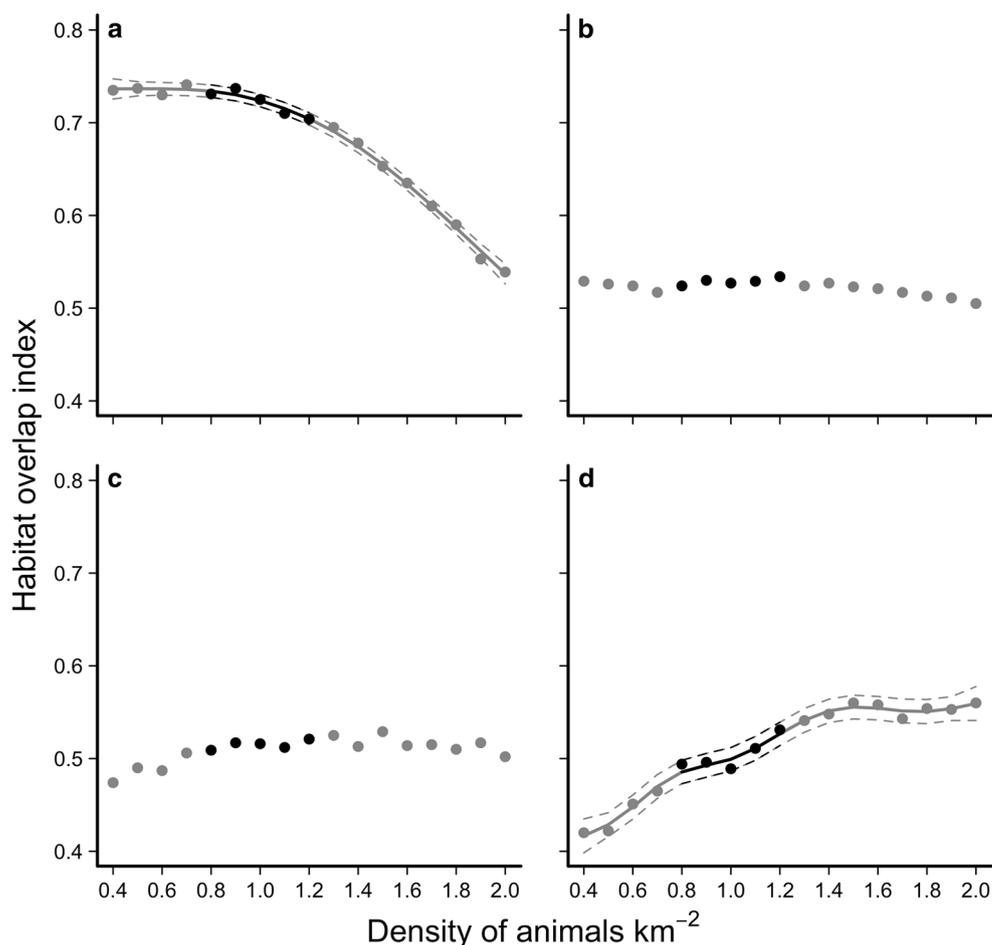
Fig. 4 Surface plots showing the mean RSF estimates [logit(probability of use)] of **a, c, e** moose and **b, d, f** elk selection for distance (*Dist.*) to paved roads, unpaved roads, and elevation as a function of species-specific densities (2000–2011) in RMNP. **a–c** Absence of filled contours indicates non-significant ($P > 0.05$) changes in selection with increasing density. Predictions were made for within the observed range of densities using a thin plate spline surface with the optimal smoothing parameter chosen by generalized cross-validation. Additional covariates in the RSFs were held constant at their mean value. RSF $\beta \pm$ SE for each covariate is reported in the corresponding panel



or biotic and abiotic conditions therein (Rosenzweig 1991; McPeck 2012). A wide body of literature supports the notion that habitat partitioning by species is a possible outcome of exploitation competition (Morris 1999; Stewart et al. 2011; Macandza et al. 2012). How this process is affected by changes in population size, however, remains poorly understood for free-ranging, large herbivores in natural systems.

Our study shows that landscape-scale habitat selection during winter of two large ungulate species is density dependent and influences how habitat is partitioned among species. Both elk and moose actively selected for mixed forest when densities were at their lowest. Mixed forest stands are known to be of high value for both species during winter due to the abundance of both forage and cover (van Beest et al. 2013a; Milligan and Koricheva 2013).

Fig. 5 Habitat overlap indices for moose and elk as a function of co-occurring population densities calculated with a bootstrap procedure (1,000 permutations) for each fixed effect in the RSF models: **a** land-cover types, **b** distance to paved roads, **c** distance to unpaved roads, and **d** elevation. Lines and 95 % confidence intervals are fitted only for significant relations as estimated with a generalized additive model with the optimal smoothing parameter chosen by generalized cross-validation. Grey circles and lines indicate extrapolated density values, whereas black circles and lines indicate densities as observed in RMNP during 2000–2011



Use of this land-cover type reflects a strategy to optimize energy intake while reducing the risk of predation and human hunting, a trade-off known to influence the behaviour of both elk and moose (Kittle et al. 2008). As densities increased, the relative use of mixed forest declined for both species (though it remained higher than availability), while the relative use of secondary, poorer quality land-cover types increased (as expected by prediction 1 and from density-dependent habitat-selection theory).

Based on species-specific, density-dependent habitat-selection estimates, total habitat overlap appeared unrelated to density when considering all our land-cover types and environmental features (paved and unpaved roads and elevation) simultaneously. Stewart et al. (2002) posited that habitat partitioning between elk and mule deer (*Odocoileus hemionus*) becomes progressively more difficult as population densities increase and forage resources decrease. We therefore expected habitat overlap between moose and elk to be greatest at high density (prediction 2), but overlap remained constant at ca. 0.55 irrespective of density. This value lies in the middle of the theoretical habitat overlap gradient of 0 (no overlap, habitat partitioning) and 1 (complete overlap, no habitat partitioning) and would suggest that some degree of

exploitation competition between moose and elk exist (Jenkins and Wright 1988). However, by quantifying overlap for each environmental feature independently we revealed that competitive interactions between these species are reduced via divergent selection patterns for both land-cover types and elevation as population densities change. When elk and moose co-occurred at high population densities they were able to partition habitat by occupying divergent secondary, low-quality land-cover types. At low population density, when both species favoured mixed forest and we expected habitat overlap to be high (Prediction 3b), habitat partitioning was achieved by spatial segregation across the elevation gradient. Indeed, when two species share a preference for one particular habitat type, partitioning may not be possible without compromising Darwinian fitness (Rowell 2010). We show that, in such situations, species may spatially segregate and as such reduce competitive interactions while utilizing the same high-quality, preferred habitat.

Despite much theoretical work on density-dependent habitat selection and partitioning, the challenge in interpreting empirical findings from intact systems is to determine if density is the most important condition shaping behavioural responses or whether it is confounded by other

environmental influences such as predation risk (Montgomery et al. 2013), human hunting (Dugal et al. 2013) or both. Antipredator behaviour (due to human hunting or natural predators) is expected to be strongest at low prey population density and to decline as prey densities increase because individuals become increasingly food stressed (Peacor 2003). Hunting pressure around RMNP is high in autumn and early winter and as such agricultural fields and built-up areas are likely perceived as high-risk areas by both elk and moose. This is reflected by their general avoidance of these areas at low population density, despite the risk of predation by wolves within the park (van Beest et al. 2013a). This finding could suggest that hunting pressure is considered a greater threat by elk and moose than is predation risk by wolves. Lack of data on the distribution of wolves over the complete time frame of our analyses prevented us from explicitly incorporating predation risk into this study. However, our results fit with the notion that antipredator behaviour is density dependent. Within RMNP and at low population densities, both species optimized foraging activities by selecting patches with abundant forage and cover (i.e. mixed forest) where predators are less likely to detect and encounter prey and human hunting is absent. As densities increased, and individuals became more food stressed, antipredator behaviour weakened as both species progressively selected for riskier patches (i.e. built-up areas for moose and coniferous forest and agricultural land for elk) where human activity is higher and predators are more likely to detect and encounter prey. Predation by wolves may also be a contributing factor to the natural decline in moose population size in RMNP (Fig. 1b) through the process of prey-switching behaviour (Chesson 1984); where the predator switches to more abundant prey (moose) when their primary prey (elk) decreases in abundance. However, other factors such as nutritional deficiency or climate-induced effects on body condition may also have influenced the decline in moose population density as has been demonstrated for moose populations elsewhere (Murray et al. 2006; van Beest and Milner 2013).

Inference of our results on density effects on habitat selection and partitioning apply to the landscape-scale. It is generally accepted that habitat selection is scale dependent (Johnson 1980). As such, habitat overlap and exploitation competition may also vary across spatial scales. Indeed, Peters et al. (2013) showed that competitive interactions for space and habitat between moose and woodland caribou (*Rangifer tarandus caribou*) were relatively low when viewed at coarse spatial scales (landscape-scale), while the opposite was observed at finer scales (home-range scale). Scale-dependent habitat selection has been found for both elk (Hebblewhite and Merrill 2007; Kittle et al. 2008) and moose (van Beest et al. 2010; Oehlers et al. 2011). However, estimates of fine-scale, density-dependent habitat selection and overlap between these species are currently

lacking. A potentially valuable hypothesis to test is that competitive interactions between these two sympatric ungulates are stronger at a finer spatial scale than at the coarse spatial scale considered here.

Population size of moose and elk in our study declined simultaneously. There are various other scenarios in how population sizes of sympatric species can change (e.g. density varies for one species only, while for others it remains stable, or densities of species change in opposite directions), each with distinct levels of intra- and interspecific competition, and patterns of habitat selection and resource partitioning may vary accordingly (Stewart et al. 2002, 2011). For example, Focardi et al. (2006) showed that a slight increase in population density of fallow deer (*Dama dama*) led to the spatial displacement and increased use of poor-quality habitat by roe deer (*Capreolus capreolus italicus*) reducing the species phenotypic performance and population size. In addition, the rate of population change can affect the strength of competitive interactions between and within species. Where population size changes gradually and species have coexisted for a long period, behavioural changes due to competition may be difficult to detect compared to rapid population changes, which in some cases may produce patterns that deviate from general competition theory (Brown and Rosenzweig 1986; Nicholson et al. 2006).

Much is still to be learned about the mechanisms that influence both population size and animal behaviour of similar species within ecological communities. Especially challenging is to distil the combined influence of species-dependent predation risk and population density on intra- as well as interspecific competition. This formidable task involves monitoring the movement of individuals across multiple species and trophic levels, but would greatly improve our understanding of the scale-dependent effect of these two extrinsic conditions on species coexistence. Besides its value to test and progress ecological theory, such a holistic approach would greatly benefit and facilitate species management and conservation.

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